

# Great Basin Aquatic Systems History

*Robert Hershler, David B. Madsen, and Donald R. Currey*

EDITORS

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## ABSTRACT

Hershler, Robert, David B. Madsen, and Donald R. Currey, editors. Great Basin Aquatic Systems History. *Smithsonian Contributions to the Earth Sciences*, number 33, 405 pages, 190 figures, 21 tables, 2002.—The 14 papers collected herein treat diverse aspects of the aquatic history of the Great Basin of the western United States and collectively attempt to summarize and integrate portions of the vast body of new information on this subject that has been acquired since the last such compilation was published in 1948. In the first section, four papers (Lowenstein, Negrini, Reheis et al., Sack) focus on physical aspects of Great Basin paleolake histories, whereas a fifth paper (Oviatt) summarizes the contributions to the study of Bonneville Basin lacustrine history made by two early giants of the field, Grove Karl Gilbert and Ernst Antevs. In the second section, four papers synthesize perspectives on Great Basin aquatic history provided by diatoms and ostracods (Bradbury and Forester), fishes (Smith et al.), aquatic insects (Polhemus and Polhemus), and aquatic snails (Hershler and Sada), whereas a fifth (Sada and Vinyard) summarizes the conservation status of the diverse aquatic biota that is endemic to the region. In the final section, three papers integrate terrestrial biotic evidence pertaining to Great Basin aquatic history derived from pollen from cores (Davis), floristics (Wigand and Rhode), and the mammal record (Grayson), whereas a fourth (Madsen) examines the relationship between Great Basin lakes and human inhabitants of the region. Although diverse in scope and topic, the papers in this volume are nonetheless linked by an appreciation that integration of geological, biological, and anthropological evidence is a necessary and fundamental key to a mature understanding of Great Basin aquatic systems history.

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# Contents

	<i>Page</i>
Introduction, by David B. Madsen, Robert Hershler, and Donald R. Currey . . . . .	1

## LAKE HISTORIES

Pluvial Lake Sizes in the Northwestern Great Basin throughout the Quaternary Period, by Robert M. Negrini . . . . .	11
Pliocene to Middle Pleistocene Lakes in the Western Great Basin: Ages and Connections, by Marith C. Reheis, Andrei M. Sarna-Wojcicki, Richard L. Reynolds, Charles A. Repenning, and Martin D. Mifflin . . . . .	53
Pleistocene Lakes and Paleoclimates (0 to 200 Ka) in Death Valley, California, by Tim K. Lowenstein . . . . .	109
Bonneville Basin Lacustrine History: The Contributions of G.K. Gilbert and Ernst Antevs, by Charles G. Oviatt . . . . .	121
Fluvial Linkages in Lake Bonneville Subbasin Integration, by Dorothy Sack . . . . .	129

## AQUATIC BIOTIC PERSPECTIVES

Environment and Paleolimnology of Owens Lake, California: A Record of Climate and Hydrology for the Last 50,000 Years, by J. Platt Bradbury and R.M. Forester . . . . .	145
Biogeography and Timing of Evolutionary Events among Great Basin Fishes, by G.R. Smith, T.E. Dowling, K.W. Gobalet, T. Lugaski, D.K. Shiozawa, and R.P. Evans . . . . .	175
Basins and Ranges: The Biogeography of Aquatic True Bugs (Insecta: Heteroptera) in the Great Basin, by Dan A. Polhemus and John T. Polhemus . . . . .	235
Biogeography of Great Basin Aquatic Snails of the Genus <i>Pyrgulopsis</i> , by Robert Hershler and Donald W. Sada . . . . .	255
Anthropogenic Changes in Biogeography of Great Basin Aquatic Biota, by Donald W. Sada and Gary L. Vinyard . . . . .	277

## NON-AQUATIC BIOTIC AND HYDROCLIMATIC PERSPECTIVES

Late Neogene Environmental History of the Northern Bonneville Basin: A Review of Palynological Studies, by Owen K. Davis . . . . .	295
Great Basin Vegetation History and Aquatic Systems: The Last 150,000 Years, by Peter E. Wigand and David Rhode . . . . .	309
Great Basin Mammals and Late Quaternary Climate History, by Donald K. Grayson . . . . .	369
Great Basin Peoples and Late Quaternary Aquatic History, by David B. Madsen . . .	387

# Introduction

*David B. Madsen, Robert Hershler, and Donald R. Currey*

It has long been known that the huge, arid region of internal drainage in western North America known as the Great Basin contained a series of large, intermontane lakes during wetter, or pluvial, periods of the late Cenozoic. During the last 100 years numerous geologists and biologists, including many preeminent scientists beginning with Grove Karl Gilbert (1843–1918) and Israel Cook Russell (1852–1906), have studied the extent, integration, and contemporaneity of these lakes, and the relation between regional hydrographic history and biogeography. The first attempt to synthesize this information was in June 1942, when the Western Division of the American Society of Ichthyologists and Herpetologists met in Salt Lake City, Utah. The highlight of the meeting was a symposium on the glacial and postglacial history of the Great Basin, which was jointly arranged with the Pacific Division of the American Association for the Advancement of Science (Crocker, 1942). Papers presented at the meeting included summaries of the geological development of the Great Basin, pluvial lake distribution and pertinent ichthyological evidence, and paleoclimates, which were later collected in *The Great Basin, with Emphasis on Glacial and Postglacial Times* (Antevs, 1948; Blackwelder, 1948; Hubbs and Miller, 1948). This modest volume has stood as a landmark in the study of what Grayson (1993:xvi) referred to as the “natural prehistory” of the Great Basin.

Immense strides have been made in the study of Great Basin aquatic history during the last 50 years. On the physical side, our understanding of geological evolution of the Great Basin has been revitalized in the wake of modern concepts of mountain building, tectonics, and volcanology. Geochronology has provided many new dating methods to aid interpretation of key geologic events. New methodologies also have enabled much more precise delineation and dating of ancient lake beds and better discernment as to whether such data represent records of long-lived lakes or ephemeral water bodies (playas). Climatic

modeling has developed into an important field that further aids elucidation of pattern and sequence of aquatic-system development. On the biological side, evidence derived from fishes (both living and fossil) has been expanded and refined, and other aquatic biota now has been similarly studied. The coupling of biogeographic analysis with phylogenetics has provided explicit, testable methods of inferring historical relationships among geographic areas (drainages). The blossoming field of phylogeography (Bermingham and Moritz, 1998) offers additional tools for fruitful analysis at the population level, although this has been little applied to aquatic biota of the Great Basin (but see Duvernell and Turner, 1998).

The purpose of this volume is to assemble and integrate this large body of relevant data from the geological and biological schools as it pertains to the history of aquatic systems in the Great Basin. This is hardly a new concept, but instead it reiterates the spirit of Hubbs and Miller (1948:120):

Even greater advances should ensue, when the biological and geological approaches are more definitely integrated. We eagerly look forward to the time when we may join with the glacial geologist to journey, helping hand in hand, across the desert mountains and flats of the Great Basin, together attempting to unlock some of the doors that are yet closed to us.

This volume is a product of the Great Basin Aquatic System History (GBASH) Symposium, which was convened in Salt Lake City at the University of Utah from 17 September to 21 September 1997 to celebrate the 50<sup>th</sup> anniversary of the publication of papers from the original 1942 symposium. More than 75 individuals attended the GBASH conference, including invited speakers, poster presenters, representatives of land management agencies, and the general public. Participants enjoyed a highly structured program designed to summarize recent advances in Great Basin natural history in an integrated, interdisciplinary fashion. Presenters included an array of geologists, climatologists, botanists, zoologists, and anthropologists under the general direction of conference chair Donald R. Currey. The presentation format for the 25 invited papers followed the same tripartite structure we employ herein. Fourteen of those papers were revised subsequent to the symposium and are collected in this volume. Together these papers complement the more generalized treatments of Great Basin aquatic history that are currently available.

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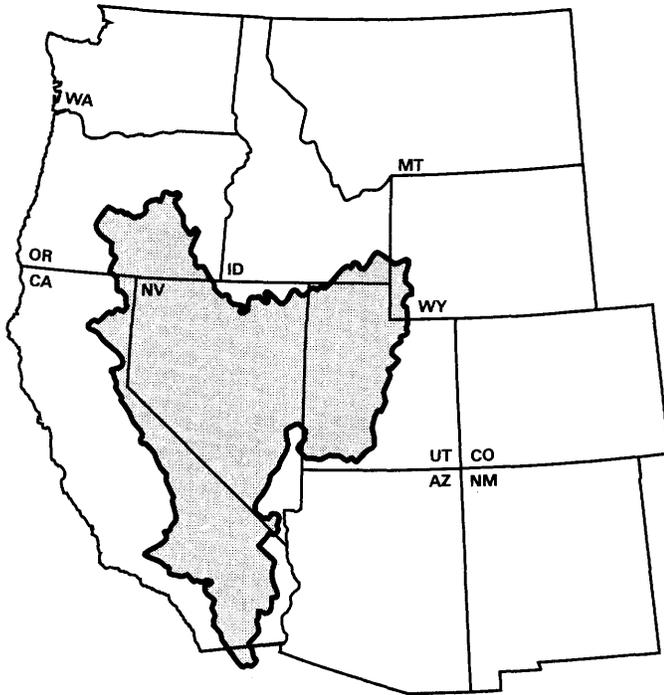


FIGURE 1.—The limits of the Great Basin, as defined by areas of internal drainage (after King, 1986).

### Defining the Great Basin

The Great Basin is a vast complex of internal drainage systems lying in interior western North America (Figure 1). These systems are composed primarily of high, north-to-south trending mountains and long, narrow valleys into which mountain streams and rivers drain. Depending upon how it is defined (and it can be defined in a number of ways), the Great Basin extends as far north as 44° north latitude, as far south as 33° north latitude, as far east as 110° west longitude, and as far west as 121° west longitude. Although the many definitions of the Great Basin are appropriate for specific purposes, none exceeds that of John C. Frémont's (1845:175) original description in terms of simple utility:

The Great Basin—a term I apply to the intermediate region between the Rocky mountains and the next range [the Sierra Nevada and the Cascade Range], containing many lakes, with their own system of rivers and creeks, (of which the Great Salt is the principal,) and which have no connexion with the ocean, or the great rivers which flow into it.

A number of general accounts reviewing the natural history of the Great Basin are available (e.g., Houghton, 1976; McPhee, 1981; Trimble, 1989; and particularly, Grayson, 1993), and there is also a variety of extensive treatments of specific topics (Lanner, 1983; Ryser, 1985; Fiero, 1986; Mazingo, 1987; and Sigler and Sigler, 1987). As a result, we have not attempted to produce yet another generalized description of the Great Basin herein. Furthermore, because a variety of biological, geomorphological, and hydrological topics are covered

in the papers that follow, it is important to recognize that the physiographic, hydrographic, and floristic definitions of the Great Basin employed in these papers are somewhat different.

Physiographically, the Great Basin is part of the Basin and Range Province (Hunt, 1967) that, although coterminous with the hydrographic Great Basin in the north, extends into southern Arizona and New Mexico and covers much of northern Mexico (Figure 2). The fault-block mountains that characterize the province began forming during the middle Tertiary, approximately 40 million years (My) before present (B.P.) (King, 1977). This system of mountains and valleys was formed as part of an ongoing extensional process related to plate tectonics (Zoback et al., 1981), and the Great Basin continues to expand as the Pacific Plate shears off the western margin of the North American plate (Stewart, 1971; Fiero, 1986). This east-west expansion has created a series of north-to-south trending fault-block mountains separated by long, narrow graben and/or half-graben valleys filled with Quaternary alluvium. The larger valleys exceed 100 miles (161 km) in length and 30 miles (48 km) in width. The Great Basin is bounded on the west and east by the higher ranges of the Sierra Nevada and the western Rocky

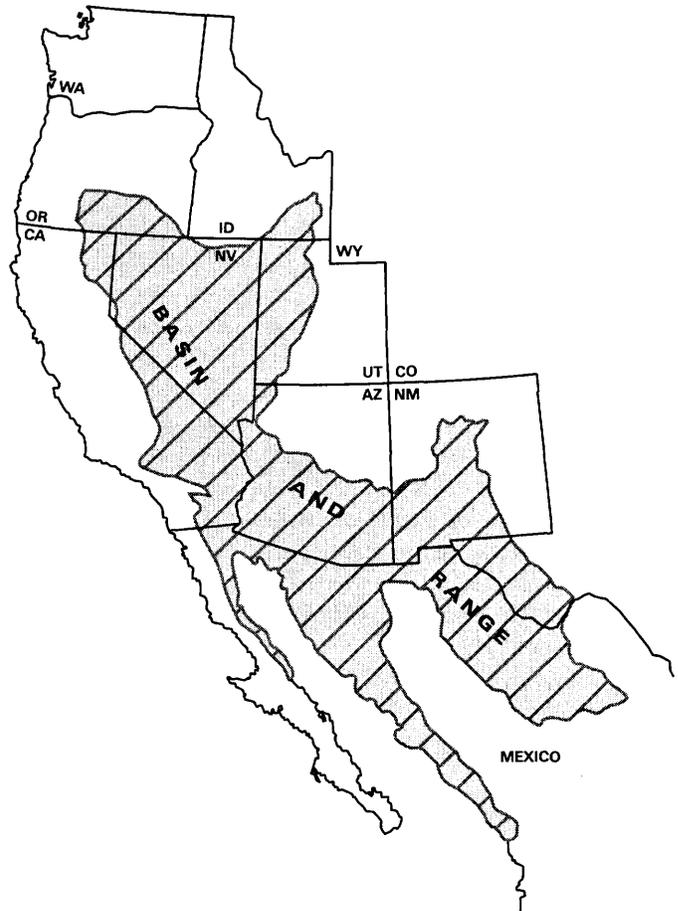


FIGURE 2.—The limits of the Basin and Range Province (after Stewart, 1971; Fiero, 1986).

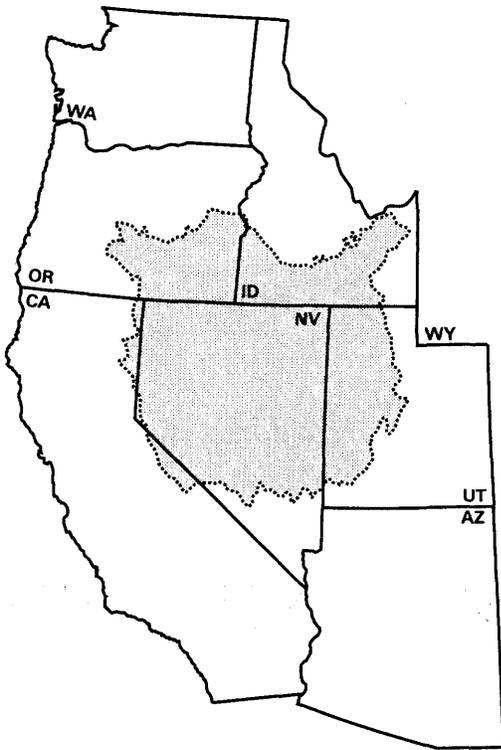


FIGURE 3.—The limits of the floristic Great Basin (after Cronquist et al., 1972).

Mountains, respectively, but many of the smaller interior ranges reach almost as high because the Great Basin is dome-shaped in cross section. Many ranges reach 12,000–13,000 ft (3660–3960 m) and extend 5000–6000 ft (1524–1829 m) above valley floors.

The biotic Great Basin is defined primarily by the distribution of plant communities rather than by the animals that are dependent upon them (Gleason and Cronquist, 1964). The most widely employed floristic definition is that of Cronquist et al. (1972) (Figure 3). In this interpretation, the floristic Great Basin extends from the Sierra Nevada on the west to the Wasatch Front ranges of Utah on the east (Cronquist et al., 1972; Osmond et al., 1990). The eastern boundary is not as sharp as that on the west, however, and many early treatments of Great Basin flora (e.g., Shreve, 1942) included much of the northern Colorado Plateau in the floristic Great Basin. Plant communities are dominated by sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), and saltbush (*Atriplex canescens*) on valley floors, juniper (*Juniperus osteosperma*) and single-leaf piñon (*Pinus monophylla*) on lower mountain slopes in the central and southern Great Basin, and white fir (*Abies concolor*), Engelmann spruce (*Picea emglemannii*), blue spruce (*Picea pungens*), Douglas fir (*Pseudotsuga menziesii*), and quaking aspen (*Populus tremuloides*) at higher elevations.

These communities extend north into the Snake River Plain, and the floristic Great Basin, as a result, does not conform well with the Great Basin as defined either physiographically or hy-

drographically. There is similar terminological confusion regarding the southern margin of the floristic Great Basin because this boundary is defined mostly by the appearance of creosote bush (*Larrea tridentata*), yucca (*Yucca brevifolia*), and other plants of the Mojave Desert south of about 37° north latitude. When either a hydrographic or physiographic definition of the Great Basin is employed, the Great Basin actually contains three of the four biotic North American deserts (Figure 4).

The Great Basin can be described most definitively in terms of a series of contiguous interior drainage systems. Although subject to some debate over whether or not a few individual drainage basins do indeed have internal drainage (e.g., Mifflin and Wheat, 1979; Smith and Street-Perrott, 1983; King, 1986), this hydrographic definition is the most detailed of those available because drainage basin boundaries can be identified with precision. Several hydrographic definitions have been produced, which differ because of the varying number of drainage

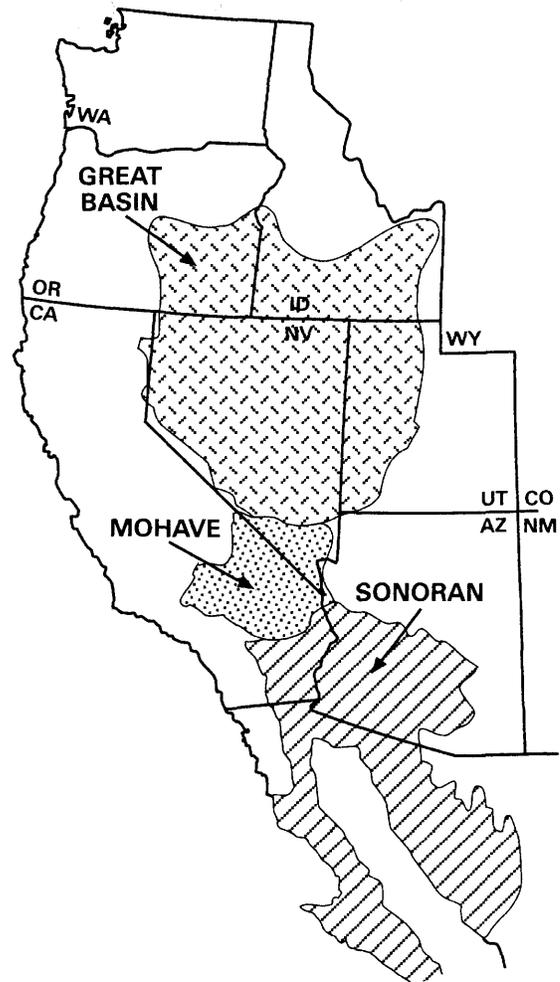


FIGURE 4.—The three biotically defined North American deserts with the hydrographically defined Great Basin (after Shreve, 1942; Spaulding et al., 1983).

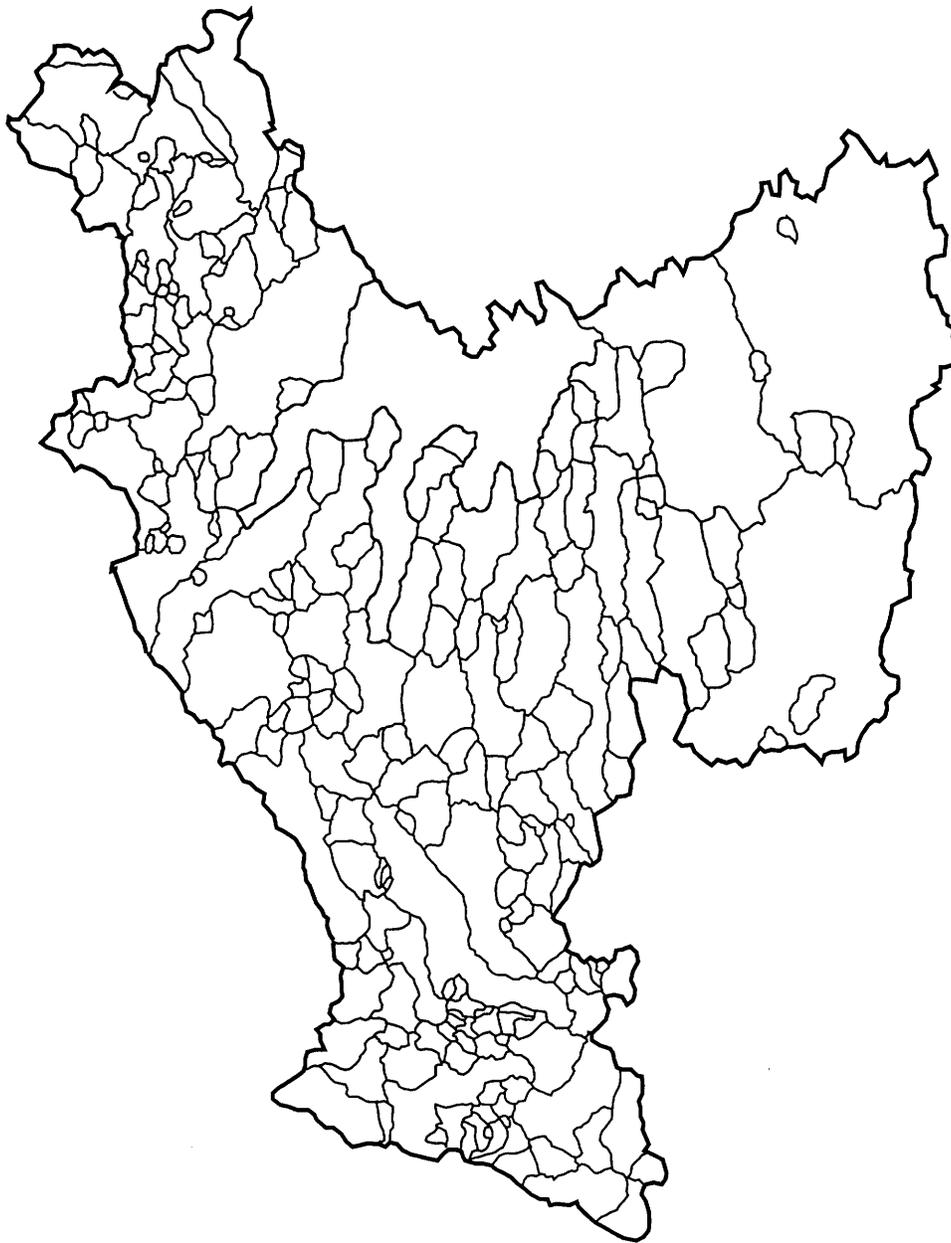


FIGURE 5.—Hydrographic basins within the Great Basin (after G.Q. King, unpublished data).

basins included. A hydrographic definition of the Great Basin is most useful herein because our interest is in Great Basin aquatic systems, and we employ that of King (1986), who identified 187 separate drainage basins within the Great Basin as a whole (Figure 5).

Many of these individual drainages coalesced to form larger drainage units during cooler and wetter periods when lake levels rose and overflowed into adjoining basins. The largest of these, by far, are the Lahontan Basin on the west and the Bonneville Basin on the east, where the relatively more massive Wasatch Mountains and Sierra Nevada, respectively, cap-

ture substantial amounts of precipitation. During warm and dry intervals, the rivers of the Lahontan Basin, such as the Truckee, the Humboldt, the Carson, and the Walker Rivers, flowed into separate basins and form individual lakes, such as Pyramid and Walker Lakes. Under higher precipitation and lower evaporation regimes, however, these basins filled differentially, forming variable combinations of basin systems as lake waters rose (Davis, 1982). At their maximum, these waters formed a single lake, covering nearly 8670 square miles (22,440 km<sup>2</sup>), during the last glacial cycle. The situation is similar in the eastern Great Basin where the Sevier and Great

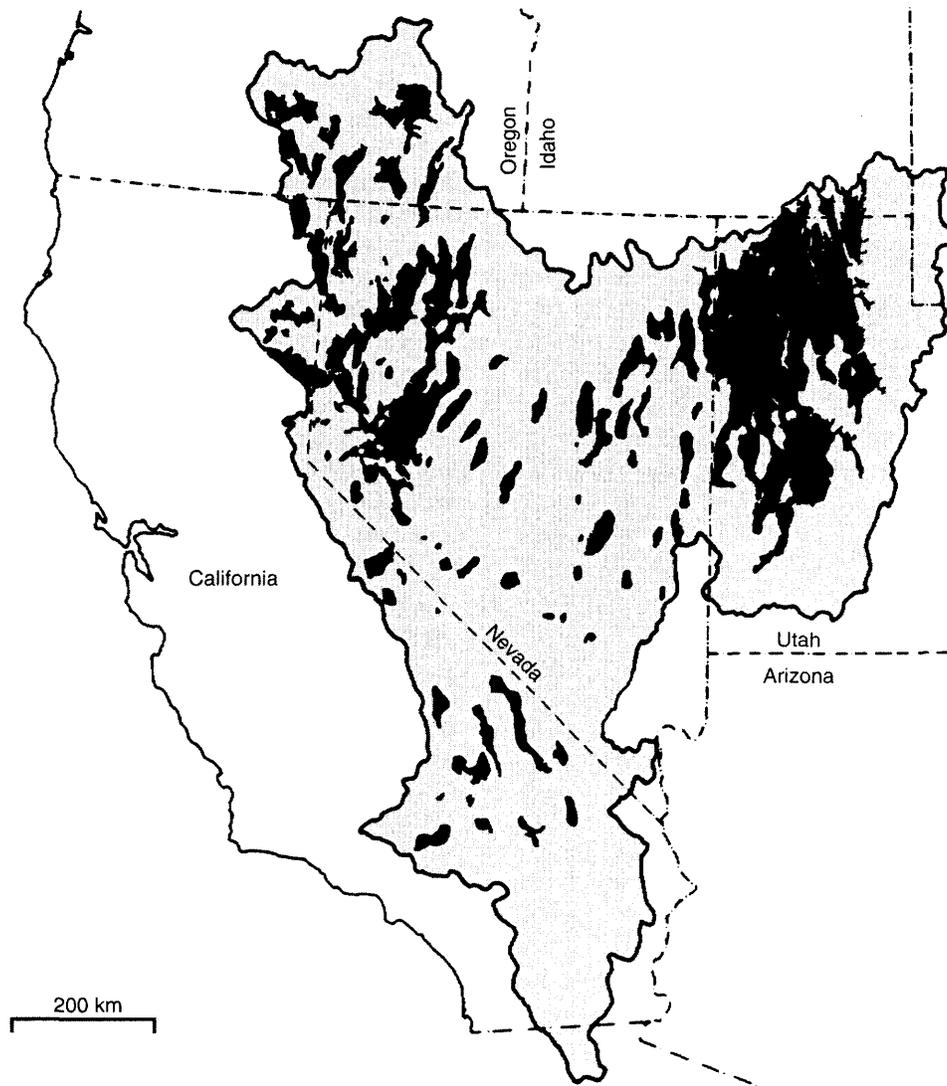


FIGURE 6.—Large lakes within the Great Basin during the height of the last pluvial period (18–16 Ka) (after Williams and Bedinger, 1984).

Salt Lake subbasins at times have been either completely separate, connected by an overflow channel, or coalesced into a single lake. At its height, Lake Bonneville extended more than 500 miles (805 km) from north to south, covered more than 19,900 square miles (51,640 km<sup>2</sup>), and overflowed into the Snake River and the Columbia River drainage system. At such times the Bonneville Basin was not, hydrographically speaking, part of the Great Basin at all.

A number of other basins within the Great Basin also overflowed during wet periods, but they formed a series of interconnected lakes rather than a single, large lake. The most extensive chain of lakes and basins were formed in the southwestern Great Basin, where Mono, Owens, China, Searles, and Panamint Lakes (and other smaller lake basins) were connected at the peak of pluvial periods by a series of overflow channels

that eventually extended into Death Valley (Smith and Street-Perrott, 1983). A number of shorter, interconnected lake systems, such as the Malheur Lake–Harney Lake chain in Oregon, were found in other parts of the Great Basin. Most of the basins in the central and southern Great Basin contained only isolated lakes during moist intervals because the mountains that form their margins are limited both in extent and elevation; however, several of these isolated lakes, such as Pleistocene Lake Franklin in central Nevada, were relatively large because of the high elevation of both the basin floor and the surrounding mountain crests in the central Great Basin. More than 80 percent of the 187 Great Basin drainages contain playas, and most of these basins likely supported lakes at least seasonally during the peak of the last pluvial interval (e.g., King, 1986; Williams and Bedinger, 1984) (Figure 6).

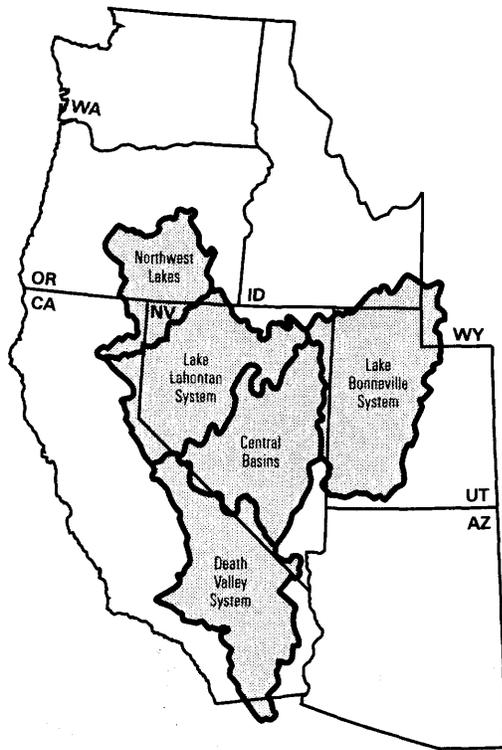


FIGURE 7.—Major subregions of the Great Basin (after Houghton, 1976).

Major subdivisions within the Great Basin have been defined in a number of ways, much like the basin as a whole. These subdivisions, also like the basin as a whole, differ markedly depending upon the criteria that are employed in making the divisions. Cronquist et al. (1972) divided the Great Basin floristic province into 15 separate sections. This number can be reduced considerably because parts of seven of these sections lie well outside the Great Basin, as defined either hydrographically or physiographically, on the Snake River Plain and the Colorado Plateau. On the other hand, they include none of the plant communities of the Mojave or Sonoran Deserts in the southern hydrographic Great Basin. Many of these floristic subdivisions cross drainage system boundaries. Both Hunt (1974) and Houghton (1976) divided the Great Basin into five major subregions based upon a combination of hydrographic and physiographic factors (Figure 7). These subdivisions are in relatively close agreement, differing primarily in the labels that are applied to them, and they provide a far simpler and more coherent division of the Great Basin than that of Cronquist et al. (1972). These include the Bonneville Basin to the east of the central basin area, the Lahontan Basin to the west of the central area, a Northwest Lakes (or Lava and Lakes) area to the north of the Lahontan Basin, and a Southern or Death Valley system to the south of the central area.

The confusion surrounding various biotic, physiographic, and hydrographic definitions of the Great Basin is symptomatic of the difficulties in understanding the history of the Great Ba-

sin aquatic systems. The Great Basin is related in many different ways to the areas around it, and it is difficult to tease out how changes in those relationships through time have differentially affected Great Basin biomes. For example, at times the Bonneville Basin has been hydrographically part of the Great Basin, and at other times it has been part of the Columbia River drainage system. As a result, the aquatic biota of this basin has a history that is both richer and more complex than that of many other Great Basin drainages. These different definitions are also illustrative of the difficulties in making comparisons across drainages within the Great Basin. Lakes in the south, for example, are surrounded by vegetation that is so markedly different from that surrounding lakes in the north that floristically they are not even in the Great Basin. Yet it is these differences that lie at the heart of the Great Basin and that, by extension, lie at the heart of the papers in this volume. The Great Basin is at once both obvious and enigmatic, making attempts to explore and interpret its natural history both irritating and rewarding.

### Chronological Aspects of Great Basin Aquatic Systems

A Great Basin aquatic systems history must include an understanding of the changing climatic conditions that have largely structured fluctuations in the size of Great Basin lakes and the development of biotic communities in the region. These long-term climatic changes are related most directly to alterations in the relative distance between the earth and the sun and, hence, vary with perturbations in the earth's orbit and axis. These climatic changes operate on a number of different scales, ranging from about 20,000 to 100,000 or more years, and, depending upon where the earth is in each of these Milankovitch cycles, they can reinforce or counteract each other. For example, the wobble in the earth's axis alternately moderates and exacerbates the change in the amount of energy received from the sun as the earth's orbit changes on a longer scale. For Late Quaternary climates, the 19,000- and 23,000-year precession cycles and the 41,000-year obliquity cycles are particularly important (e.g., Grootes and Stuiver, 1997). Climatic change on a millennial scale of 1000–2000 years also has been recognized in proxy records from ice cores and from cores taken from the ocean and large continental lakes. As yet, however, it is not clear how short-term Dansgaard-Oeschger cyclical variations may relate to the celestial mechanics that drive the longer cycles. All of these cycles appear to produce globally linked climatic changes, although the nature of these changes varies spatially.

The longer-term cycles defined in the oxygen isotope record of deep-sea cores are also readily recognized in the fluctuation histories of many Great Basin lakes (e.g., Smith and Bischoff, 1997; Benson et al., 1998). Several of the papers in this volume explore the effects of these longer-term climatic cycles on Great Basin lakes, and there is no need to discuss the issue here. Less well known, however, is the relationship between millennial-scale climatic changes and the fluctuation histories of

Great Basin lakes. Most dramatically, it is becoming increasingly clear that the transitions between the steady-state conditions that characterize these millennial-scale cycles are relatively abrupt, often on the order of a decade or less, and certainly within the lifetime of a human being. Evidence from Greenland ice cores and from cores taken from the North Atlantic Ocean indicates that these cycles assumed a characteristic form during the glacial period. They were initiated by a rapid rise in temperature of  $5^{\circ}$ – $8^{\circ}$  C in a matter of decades, gradually returned to moderate conditions over the course of about 1000 years, and ended with a rapid return to very cold temperatures prior to the start of a warming event that initiated a new cycle. The amplitude of the cycles appears to have been much smaller during the Holocene (on the order of  $1^{\circ}$ – $3^{\circ}$  C), but the pattern seems to have been relatively similar. Twenty-four cycles have been identified in the last glacial period, and nine have been recognized in these detailed ice core records during the 12,000 years of recorded human occupation in the Great Basin (e.g., Bond et al., 1997). These millennial-scale cycles extend back at least 100,000 years (e.g., Brooks et al., 1996) and appear to be part of the entire Pleistocene record.

Although it is becoming evident that change in the water budget of many Great Basin lakes is correlated with millennial-scale cycles evident in the ice core record (e.g., Benson et al., 1997; Oviatt, 1997), all of the late glacial and Holocene cycles have yet to be recognized locally. This is probably due to a combination of factors, such as the relatively coarse nature of local environmental records and the presence of other, longer cycles with periodicities of 6100 and 11,100 years that may obscure local manifestation of millennial-scale fluctuations (e.g., Mayewski et al., 1997). Once detailed and sensitive records, such as those from tree rings and lake varves, are available, many, but perhaps not all, of these cycles may become evident.

Regardless, it is as important to incorporate a notion of time into an understanding of Great Basin aquatic systems as it is to understand the spatial dimensions that define them. At times Great Basin valleys were filled with water, and at other times they became completely desiccated; lakes came and went; hydrological systems connected and disconnected. These cyclical changes, together with the basin and range topography, comprise the basic structure that underlies Great Basin aquatic systems.

### Organization of the Volume

The first section of this volume includes papers treating the physical history of Great Basin paleolakes. Negrini's comprehensive summary of pluvial lake histories in the northwestern Great Basin (and evaluation of Antevs' model for Quaternary climate change) will prove useful not only to geologists but also to those seeking information relative to aquatic biogeography. Millennial-scale oscillations are evident in this sequence, but it is apparently slightly out of phase with those of the eastern Great Basin lakes. Similarly, the paper by Reheis et al.,

which carefully documents new evidence supporting an enlarged Lake Lahontan drainage system during the late Neogene, also fits well the cross-disciplinary focus of this symposium. They suggest that lake levels were as much as 70 m higher during the early to middle Pleistocene than during the late Pleistocene highstand—a sequence that is also quite different from that found in the eastern Great Basin. The highly dynamic nature of Quaternary paleoclimates and associated hydrological cycles in the Great Basin is emphasized by Lowenstein, who reviews pertinent high-resolution data from lake beds of the Death Valley hydrographic system. Lowenstein makes it clear that rapid climate-change events evident in the Greenland ice core and in North Atlantic core records also are present in Great Basin lake histories. Oviatt summarizes the lasting contributions of Gilbert and Antevs, two of the contributors to the 1948 Great Basin volume, to the study of aquatic history of the Bonneville Basin. Sack marshals geomorphic and hydrologic evidence to unravel changes in subbasin relationships within a component of the Bonneville Basin, again indicating that complexity is a hallmark of Great Basin aquatic systems history.

The section on aquatic biology focuses on the latest contributions that biotic data have made to our understanding of Great Basin aquatic systems history, and it is intended as a supplement to the earlier papers collected by Harper and Reveal (1978). Regional aquatic biota includes various taxa that disperse readily, speciate slowly, and whose distribution and occurrence more reflects ecological and climatic conditions than history of drainage interconnections. The fossil record of such organisms thus can provide a detailed picture of environmental history. In the paper by Bradbury and Forester, high-resolution paleontologic data for two such groups from lake bed cores (diatoms and ostracods) are integrated with other biotic and physical evidence to infer the late Pleistocene history of Owens Lake within the context of Sierra Nevada glaciation and regional climatic history. On the other end of the spectrum, speciose groups, whose members are often locally endemic, can provide important clues of drainage interconnections, although this utility is strongly dependent upon the availability of robust phylogenetic hypotheses as the basis for analysis. Fishes have long paved the way in this arena, and the paper by Smith et al. represents a significant advance from the classical treatment of Hubbs and Miller (1948). In this paper phylogenies of several groups, based on mitochondrial DNA sequences, together with a comprehensive review of fossil evidence, are used to refine previous interpretations of historic drainage relationships and rates of fish evolution. Fish evidence suggests the importance of old drainage relationships and vicariant events that preceded the late Pleistocene pluvial period, as presaged by Minckley et al. (1986). Papers on aquatic snails (Hershler and Sada) and insects (Polhemus and Polhemus) suggest additional ancient drainage relationships that predate modern topography, although these hypotheses await testing within the context of phylogenetic analysis. Great Basin biogeography has changed

(extirpation of biota, introduction of exotic taxa, etc.) as a regrettable consequence of anthropogenic activities relating to water development in this arid region. It is appropriate to ask whether, using the phraseology of Kornfield and Echelle (1984:251), attention to "tending of the flock" is currently sufficient to ensure long-term persistence of the unique aquatic ecosystems in the Great Basin. The chapter by Sada and Vinyard summarizes the conservation status of aquatic biota endemic to the Great Basin. One cannot but conclude that conflicting development and conservation needs can be better balanced.

The final section on nonaquatic biology and hydroclimatic perspectives is focused on the climatic mechanisms that drive changes in Great Basin lake levels and on the biological communities that surround the Great Basin lakes. Because the history of these biotic systems is, in turn, mostly determined by fluctuations in the size of the lakes, these changes are necessarily an integral part of Great Basin aquatic systems history. The papers in this section vary between generalized accounts applicable to the Great Basin as a whole and specific accounts related to a single lake-basin history, and between consideration of very long-term changes and of relatively short-term records. As such, these papers reflect the breadth of studies involving Great Basin ecosystems that are currently underway. Davis focuses on the long-term vegetational history of the Bonneville Basin, as delineated from analysis of the pollen in deep cores from the Great Salt Lake. He suggests that there was a gradual evolution of desert flora during the last five million years that was punctuated by a number of noteworthy events. Pluvial-interpluvial cycles began after about 750,000 years ago, and Davis suggests that an increase in pollen concentration indicates the Bear River was diverted into the Bonneville Basin shortly before about 300,000 years ago. Wigand and Rhode provide a detailed compilation of Great Basin floristic changes during the last 150,000 years, focusing primarily on the last 15,000–20,000 years. Using an extensive array of data derived from pollen, midden, and tree-ring records from the northwestern, southern, and northeastern Great Basin, they suggest that

Great Basin ecosystems have not evolved in a holistic fashion. Rather, Great Basin floristic communities are a continually changing mosaic of individual organisms, and Wigand and Rhode suggest that modern and prehistoric communities are not appropriate analogues for one another. Grayson uses a detailed, small-mammal record derived from the collecting activity of owls to assess the nature of climatic change during the Pleistocene–Holocene transition and the early Holocene in the Great Salt Lake basin. He suggests that the early Holocene was both cooler and wetter than at present, in contrast to climate models that indicate otherwise. He too notes that faunal communities are composed of species that react differently to changing climatic conditions and finds support for species-richness response models that predict increasing diversity with increasing precipitation. Finally, Madsen reviews the relationship between Great Basin lakes and Great Basin peoples. He notes that this relationship is mostly structured by the dichotomy between the relatively rich and productive riverine and lacustrine ecosystems and the relatively dry and less productive landscapes that surround them. As a result, changes in the size and distribution of lakes have been critical components in the development of prehistoric human society in the Great Basin.

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# Pluvial Lake Sizes in the Northwestern Great Basin throughout the Quaternary Period

*Robert M. Negrini*

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## ABSTRACT

Sediments deposited by pluvial lakes of the northwestern Great Basin are good repositories of paleoclimate data, which have been used to test models of global climate change whose scale ranges from multidecade to megayear. The principal driving models include (1) Milankovitch-scale ( $10^6$ – $10^4$  yr) jet stream migration in response to changes in the sizes of continental glaciers, (2) millennial-scale ( $10^4$ – $10^2$  yr) climate change as a hemispheric response to large-scale climate changes in the North Atlantic Ocean (i.e., Dansgaard–Oeschger cycles, Heinrich Events, and Bond Cycles), and (3) Antevs' (1948) phenomenological model of climate change in the Holocene, which primarily predicts, on the average, a relatively warm and dry interval in the middle part of the Holocene. Changes in the Earth's orbital geometry are the ultimate causes for Milankovitch-scale climate changes. Changes in the solar constant might prove to be the ultimate cause for climate change with periods long enough to overlap the part of the spectrum occupied by the Holocene changes and by the millennial-scale climate changes; however, the magnitude of change expected from solar processes would be much smaller than those associated with millennial-scale climate changes, so if there is a causal connection, it would have to be strongly nonlinear.

Climate records from the northwestern Great Basin, particularly those from pluvial Lakes Modoc, Lahontan, and Chewaucan, support models related to Milankovitch-scale climate changes by exhibiting the appropriate periodicities and/or phases of predicted climate change and by exhibiting the appropriate dynamic spectral content of climate change throughout time (e.g., the change from a dominance of periods lasting 400 thousand years (Ky) and 41 Ky to a dominance of 100 Ky starting at ~900 thousand years ago

(Ka)). Records of millennial-scale change from the northwestern Great Basin are beginning to appear in the literature, but at the time of this review, no published records have been dated precisely enough for comparison with the archetypical records from North Atlantic marine and ice cores. A collective record associated with pluvial lakes throughout the northwestern Great Basin indicates a weak trend toward overall lower lake levels and warmer, drier climate during the middle Holocene, thereby supporting Antevs' (1948) model of Holocene climate change for the Great Basin.

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## Introduction

Approximately 50 years ago, Ernst Antevs (1948) proposed a model of Quaternary climate change for the Great Basin. The inductive reasoning that led to this model was based in part upon observations made by Allison (1945) and Russell (1895) of changes in pluvial lake levels through time in the northwestern Great Basin. The pluvial lakes of the internally drained Great Basin hydrological province have continued to be a valuable source of nonmarine paleoclimate data primarily because the sizes of these lakes are especially sensitive to changes in precipitation and evaporation (e.g., Morrison and Frye, 1965; Mifflin and Wheat, 1979; Smith and Street-Perrott, 1983; Benson and Thompson, 1987a; Benson et al., 1990; Morrison, 1991a; Spaulding, 1991; Oviatt et al., 1992; Grayson, 1993; Benson et al., 1995). Furthermore, these size changes are recorded by the presence of a wide range of observable features in the lake system, including tufa deposits, strandlines, and biota, and by a wide range of measurable features, including the geochemistry, physical lithology, and magnetism of lake sediments (Currey, 1994b). Finally, because most of the basins have been actively subsiding along marginal faults for much of the late Cenozoic era, their deposits potentially carry paleoclimate records throughout the Quaternary and earlier into the latest Tertiary period.

Records from lakes in the northwestern part of the Great Basin are set apart from those of the rest of the Great Basin because

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this region is located downwind from the volcanoes of the Cascade Range. Consequently, volcanic ashes are ubiquitous in lake-bottom sediments and are commonly found in context with other geomorphic features associated with these lacustrine systems. For example, a 17 m section of lake-bottom sediments exposed near Summer Lake, Oregon, contains more than 50 tephra layers, and the overlying sand dunes contain fragments of the Mazama tephra (Allison, 1982; Davis, 1985). The geochemical, petrographic, and, to a lesser extent, the paleomagnetic signatures of such ashes allow excellent intrabasinal correlations among outcrops and cores as well as extrabasinal correlations with other well-dated sequences of lake sediments or volcanic deposits. The absolute ages of the ashes often can be determined directly by using a variety of radiometric and luminescence methods, thus extending the age control of these sediments beyond the range of radiocarbon dating (Berger, 1991; Sarna-Wojcicki and Davis, 1991).

This paper is a review of research on northwestern Great Basin pluvial lake levels published since Antevs' 1948 paper. Antevs' original hypotheses are summarized first, followed by a review of improvements made on these models during the last 50 years. Next is a brief review of other climate-change models that potentially impact the northwestern Great Basin. Finally, advances in the associated observations (i.e., the prehistory of northwestern Great Basin lakes) made during the last several decades are summarized, focusing on studies done after previously published, related reviews (e.g., Davis, 1982; Smith and Street-Perrot, 1983; Benson and Thompson, 1987a; Morrison, 1991a, 1991b; Grayson, 1993). The spatial coverage includes pluvial Lake Lahontan and all of the Great Basin pluvial lakes to the north and west of Lake Lahontan for which published research is available (Figure 1). The temporal scope of this paper is the Quaternary period, during which the late Tertiary Great Basin was influenced by the advance and retreat of continental glaciers. The latest Quaternary receives the most emphasis because of the prevalence of data from that time interval. Unless otherwise noted, this paper follows Russell (1895), Hubbs and Miller (1948), and Morrison and Davis (1984a) in the use of the same proper name for all successive pluvial lakes that occupied each major basin.

### Models of Great Basin Climate Change

#### ANTEVS' JET STREAM MIGRATION MODEL FOR PLEISTOCENE CLIMATE CHANGE

Near the end of the nineteenth century, Russell (1895) surmised that the rise and fall of pluvial Lake Lahontan was synchronous with the advance and retreat of continental glaciers in North America. Antevs (1925, 1938, 1948, 1955) agreed with this premise and advanced the idea into a more complete model whereby pluvial episodes in the Great Basin resulted from the southward deflection of the northern jet stream storm track (and associated weather regimes) by North American continen-

tal ice sheets. Some of the details in Antevs' model have since been proven to be wrong. For example, his absolute chronologies of climate change were in error principally because his dating methods were limited to long distance correlations of discontinuous varve sequences and to salt balance calculations. In addition, he was overly attached to the assumption of precisely synchronous climate change in Europe and North America (Antevs, 1955:324; 1962; Frye et al., 1965:57). Nevertheless, Antevs' model linking ice-sheet extent to pluvial lake sizes has, to a first order, stood the test of time and, as a result, has become the prevailing model for research on high-amplitude Quaternary climate change in the Great Basin (e.g., Benson and Thompson, 1987a; Benson et al., 1990; Morrison, 1991a; Spaulding, 1991; Benson et al., 1995).

#### IMPROVEMENTS TO ANTEVS' PLEISTOCENE MODEL

##### *Estimating the Size of the Ice Sheets through Time*

**DIRECT EVIDENCE.**—The timing of lake-level change predicted by Antevs' model is, of course, dependent upon the size of the continental glaciers through time. With the development of additional absolute dating techniques and the inclusion of additional data, constraints on the extent of North American continental glaciers through time have improved considerably since Antevs' 1948 paper (e.g., Crandell, 1965; Frye et al., 1965; Goldthwait et al., 1965; Lemke et al., 1965; Muller, 1965; Péwé et al., 1965; Schafer and Hartshorn, 1965; Wayne and Zumberge, 1965; Wright and Ruhe, 1965; Hamilton and Thorson, 1983; Mickelson et al., 1983; Waitt and Thorson, 1983; Andrews, 1987; Booth, 1987). This improved knowledge base has led to more robust testing of Antevs' jet stream migration model. Unfortunately, even these advances cannot make up for the obvious fact that most of the direct evidence for the extent of the North American continental glaciers during the Quaternary period has been erased by the last glacial advance. As a result, abundant direct evidence of glacial size is only available for the last maximum and subsequent retreat positions.

**INDIRECT EVIDENCE.**—One of most important advances in Quaternary climate models during the last 50 years was the discovery that the relative concentration of the oxygen isotopes in the shells of marine microfossils provides a good first-order proxy for global ice volume for the entire Quaternary period (Shackleton, 1967; Imbrie and Kipp, 1971; Imbrie and Imbrie, 1979). This concentration is conventionally expressed as  $\delta^{18}\text{O}$ , the difference between a ratio of  $^{18}\text{O}$  and  $^{16}\text{O}$  in a given sample and that same ratio observed in a standard sample. Of particular importance to Antevs' model and to the Great Basin is the usefulness of this proxy to represent the size of the North American ice sheets through time. Indeed, despite low-amplitude, high-frequency discrepancies and an approximately 1000-year time lag, the decrease of  $\delta^{18}\text{O}$  in marine microfossils has been shown to occur more or less synchronously with the 14–6 Ka

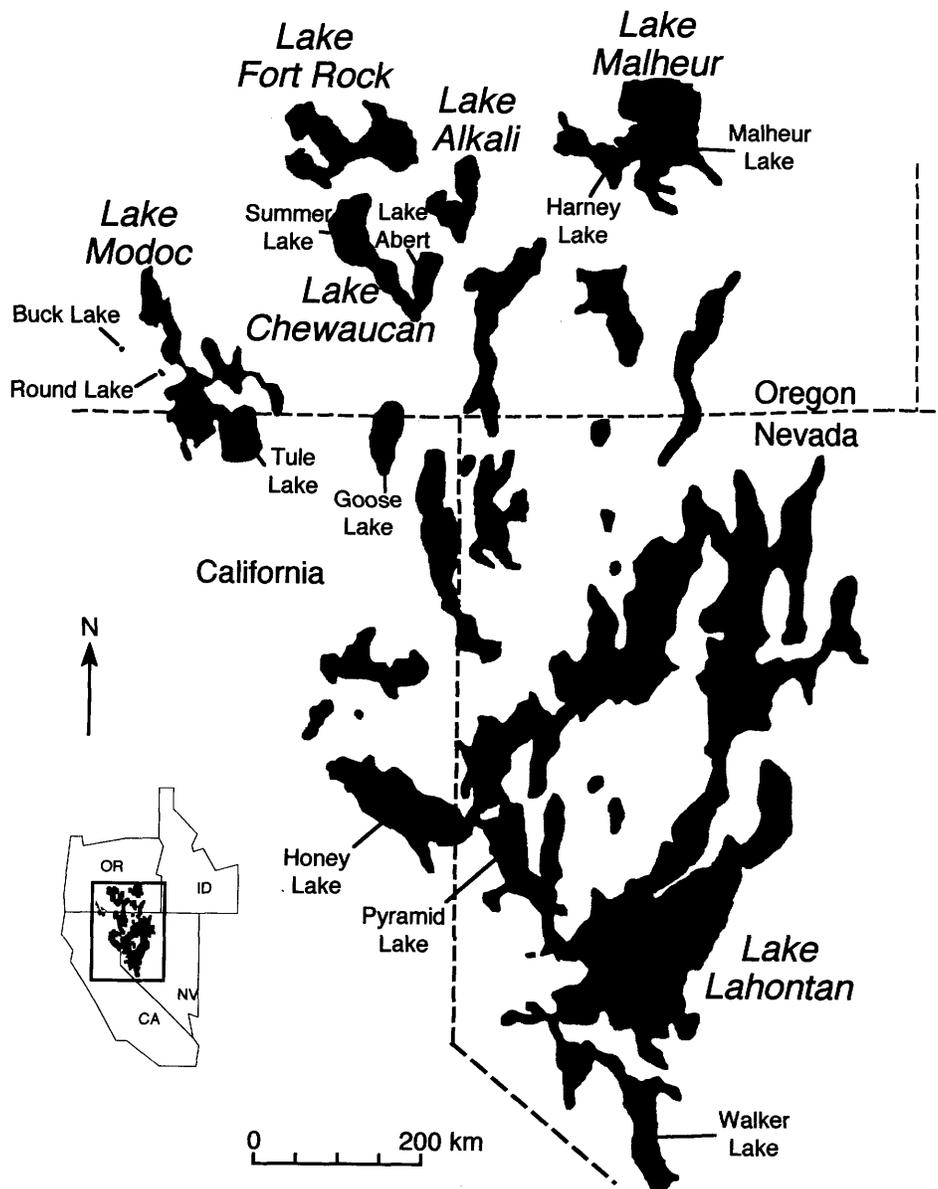


FIGURE 1.—Pluvial lakes of the northwestern Great Basin. Lake sizes during pluvial maxima are shown in gray. Modern remnant lakes are shown in black. The names of pluvial lakes discussed in this paper are shown in italicized print with large font size; the names of relevant modern remnants are indicated with smaller font.

retreat of the North American ice sheets (Mix, 1987; Ruddiman, 1987). Considering that many of the radiocarbon ages used to date both the marine records and the terrestrial limits of the ice sheets were from entirely different materials exposed to radically different geochemical environments, the timing of the two records agrees quite well. Furthermore, there is no reason to believe that this result is not representative of previous glaciations.

Another advantage in using marine isotope records as a proxy for ice-sheet size is that their ages can be determined with an accuracy, precision, and continuity previously unknown for middle- to late-Pleistocene sedimentary records.

The dating method used assumes that a large component of climate change is driven by variations in solar insolation incident on the earth's northern hemisphere, which in turn are driven by variations in the earth's orbital geometry, the so-called Milankovitch cycles (Hays et al., 1976; Imbrie et al., 1984; Martinson et al., 1987; Berger et al., 1992). These variations consist of the precession of the earth's axis of rotation about the ecliptic normal (an ~21 Ky period), the oscillation of the axial obliquity angle (an ~41 Ky period), and the oscillation of the eccentricity of the orbit (an ~100 Ky period). Marine oxygen isotope records are dated by tuning their phase and amplitude spectra

to those of the Milankovitch cycles. This analysis includes the expected lag in the melting of the ice sheets and the associated lowering of marine  $\delta^{18}\text{O}$ . Because the timing of Milankovitch cycles can be accurately and precisely extrapolated backward in time for hundreds of thousands of years from modern and historical astronomical observations, the age control for the oxygen isotope global ice volume proxy is arguably precise to within a few thousand years to at least as far back as 300 Ka (Martinson et al., 1987). There is strong support for the accuracy of the marine oxygen isotope chronology well back into the early Quaternary (Johnson, 1982; Baksi et al., 1992; Izett and Obradovich, 1994; Edwards et al., 1997; Kerr, 1997). It should be noted that terrestrial temperature proxies from ice cores and vein calcites, which should respond more quickly to insolation variations than the marine oxygen isotope records, at times agree very precisely with the marine records but at other times are quite discordant (e.g., Winograd et al., 1992; Winograd et al., 1997). This inconsistency calls into question the constancy of the lag times used in the orbital tuning of the marine oxygen isotope chronology and, thus, the accuracy of this chronology.

An abrupt increase in mean  $\delta^{18}\text{O}$ , a corresponding decrease in the mean percentage of  $\text{CaCO}_3$ , and a coeval increase in variability of both of these indices in marine sediments point to the onset of ice sheets in the northern hemisphere at about 2.5 Ma (Ruddiman and Wright, 1987, and references therein). These early ice sheets apparently fluctuated in size at obliquity-like periods of 41 Ky from ~2.5 Ma until ~900 Ka (Ruddiman et al., 1986; Ruddiman and Wright, 1987; Ruddiman and Raymo, 1988). From 900 Ka to the present, the 23 Ky precession-like period became as important as the 41 Ky period, and both became subordinate to the 100 Ky eccentricity-like period (Imbrie, 1985; Ruddiman and Wright, 1987). The above-described character of the marine-sediment proxies for ice-sheet extent can be used in conjunction with Antevs' model to predict similar features in records of pluvial lake-level sizes through time. Furthermore, assuming that the lake-level data have the requisite amplitude resolution and age control, finer-scale features in the marine proxies, such as the oxygen isotope stage (OIS) and the substage boundaries of Hays et al. (1976), also can conceivably be employed as predictive tools.

#### *Quantifying the Jet Stream Model*

**ATMOSPHERIC CIRCULATION MODELS.**—Spurred by advances in computer technology during the last 25 years, Antevs' model has been expressed quantitatively as part of a more general effort to model global atmospheric circulation in response to a variety of factors (Kutzbach, 1987; COHMAP, 1988; Kutzbach and Ruddiman, 1993). From such models, jet-stream position versus time has been predicted in response to changing global climatic conditions for the last 18 Ky. The models are based upon the fundamental laws of physics and are

constrained by a myriad of boundary conditions, including the surface area and elevation of continental ice sheets, latitude- and time-dependent Milankovitch-driven changes in solar insolation, atmospheric chemistry (e.g., the concentration of  $\text{CO}_2$ ), sea-surface temperatures, albedo of the earth's surface, etc. Such efforts have shown that, to a first order, significant changes in precipitation, temperature, and weather distribution patterns should, indeed, occur in response to the advance of the continental ice sheets as proposed in Antevs' original model for the Great Basin (Kutzbach and Wright, 1985; Manabe and Broccoli, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987; COHMAP, 1988).

Although the results of the above-described models generally support Antevs' jet stream migration model, the spatial and temporal grid spacings in the models are relatively large compared with the spatial and temporal resolution and the accuracy of the observational database. That is, the general atmospheric circulation models do not generate specific-enough predictions regarding the effect of the jet stream on the magnitude and timing of pluvial lake size in a region as small as the northwestern Great Basin. For example, such models show a maximum southward mean position of a strong winter jet stream at ~25°–35° N from before 18 Ka to as late as 15–12 Ka (Kutzbach, 1987, fig. 11; Thompson et al., 1993). In contrast, northwestern Great Basin lakes are spaced only tens to hundreds of kilometers apart, and the lake-level prehistory of at least one of them (Lake Lahontan) is known throughout this time interval with a precision as small as a few hundred years (see "Latest Pleistocene," below). As knowledge of the lake-level prehistories for the other lakes approaches that for Lake Lahontan, higher-resolution models will be required.

**EFFECT OF JET STREAM MIGRATION ON LAKES.**—More-localized modeling has been conducted to determine if predicted climate conditions would result in lake-size changes that agree with observations (Mifflin and Wheat, 1979; Benson, 1986; Benson and Paillet, 1989; Hostetler and Bartlein, 1990; Hostetler and Benson, 1990; Hostetler, 1991; Freidel, 1993). Input for these models includes the general climate conditions dictated by the output of the larger-scale models, independent observations of pluvial climate conditions (e.g., temperature and precipitation estimates from fossil pollen analyses), or extreme values from modern measurements (e.g., river discharge values from the 1983 wet year). Such efforts have demonstrated that pluvial lakes can indeed reach their maximum sizes under the conditions corresponding to a mean annual position of the jet stream storm track near or south of the latitude of the lake in question in response to decreased evaporation from lower temperatures and increased cloud cover and in response to enhanced precipitation in the drainage basins. The amount of required increase in precipitation is reduced significantly by greatly reduced evaporation if the temperature decreases enough to freeze the lakes during the winter.

DANSGAARD-OESCHGER CYCLES, HEINRICH EVENTS, AND  
BOND CYCLES AS MODELS FOR HIGH-AMPLITUDE  
PLEISTOCENE CLIMATE CHANGE

In the last two decades, high-frequency climate events and cycles not explainable by Milankovitch cycles have been observed in several different types of climate records, especially high-resolution ice cores and marine sediment cores (Broecker, 1994). In particular, Dansgaard-Oeschger (D-O) cycles are variations in several climate parameters and were first observed in Greenland ice cores (Dansgaard et al., 1982; Dansgaard et al., 1993). They have a distinctive square-wave morphology and periods of a few thousand years. These cycles usually oscillate about a progressively cooler temperature mean until a relatively instantaneous Heinrich event occurs. Heinrich events are marked by distinct marine sedimentary deposits that indicate extensive ice rafting from North America into the North Atlantic Ocean (Heinrich, 1988). These lithologic deposits are coeval with the coldest of the cold parts of the D-O cycles since the last Heinrich event. A rapid warming usually follows, marking the beginning of a new sequence of D-O cycles that, in turn, end in the next Heinrich event (Bond et al., 1993). Each set of D-O cycles and its associated terminal Heinrich event is collectively referred to as a Bond cycle (Broecker, 1994). Within Bond cycles, each cold part of the higher-frequency D-O cycles also are correlated with high percentages of lithic detritus presumably rafted on icebergs (Bond and Lotti, 1995).

The balance of evidence suggests the above phenomena are global in nature. Heinrich events, in fact, appear to have occurred near major global climate boundaries (e.g., at the transition from OIS 6 to 5, from 5 to 4, and from 2 to 1 (Broecker, 1994). The most-favored mechanisms for connecting Heinrich events (and now the cool parts of the D-O cycles) with global climate change are (1) the impact of fresh water into the North Atlantic Ocean on the marine thermohaline circulation and related atmospheric/oceanic transfer of heat and water vapor, and (2) the impact on the position of prevailing weather patterns caused by a rapid retreat of the Laurentide ice sheet (Broecker, 1994; Bond and Lotti, 1995). Although the causes of D-O cycles, Heinrich events, and Bond cycles have not been identified unequivocally, their widespread nature and distinct timing have led to their use as potential phenomenological models for high-frequency climate change in the Great Basin (e.g., Oviatt, 1997; Benson et al., 1998).

ANTEVS' NEOTHERMAL MODEL FOR HOLOCENE  
CLIMATE CHANGE

The understanding of Holocene climate change is important for several reasons, including its bearing on the distribution and nature of archeological sites (Baumhoff and Heizer, 1965; Aikens, 1983; Mehringer, 1986; Madsen, 2002) and its importance in establishing a baseline for anthropogenic climate change (Scuderi, 1993). Unfortunately, for the most part, models of

Holocene climate change are still in the inductive stage. They are either entirely descriptive or consist of time-varying global phenomena that have only speculative, generalized links to climate. Part of the problem for the northwestern Great Basin lies in the unremarkable nature of the observations relative to those in the latest Pleistocene. Holocene pluvial lake-level changes in this region either are very low in magnitude or, if high-magnitude changes do exist, are of too high a frequency (<100-year periods) to be easily observed in the geological record. Despite these problems, the existing models of Holocene climate change are worth reviewing as points of departure.

Antevs (1948, 1955) based his model for Holocene (or, in his terms, "Neothermal") climate change in the Great Basin on observational evidence from North America and Sweden and on the assumption of synchronous climate change for the entire Northern Hemisphere (Grayson, 1993). Loosely interpreted, Antevs divided the Holocene into three intervals of roughly equal duration, as shown in Figure 2a. The early Holocene Anathermal age (10–7.5 calendar thousand years ago (cal Ka); 8.4–6.6 radiocarbon thousand years before present ( $^{14}\text{C}$  Ky B.P.)) was characterized by modern-like temperatures that gradually increased throughout the interval and by aridity levels that were slightly moister than today. The middle Holocene Altithermal age (7.5–4.5 cal Ka; 6.6–4.0  $^{14}\text{C}$  Ky B.P.) was distinctly warmer than present, and it was characterized by higher aridity. In the late Holocene Medithermal age (4.5 cal Ka to present), conditions returned to cooler temperatures and less aridity, although they were slightly more arid than the Anathermal. Quantitative modeling has not yet been attempted to determine the extent of lake-level rise and fall in response to Holocene climate change; however, assuming Antevs' model is correct, it is reasonable to extrapolate from this model that northwestern Great Basin pluvial lakes would have been at late Holocene levels or slightly higher during the early Holocene and at their lowest levels during the middle Holocene.

As with Antevs' jet stream migration model, the particulars of his Neothermal model have fallen prey to additional data that have been analyzed with more modern techniques. For example, his attribution of moister conditions for the Anathermal age is based in part upon several meters of lake sediments found above the Mazama tephra in an outcrop that is 25 m above the present-day lake level of Summer Lake, Oregon (Allison, 1945; Antevs, 1948). After the advent of geochemical fingerprinting of tephra layers and better absolute dating techniques, it became clear that Allison's tephra was, instead, the considerably older (~45–50 Ky old) Mount St. Helens Cy tephra (Allison, 1966a; Davis, 1985; Berger and Davis, 1992). Generally speaking, however, when data are averaged temporally over hundreds of years and spatially over the entire northwestern Great Basin, Antevs' original hunch has proven to be more or less correct, although a strict adherence to this model is commonly advised against, mostly because of its limited applicability to very specific localities and times (Bryan and

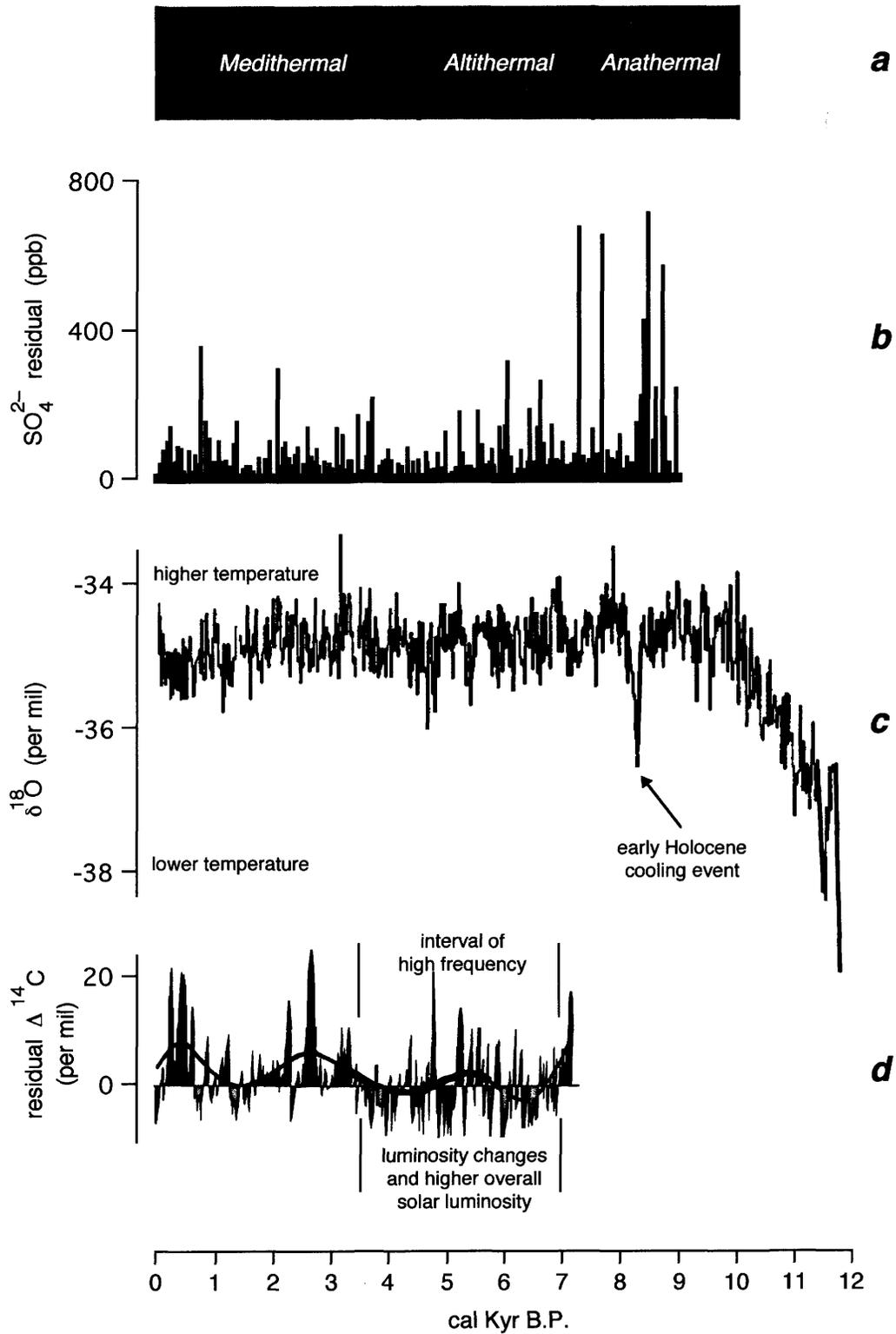


FIGURE 2.—*a*, Approximate age range of Antevs' Neothermal ages. *b*, Frequency and severity of Holocene eruptions as indicated by residual sulfate anomalies from the GISP2 ice core (after Zielinski et al., 1994, fig. 4). *c*, Holocene temperature as indicated by oxygen isotope data from the GISP2 ice core (after Stuiver et al., 1995, fig. 5). *d*, Solar luminosity throughout the middle and late Holocene as inferred from  $^{14}\text{C}$  concentration anomalies corrected for variations in magnetic field intensity (after Damon et al., 1989, fig. 4; Magny, 1993, fig. 3).

Gruhn, 1964; Mehringer, 1986; Grayson, 1993; Wigand and Rhode, 2002).

Aside from the issue of its applicability, Antevs' model is less than satisfying because it is entirely descriptive in nature. That is, there is no cause attributed to the transitions between, and the durations of, Antevs' three Neothermal ages. Toward this end, Antevs' model appears to be consistent, at least in a qualitative sense, with his jet stream migration model until the end of the middle Holocene. That is, the moist, not-quite-hot Anathermal could be considered to be related to slightly more frequent storms in the northern Great Basin if the storm track had not quite retreated to its modern position associated with ice-free conditions. The Altithermal, which reached its peak hot, dry conditions 5.5–6.0 cal Ka, corresponds quite well with the final disappearance of the North American ice sheets. The return of moderately warm, arid to semiarid conditions in the Medithermal age after 4.5 cal Ka is not explained by this model because the North American ice sheets have not returned.

Results from quantitative modeling, however, indicate that the northern jet stream storm track would have reached its modern position and intensity (or lack thereof) by 9 Ka or earlier, which is well before the peak of the Altithermal age (Kutzbach, 1983, 1987). Thus, subsequent reductions in the size of an already insignificant ice sheet should not have affected Great Basin climate. On the other hand, although atmospheric circulation models also take into account the more subtle shift in weather patterns caused solely by Milankovitch-driven changes in insolation in the absence of ice sheets, the low-amplitude changes in precipitation and temperature that result directly from such insolation changes are usually below the sensitivity level of these models (Kutzbach, 1987). On a more localized scale, Benson (1986) has shown that changes in the evaporation rate that were induced solely by insolation changes were an order of magnitude lower than those needed to fill pluvial Lake Lahontan in conjunction with increased discharge. Thus, if insolation variations were nonetheless responsible for the subtle changes in lake level observed in the northwestern Great Basin during the Holocene, then they must have acted in the absence of the other factors that Benson found to be much more important (e.g., the difference between air and water-surface temperatures, the type of clouds, and the degree of cloudiness). In any case, the peak value of summer insolation at the latitude of the northwestern Great Basin occurred at ~11 Ka, well before the onset of the middle Holocene Alithermal age. Again, timing is a problem with regard to nondescriptive modeling of Holocene climate in the northwestern Great Basin.

#### OTHER MODELS FOR HOLOCENE CLIMATE CHANGE

##### *Volcanic Eruptions*

Large volcanic eruptions significantly increase the concentration of atmospheric aerosols and, as a result, decrease global

temperatures slightly ( $<1.5^{\circ}\text{C}$ ) for a few years until the aerosols settle out (Stuiver et al., 1995). The 1991 eruption of Mount Pinatubo lowered the earth's mean temperature by as much as  $\sim 0.5^{\circ}\text{C}$  for a year or two, as determined both by direct observations and by models that postulated the effects on the atmosphere caused by the observed increase in aerosol concentration (Hansen et al., 1992; Houghton et al., 1996, fig. 14). The effects of larger eruptions on climate (e.g., Tambora in 1815), as inferred from increased levels of acidity in Greenland ice cores, do not seem to last much longer (Hammer et al., 1980, fig. 2).

Despite the short-term nature of the effects of single eruptions on climate, some time intervals containing frequent, large eruptions may coincide with intervals characterized by lower temperatures over much of the earth. For example, Hammer et al. (1980, fig. 5) demonstrated longer-term (decade to century) correlations between periods of lowered Northern Hemisphere temperature (by  $0.5^{\circ}\text{C}$ – $1.0^{\circ}\text{C}$ ) and intensified and/or more frequent volcanism. On the millennial scale, Stuiver et al. (1995) used  $\delta^{18}\text{O}$ -derived temperature estimates from the GISP2 ice core to argue that volcanism caused no more than a  $0.1^{\circ}\text{C}$  average decrease in temperature during the last 1000 years.

The last 1000 years, however, may not be representative of the entire Holocene. Zielinski et al. (1994) presented an intriguing record of volcanic eruptions for the past 9000 years, based upon their analysis of sulfate concentrations in the GISP2 ice core (Figure 2*b*). They found that extremely large eruptions occurred more frequently during the early Holocene ( $\sim 9.0$ – $7.0$  cal Ka) as opposed to the remainder of the Holocene. These authors tentatively concluded that this increased volcanism contributed to observed climatic cooling in the Northern Hemisphere during a time interval that otherwise would have been warmer because of higher summer insolation values in the Northern Hemisphere. Thus, Holocene climate change could conceivably be explained by the combined effects of volcanism and insolation variations. That is, the highest insolation values in the early Holocene could have been counteracted by the effects of anomalous volcanism. The middle Holocene (Antevs' Altithermal age) would have been a time of higher temperatures driven by still-high insolation values, but the cooling effect of the anomalous early Holocene volcanism would have ended. As Northern Hemisphere insolation values decreased steadily to present values, cooler temperatures would have prevailed in the late Holocene. This combined model is appealing, but it remains to be shown that the larger, more frequent eruptions of the early Holocene would result in a significantly larger temperature anomaly than the mere  $0.1^{\circ}\text{C}$  effect determined by Stuiver et al. (1995) for the last 1000 years. It also must be shown that the increased level of sulfate in the GISP2 ice core during the early Holocene was caused by globally significant eruptions rather than by local events in the vicinity of Greenland (Zielinski et al., 1994).

### *Solar Variability*

Low-amplitude temperature change during the Holocene also has been attributed to variations in solar insolation caused, in turn, by inherent variability in the sun's luminosity on the order of 0.1% (Stuiver, 1965, 1980; Denton and Karlén, 1973; Reid, 1987; Stuiver et al., 1991; Stuiver et al., 1995). This causal relationship is most directly based upon correlations of the timing of various global climate estimates during the last century with both the number of sunspots (Eddy, 1977; Reid, 1987) and the period of the sunspot cycle (Friis-Christensen and Lassen, 1991). Such variations in solar luminosity can account for an increase of as much as 0.25° C, which is approximately 50% of the long-term temperature increase observed since the middle of the nineteenth century. These values are based upon recent studies that modeled the effect on global temperature caused by the relative contributions of heat input from changes in solar luminosity and from changes in the concentrations of greenhouse gasses and aerosols (Kelly and Wigley, 1992; Lacis and Carlson, 1992; Schlesinger and Ramanakuty, 1992).

Proxy indices have been generated to extend estimates of changes in solar activity back through the last several tens of thousands of years. These indices are based upon observed correlations of lower solar luminosity with higher concentrations of cosmogenic radioisotopes (Stuiver, 1965; Stuiver and Quay, 1980; Damon et al., 1989; Stuiver et al., 1991; Stuiver et al., 1997). One such proxy index (Figure 2*d*) is based upon  $\Delta^{14}\text{C}$ , which is a ratio expressing the difference between measured radiocarbon activity and the expected activity of a sample of a particular age (Stuiver and Pollach, 1977; Sonett et al., 1990; Stuiver et al., 1991). The data shown in Figure 2*d* are residual values of  $\Delta^{14}\text{C}$  after the removal of variations caused by well-documented changes in the intensity of the earth's magnetic field (Damon et al., 1989).

Such proxies for solar luminosity have been compared with various estimates of climate change throughout the Holocene (e.g., glacier extent around the world and lake-level fluctuations in Europe), and correlations have been found corresponding to periods of duration of ~90, 200, and 2200–2300 years (Damon and Jirikowic, 1992; Magny, 1993; Stuiver and Braziunas, 1993; O'Brien et al., 1995; Stuiver et al., 1995). The largest magnitude of temperature change at these periods, as inferred from Holocene variations of  $\delta^{18}\text{O}$  in the GISP2 ice core (0.4° C; Stuiver et al., 1995), is reasonably close to the previously mentioned modeled results for solar-induced temperature change during the last century or so (see above).

Assuming that changes in the solar constant during the Holocene really do contribute to the  $\Delta^{14}\text{C}$  variations shown in Figure 2*d*, one could conceivably use this data to predict the timing and duration of the relatively subtle Holocene climate changes observed in the Great Basin. For example, the overall low values of  $\Delta^{14}\text{C}$  from 7.0 to 3.5 cal Ka would indicate an extended period of higher solar luminosity during a time period

that, for the most part, corresponds with Antevs' Altithermal age. The same time period also was characterized by higher-frequency variations in luminosity, suggesting that one might expect to find high-frequency climate changes in the middle Holocene superimposed on an overall warmer climate. Finally, relatively high values of  $\Delta^{14}\text{C}$  shown in Figure 2*d* at time intervals of 6.0–5.2, 3.4–1.7, and 0.6–0.2 cal Ka predict low values of solar luminosity at those times. Magny (1993) noted that cooler, moister climate in the European Alps indeed occurred at approximately those times, as evidenced by three dominant intervals of lake-level transgressions during 6.5–4.5, 3.5–2.0, and 0.60–0 cal Ka. Furthermore, the solar-luminosity proxy and an earlier period (8.7–8.0 cal Ka) of transgressions noted by Magny (1993) correlate reasonably well with the low-amplitude, century- to millennial-scale, global cooling events (8.8–7.8, 6.1–5.0, 3.1–2.4, and 0.6–0 cal Ka) recognized both in glaciochemical time series from the GISP2 ice core and in previously published, coeval paleoclimate indicators from around the globe (O'Brien et al., 1995). This set of observations suggests that solar variability is worthy of further investigation as a potential cause of low-amplitude climate change in the Holocene.

### *A Short-Term, High-Amplitude Cooling Event in the Early Holocene*

A spike-like, early Holocene cooling event centered at ~8.4–8.0 cal Ka (e.g., Figure 2*c*) is recognized in several climate records from around the world (Alley et al., 1997) and may be potentially observable in pluvial lake records from the northwestern Great Basin. The geographic distribution of the type of climate change observed at each locality is similar to that of the terminal Pleistocene, Younger Dryas event (Alley et al., 1997, and references therein). Furthermore, the amplitudes of the anomalies in several climate proxies for the early Holocene cooling event are comparable (approximately one-half) to those of the same proxies for the Younger Dryas event. For example, a temperature decrease in Greenland of about 6° C was implied for the early Holocene event by a 2‰ decrease in  $\delta^{18}\text{O}$  in the GISP2 ice core (Alley et al., 1997). The Younger Dryas event has often been attributed to diminished thermohaline circulation induced by a sudden influx of fresh water into the North Atlantic Ocean (Broecker et al., 1990; Alley et al., 1997), suggesting that a similar influx caused the early Holocene event; however, Alley et al. (1997) noted that no such influx of fresh water is evident in the geologic record during this time interval. Alternatively, this cooling event is coincident with the time interval containing four closely spaced, very large volcanic eruptions, as inferred by the residual sulfate record from the GISP2 ice core (Zielinski et al., 1994). It is tempting to draw a causal relationship between the two phenomena, but, again, it has yet to be shown that large eruptions disrupt climate for periods significantly greater than a couple of years (see "Volcanic Eruptions," above).

## Pluvial Lake Sizes through Time in the Northwestern Great Basin

### METHODS

During the last 50 years, pluvial lake studies in the northwestern Great Basin have benefited from an increasingly diverse array of new or improved methods with which to determine the timing and magnitude of lake-size changes. These methods include radiometric and luminescence dating (Rosholt et al., 1991; Berger, 1988), petrographic and geochemical fingerprinting of tephra layers (Sarna-Wojcicki and Davis, 1991), paleoecology of lacustrine biota (Forester, 1987; Bradbury, 1991, 1992, 1997), trace element and isotope geochemistry of lake sediments (Stuiver, 1970; De Dekker and Forester, 1988; Benson and Peterman, 1995; Benson et al., 1996), particle-size analysis of sediments (McCave and Syvitski, 1992), paleomagnetic-polarity stratigraphy and secular-variation dating as applied to lacustrine sediments and volcanic tephra (Reynolds, 1977, 1979; Verosub, 1988; Rosholt et al., 1991; Negrini and Davis, 1992), environmental magnetism (Thompson and Oldfield, 1986; Verosub and Roberts, 1995), improvements in sedimentological and geomorphological models of lacustrine systems in arid environments (Currey, 1994a, 1994b), and the empirical and theoretical analyses of post-depositional deformation of basins in this region (Pezzo-pane, 1993; Bills, unpublished).

The age estimates of several key northwestern Great Basin tephra layers have been improved since the last review paper was written on northwestern Great Basin lakes, and previous reviews (e.g., Davis, 1982; Smith and Street-Perrot, 1983;

Benson and Thompson, 1987a; Morrison, 1991a, 1991b; Grayson, 1993) have not covered the use of paleomagnetic secular variation as a dating tool in the northwestern Great Basin. These two topics will be addressed below.

### *Recent Work on the Ages of Key Tephra Beds in the Northwestern Great Basin*

**EARLY PLEISTOCENE TEPHRA.**—The ages of a few early Pleistocene tephra layers have been revised recently to slightly older ages, in part as a result of improved technology of the laser-fusion  $^{40}\text{Ar}/^{39}\text{Ar}$  method (Table 1). For example, the ages of the Bishop and Lava Creek B tephra layers (and, by association, the Rye Patch Dam) have recently been revised downward by an average of a few percent to  $\sim 760 \pm 2$  Ky (Sarna-Wojcicki and Pringle, 1992; Izett and Obradovich, 1994) and  $665 \pm 10$  Ky (Izett et al., 1992), respectively. The same technique has been used to revise downward the age of the Brunhes/Matuyama geomagnetic polarity reversal to agree better with that predicted by marine  $\delta^{18}\text{O}$  stratigraphy (e.g., Johnson, 1982; Baksi et al., 1992; Izett and Obradovich, 1994).

**MIDDLE PLEISTOCENE TEPHRA.**—Several middle Pleistocene tephra layers have ages that are poorly constrained because they are either too old for the easy acquisition of precise luminescence or radiocarbon ages, too young, or of the wrong chemical composition, mineralogy, and/or grain size for the easy acquisition of precise fission-track or potassium-argon ages on distal volcanic ashes (Naeser and Naeser, 1987; Rosholt et al., 1991; Sarna-Wojcicki and Davis, 1991). As a result, many ashes in this age range have age estimates with

TABLE 1.—Tephra layers, from youngest to oldest, found in the pluvial lakes of the northwestern Great Basin.

Tephra	Pluvial lakes	Age	References
Tarupah Flat	Lahontan	600–1500 cal yr B.P.	Davis (1978)
Mazama	Lahontan, Chewaucan	$6.845 \pm 0.05$ $^{14}\text{C}$ Ky B.P.	Davis (1978), Bacon (1983); Davis (1985)
Tsoyawata	Lahontan, Modoc	$7.015 \pm 0.045$ $^{14}\text{C}$ Ky B.P.	Davis (1978), Bacon (1983); Reick et al. (1992)
Mount St. Helens Mp	Lahontan, Chewaucan	$20.5 \pm \sim 0.5$ $^{14}\text{C}$ Ky B.P.	Davis (1978), Davis (1985); Negrini et al. (1988); Negrini and Davis (1992)
Trego Hot Springs	Lahontan, Chewaucan, Modoc	$23.2 \pm 0.3$ $^{14}\text{C}$ Ky B.P.	Davis (1978), Davis (1985); Reick et al. (1992); Benson et al. (1997)
Wono	Lahontan, Chewaucan	$27.3 \pm 0.3$ $^{14}\text{C}$ Ky B.P.	Davis (1978), Davis (1985); Benson et al. (1997)
Mount St. Helens Cy	Lahontan, Chewaucan	45–50 Ky	Davis (1978), Davis (1985); Berger and Busacca (1995)
Olema	Chewaucan, Modoc	50–55 Ky	Reick et al. (1992); this paper
Pumice Castle Set	Chewaucan, Modoc, Malheur	$72 \pm 6$ Ky	Bacon (1983); Davis (1985); Reick et al. (1992); Botkin and Carambelas (1992a, 1992b); this paper
Summer Lake 2	Chewaucan	$67.3 \pm 7.2$ Ky	Davis (1985); Berger (1991)
Summer Lake V	Chewaucan, Modoc	155–200 Ky	Davis (1985); Negrini et al. (1994)
Wadsworth	Lahontan, Modoc	155–200 Ky	Davis (1978), Reick et al. (1991)
Summer Lake GG	Chewaucan	$\sim 190 \pm \sim 30$ Ky	Davis (1985); Herrero-Bervera et al. (1994); Negrini et al. (1994)
Summer Lake KK	Chewaucan, Modoc	$\sim 200 \pm \sim 30$ Ky	Davis (1985); Berger (1991); Herrero-Bervera et al. (1994)
Rockland	Lahontan, Modoc	410 Ky	Sarna-Wojcicki et al. (1985); Sarna-Wojcicki et al. (1991)
Dibekulewe	Lahontan, Modoc	$\sim 510$ Ky	Davis (1978); Negrini, Verosub et al. (1987); Sarna-Wojcicki et al. (1997)
Lava Creek B	Lahontan, Modoc	$665 \pm 10$ Ky	Davis (1978); Reick et al. (1991); Izett et al. (1992)
Rye Patch Dam	Lahontan, Modoc	$\sim 675$ Ky	Davis (1978); Reick et al. (1991); this paper
Glass Mt. D	Lahontan	$\sim 0.9$ – $1.0$ My	Sarna-Wojcicki et al. (1991); Parker (1993)
Glass Mt. G	Lahontan	$\sim 1.0$ – $1.1$ My	Morrison and Davis (1984a); Sarna-Wojcicki et al. (1991)
Rio Dell	Modoc	1.45 My	Izett (1981); Sarna-Wojcicki et al. (1987); Sarna-Wojcicki et al. (1991)
Bear Gulch	Modoc	1.94 My	Sarna-Wojcicki et al. (1991)

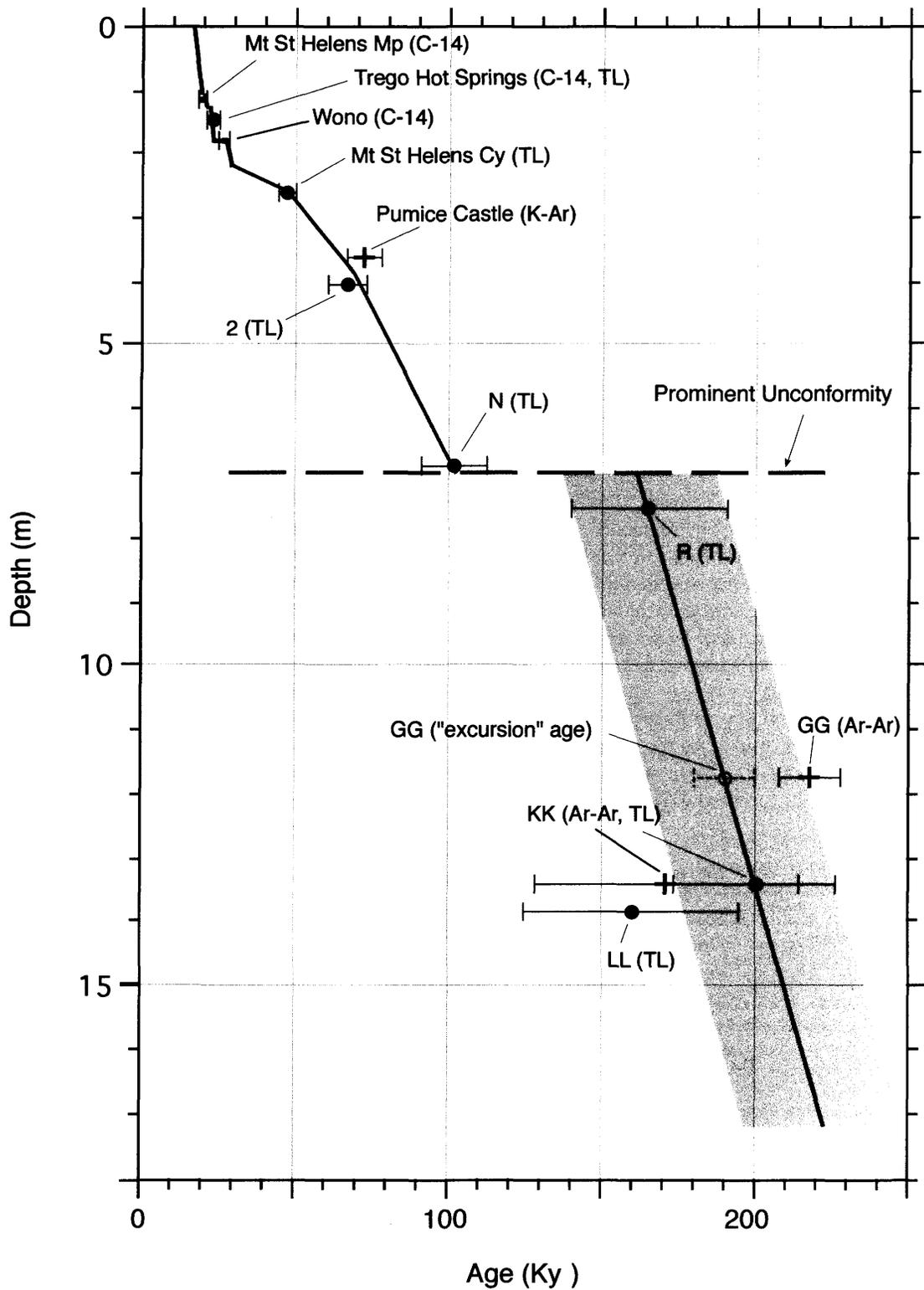


FIGURE 3.—Chronology of Lake Chewaucan sediments exposed in the Ana River canyon north of Summer Lake, Oregon. Age control is based upon a variety of methods that are summarized in Negrini et al. (1994) and in this paper. Tephra names are after Davis (1985). Note the pronounced decrease in precision for dates older than 150 Ky. Shaded region includes all age estimates as allowed by standard deviations of these ages.

uncertainties of 5%–20%. This problem is exemplified by the tephra beds from the pluvial Lake Chewaucan sediments exposed in the Ana River canyon near the town of Summer Lake, Oregon (Figure 1). As shown in Figure 3, age uncertainties of tephra from lower in the section are much greater than those from the upper part of the section (see Negrini et al., 1994, for a review of the age control at this section). The large scatter in tephra ages is reflected in the age-range (~180–230 Ky) assigned to the Pringle Falls/Biwa I geomagnetic excursion. This is a geomagnetic phenomenon recorded in several sedimentary records, including two that contain Summer Lake tephra layer GG at the Ana River locality (Negrini et al., 1994) and two that contain the correlative tephra layer D at the Pringle Falls, Oregon, locality 170 km to the northwest (Herrero-Bervera et al., 1994). McWilliams (1995) has suggested that the true age of the excursion is toward the older part of this range, based upon the similarity of its transitional virtual geomagnetic pole (VGP<sup>1</sup>) path with that of an excursion found in  $223 \pm 4$  Ky old volcanic rocks from New Zealand. Conversely, a correlation of the Pringle Falls event with an excursion found in a marine sediment record from the Blake/Bahama Outer Ridge in the northwestern Atlantic Ocean (Heney et al., 1995) suggests that the Pringle Falls excursion correlates with the  $190 \pm 10$  Ky old Jamaica event found throughout the world in marine sediments (e.g., Tauxe and Shackleton, 1994; Yamazaki and Ioka, 1994; Heney et al., 1995; Weeks et al.,

1995; Guyodo and Valet, 1996; Lehman et al., 1996). The correlation with the New Zealand excursion is problematical because the VGP path of the Pringle Falls excursion has previously been shown to have a common morphology with the VGP paths of several different polarity transitions (Tric et al., 1991). The correlation with the Jamaica event is more convincing because it is based upon distinct paleomagnetic directional and intensity features found in both the excursion itself and in the subsequent secular variation (Negrini et al., 1994; Heney et al., 1995).

**PUMICE CASTLE TEPHRA SET AND THE OLEMA AND MOUNT ST. HELENS CY TEPHRA LAYERS.**—The three tephra layers comprising the Pumice Castle set were first identified by Davis (1985) in lake sediments from a sequence of 54 waterlain tephra beds in the Ana River canyon near Summer Lake, Oregon (Figure 4). Based upon their major element compositions, Davis correlated Summer Lake tephra layers 4, 6, and 8 with the Pumice Castle-like 2, the Pumice Castle, and the Pumice Castle-like 1 tephra layers, respectively, from Crater Lake, Oregon (Bacon, 1983; Davis, 1985). Negrini et al. (1988) added support to this geochemical correlation by comparing the paleomagnetic direction of Summer Lake tephra 6 with an identical direction for the Pumice Castle tephra measured near the Crater Lake volcano by D. Champion of the United States Geological Survey (USGS) at Menlo Park. The absolute ages of the two older tephra are constrained by bracketing lavas that are dated by K-Ar at  $117 \pm 6$  Ka and  $72 \pm 6$  Ka; the youngest tephra lies above the  $72 \pm 6$  Ky old lava and below a  $52 \pm 4$  Ky old andesite flow, which also was dated with

<sup>1</sup> VGPs are magnetic pole positions pointed to by each paleomagnetic vector recorded at a particular site. Because the earth's magnetic field is not a perfect dipole, coeval VGPs recorded at different sites will not necessarily coincide.

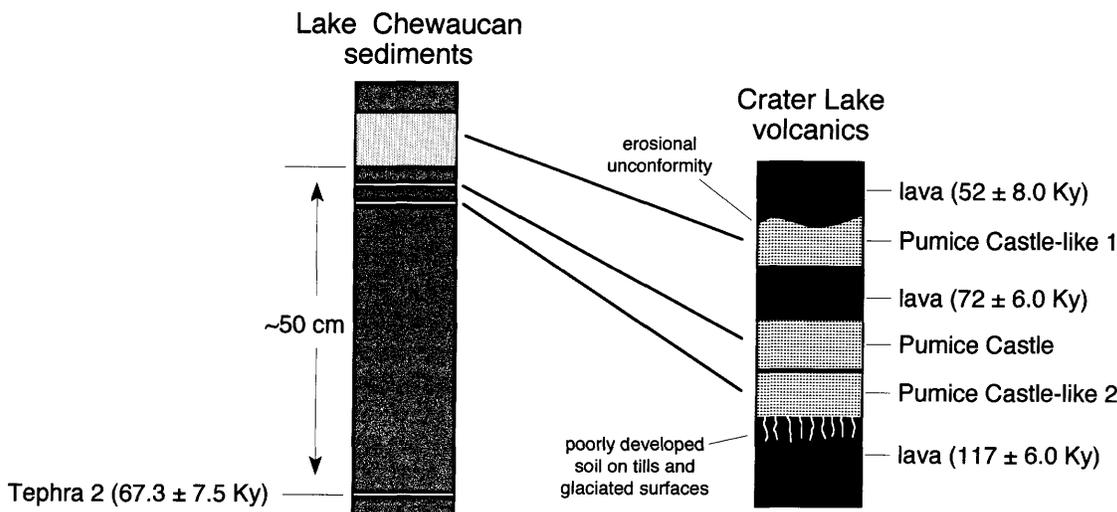


FIGURE 4.—Stratigraphic relationships supporting ~70 Ky old age of the Pumice Castle tephra set (after Bacon, 1983; Davis, 1985). These three tephra layers are nearly the same age because they are found within 10 cm of each other in fine-grained lacustrine sediments at several different localities separated by several kilometers in the Summer Lake subbasin. Thus, they are approximately as old as the  $72 \pm 6$  Ky old lava flow that separates two of them at Crater Lake, their proximal location. This age is supported by the thermoluminescence date determined for tephra 2 in the Lake Chewaucan sediments (Berger and Davis, 1992).

the K-Ar method (Bacon, 1983; C.R. Bacon and M.A. Lanphere of the USGS, in litt. to J.O. Davis, 1984; Davis, 1985).

Reick et al. (1992) reported finding the Pumice Castle-like 2 tephra, or perhaps the Pumice Castle tephra, in a core taken from the sediments of pluvial Lake Modoc. (The core was named Tulelake for the nearby town of Tulelake, California, rather than nearby Tule Lake, a remnant of Lake Modoc.) They determined this ash was deposited  $\sim 120$  Ka, in part because of its position below two samples showing negative paleomagnetic inclinations that were provisionally correlated to the 100–130 Ka Blake Reversed-Polarity Subchron (Reick et al., 1992:419, 422). This age was considered to be reasonably close to the above-mentioned  $117 \pm 6$  Ka K-Ar date on the lava flow below these tephra.

Ongoing work on the bottom sediments of pluvial Lake Chewaucan indicates that an age of  $\sim 70$  Ky, near the middle of OIS 4, is a more reasonable estimate for the Pumice Castle set of tephra beds. The three ash layers in this set are observed to be separated by only a few centimeters of lacustrine silty clays in several exposures 1–2 km apart along the Ana River canyon and in a core taken several kilometers away at an Ana River outcrop (Davis, 1985; Negrini et al., 1988; Erbes, 1996). Because this relationship argues that the three ashes were deposited within no more than a few hundred years of each other, and because a  $72 \pm 6$  Ky old lava flow is found between the correlatives of the upper two tephra found at Crater Lake (Figure 4), all three tephra layers in the Pumice Castle set must be approximately the same age as the  $72 \pm 6$  Ky old lava flow. This conclusion is supported strongly by a thermoluminescence date of  $67.3 \pm 7.2$  Ky on Summer Lake tephra 2 located 35 cm below the Pumice Castle set (Berger and Davis, 1992).

The ages of the Mount St. Helens Cy tephra and its correlatives (e.g., the Marble Bluff bed) also have been the subject of controversy. The ages of these tephra layers have most often been quoted in the range of 35–30  $^{14}\text{C}$  Ky B.P. (e.g., Davis, 1978, 1985, and references therein) on the basis of radiocarbon ages of materials found in close proximity to the tephra. In contrast, radiocarbon dating of some of the near-vent tephra deposits infers an older age for these tephra layers of perhaps greater than 40  $^{14}\text{C}$  Ky B.P., which in turn, infers a calendar date of at least 45–40 Ka (Mullineaux, 1986; Crandell, 1987; McDonald and Busacca, 1992). Thermoluminescence dates on the Cy tephra ( $46.3 \pm 4.8$  Ky) in lacustrine sediments at Summer Lake, Oregon, and on the slightly older Cw tephra ( $\sim 55 \pm 5$  Ky) in eastern Washington loess sediments support the older ages (Berger, 1991; Berger and Davis, 1992; Berger and Busacca, 1995).

The Olema tephra, originally found in cores from Clear Lake and Tule Lake, California (Sarna-Wojcicki et al., 1988), also was found in the Lake Chewaucan sediments of the WL core (N. Foit, in litt., 1993; Erbes, 1996). Given its position relative to the Pumice Castle set and Mount St. Helens Cy tephra layers in the WL core and given the above-described revisions of the ages of the latter tephra layers, the estimated age of the Olema

bed is probably closer to 55–50 Ky than to the previous estimate of 75–55 Ky (Sarna-Wojcicki et al., 1988; Reick et al., 1992).

WONO AND TREGO HOT SPRINGS TEPHRA.—New ages for the Wono tephra ( $27.3 \pm 0.3$   $^{14}\text{C}$  Ky B.P.) and the Trego Hot Springs bed ( $23.2 \pm 0.3$   $^{14}\text{C}$  Ky B.P.) have been published by Benson et al. (1997). These new ages are based upon 11 precise accelerator mass spectrometer (AMS) radiocarbon dates from adjacent organic samples in a core from Pyramid Lake.

#### *Paleomagnetic Secular Variations for Correlating Fine-Grained, Lacustrine Sediments*

Paleomagnetic secular variation (PSV) records from fine-grained sediments must satisfy strict criteria in order to establish that they record the ambient geomagnetic field vector (declination, inclination, and paleointensity) at or near the time of deposition (Verosub, 1988). This is especially true of the paleointensity component (Tauxe, 1993). If these criteria are satisfied, PSV records can be used as a method for high-resolution (century- to millennial-scale) correlation among fine-grained sediments of Quaternary age over a spatial range of continental scale. Anchored by a solid foundation of PSV reference curves for the last 30 Ky (Lund et al., 1988; Lund, 1996, and references therein), this methodology has been used on many sediments of the Great Basin (Negrini and Davis, 1992; Ewing, 1996; Liddicoat and Coe, 1997; Benson et al., 1998; Benson et al., unpublished). The potential value of this method is illustrated in Figure 5a in which the PSV signal from a North Atlantic Ocean core is compared with that from the sediments of Lake Chewaucan. This particular interval of time immediately follows the 190 Ky Pringle Falls/Jamaica/Biwa I geomagnetic excursion (Herrero-Bervera et al., 1994; Negrini et al., 1994; Henyey et al., 1995) discussed in the previous section. Note that this example demonstrates the utility of the PSV method for direct correlations between marine and terrestrial sediments. Clearly, there is an advantage to such an independent correlation of marine and nonmarine climate records without relying on either circular reasoning (i.e., the correlation of climate events to prove that the events occurred simultaneously) or a comparison of radiocarbon dates from entirely different geochemical environments. Another advantage of this method is that, under ideal conditions, it allows for continuous age control throughout the sedimentary section.

Obviously, as with all relative age-dating methods, this technique is most valuable when used in conjunction with an independent method, such as tephrochronology (Verosub, 1988; Negrini, 1993; Liddicoat and Coe, 1997). For example, the accuracy of the  $^{14}\text{C}$  chronology in the sediments of pluvial Lake Russell is confirmed using such an approach. Figure 5b is a plot of the inclination component of the PSV records from pluvial Lakes Chewaucan and Russell. The Lake Chewaucan record is from the B&B core taken from the middle of the Summer Lake playa (Erbes, 1996). The Lake Russell record is after Lund et al. (1988). The recently redated Wono tephra layer (Benson et

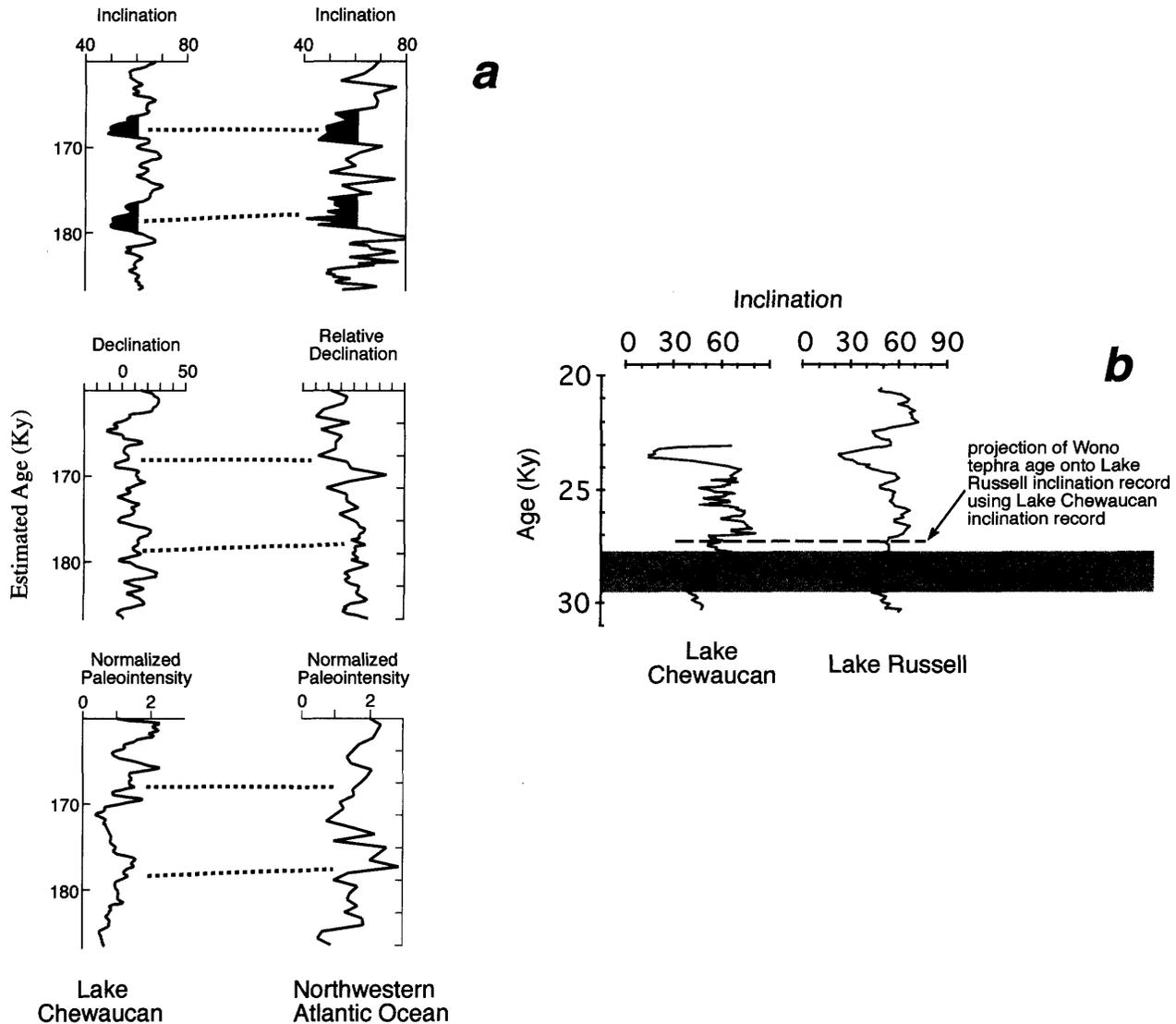


FIGURE 5.—*a*, Correlation of paleomagnetic vector components recorded in the sediments of Lake Chewaucan (Negrini et al., 1994) with those recorded in marine sediments from the northwestern Atlantic Ocean (S.P. Lund, unpublished data). The bottom of the correlated intervals begins at the end of the ~190 Ky old Pringle Falls/Jamaica/Biwa 1 geomagnetic excursion. Inclination and declination are in degrees. Declination of the marine sediments is relative rather than absolute because the core was not azimuthally oriented. The paleointensity data in both records are normalized to the mean as per Tauxe (1993:340). The dashed correlation lines of all three components were fixed by the two prominent inclination troughs shaded in black. *b*, Correlation of inclination records from pluvial Lakes Russell (Lund et al., 1988) and Chewaucan (Negrini et al., 1993). The correlation model is supported by the projection of the new age ( $27.3 \pm 0.3$   $^{14}\text{C}$  Ky B.P.) for the Wono tephra layer (Benson et al., 1997) onto the previously dated PSV record from Lake Russell.

al., 1997) is not found in the Lake Russell record but appears in the Lake Chewaucan section not too far above the interval of sediments that contains a record of the Mono Lake excursion (Negrini, 1994). Using the PSV records, the new age of this tephra layer ( $27.3 \pm 0.3$   $^{14}\text{C}$  Ky B.P.) can be precisely projected onto the Lake Russell record (Figure 5*b*), thereby confirming the accuracy of this portion of the Lake Russell chronology determined previously by radiocarbon dating of carbonates (e.g., Benson et al., 1990; Benson et al., unpublished).

## PLUVIAL LAKE RECORDS

### *Late Pliocene to Middle Pleistocene (3 Ma–30 Ka)*

**LAKE LAHONTAN.**—Our knowledge of the pluvial lacustrine history of the northwestern Great Basin is bimodal in nature. On the one hand, no other pluvial lake in the Great Basin, with the exception of Lake Bonneville, has been studied as extensively as Lake Lahontan (Figures 1, 6). On the other hand, although significant advances have been made during

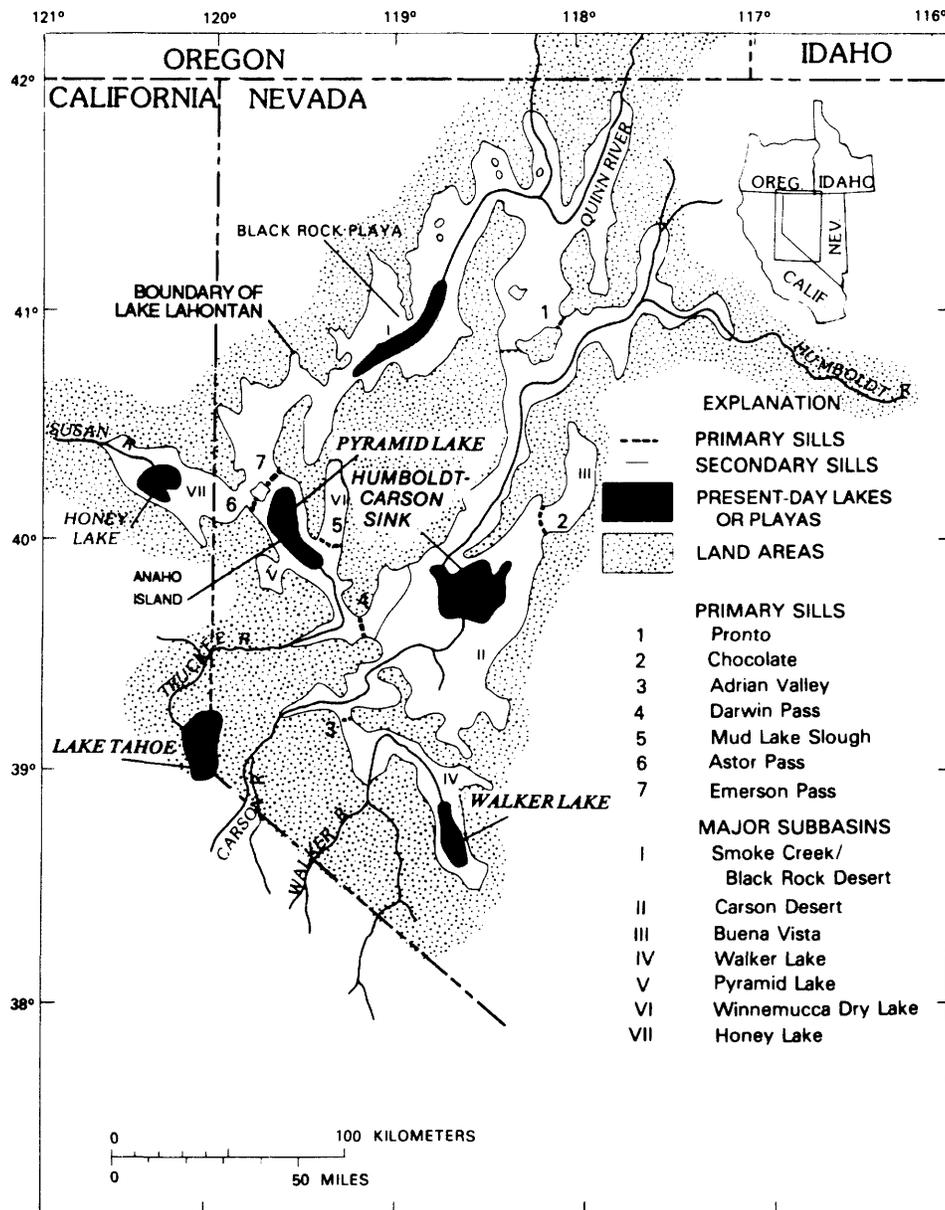


FIGURE 6.—Detailed map of Lake Lahontan pluvial system (from Benson et al., 1990, fig. 2).

the last 50 years regarding the prehistory of the other pluvial lakes in the northwestern Great Basin, we still know little about these other lakes relative to what is known about Lake Lahontan.

The emphasis on Lake Lahontan is understandable. At high-stand, this pluvial system covered more than 22,000 square kilometers, approximately 50% more than all of the other pluvial lakes in the northwestern Great Basin combined (Grayson, 1993). Its sheer size leads to the probability of finding key exposures of critical geomorphic features and lake sediments. Furthermore, the presence of large remnant lakes, particularly Pyramid Lake and Walker Lake, provide for modern analogs

and, at times, for sites of continuously deposited sediments, enabling the potential retrieval of long cores containing nearly continuous climate records.

Despite the complexity of the Lake Lahontan system (six major streams feeding seven major subbasins that are separated at different elevations by seven sills), the overall lake-level history has converged toward a coherent story for the latest Pleistocene (see "Latest Pleistocene," below). The prehistory of this pluvial system prior to 30 Ka is less well developed for the obvious reason that most of the evidence either has been superposed by the sediments of the last highstand or has been eroded or degraded through time. Nevertheless, great exposures of

sediments as old as late Pliocene in age can be found in canyons cut by the Humboldt, Walker, Carson, and Truckee Rivers (Russell, 1895; Morrison and Davis, 1984a, 1984b; Morrison, 1991b). These exposures and their associated geomorphic features (e.g., strandlines) are the foundation for the Quaternary stratigraphy of the Lake Lahontan area, which was first developed by Russell (1895) and later refined by Morrison and others (Morrison, 1964, 1991b; Morrison and Frye, 1965; Morrison and Davis, 1984a, 1984b). The latest stratigraphic framework for this region consists of a series of alloformations, as shown in Figure 7. According to Morrison and Davis (1984a:255), an alloformation is defined as "a mappable stratiform body of sedimentary rock that is defined and identified on the basis of its bounding discontinuities." For example, lacustral alloformations include all deposits of a single lacustrine episode, such as bars, deep-water sediments, deltas, tufas, etc. Interlacustral episodes could even include lake sediments in the larger remnants of a great lake, e.g., Pyramid Lake (Morrison, 1991b). This usage follows the Stratigraphic Code of the North American Commission on Stratigraphic Nomenclature (1983). Restrictions on the use of such terminology, such as the need to define alloformations as mappable units, limit the ability to directly correlate the contacts between allounits with climate-change boundaries (e.g., see later discussion of Mount St. Helens Cy tephra as a marker for the contact of the Wyemaha and Sehoor Alloformations).

Given adequate spatial sampling of the Quaternary sediments of the Lake Lahontan system, perhaps with the help of an extensive coring program, it is this author's opinion that allounits corresponding to each and every marine OIS cycle will be found somewhere in the system. Only after such data is collected will Quaternary geologists be able to make final decisions on which groups of cycles best fit into collected alloformations or, indeed, whether a separate alloformation should be assigned to each cycle. With this end in mind, the present state of the older Lahontan stratigraphy and its paleoclimatic implications are reviewed below.

The oldest sediments in the Lake Lahontan area are the "deep-lake/deltaic sediments" (Figure 7) that lie below the interlacustral Lovelock Alloformation in at least three locations: (1) 700 m south of Rye Patch Dam on the west side of the Humboldt River (Morrison and Davis, 1984a:256); (2) possibly in the Truckee River valley, 6.5 km south of Nixon, Nevada (Morrison, 1991b); and (3) at various locations in the badlands near Weber Reservoir (Morrison and Davis, 1984a; Morrison, 1991b). The absolute age of these sediments is constrained to be at least 800 Ky, based upon preliminary magnetostratigraphic results and on the identification of the ~1.0–1.1 My old Glass Mountain G tephra layer in an upper unit of these sediments near the Weber Reservoir (Morrison and Davis, 1984a; Morrison, 1991b, and references therein). A lower pre-Lovelock lacustrine unit also appears near Weber Reservoir. Its relative antiquity is inferred by the fact that it is extensively faulted and folded and that these structures are truncated by an

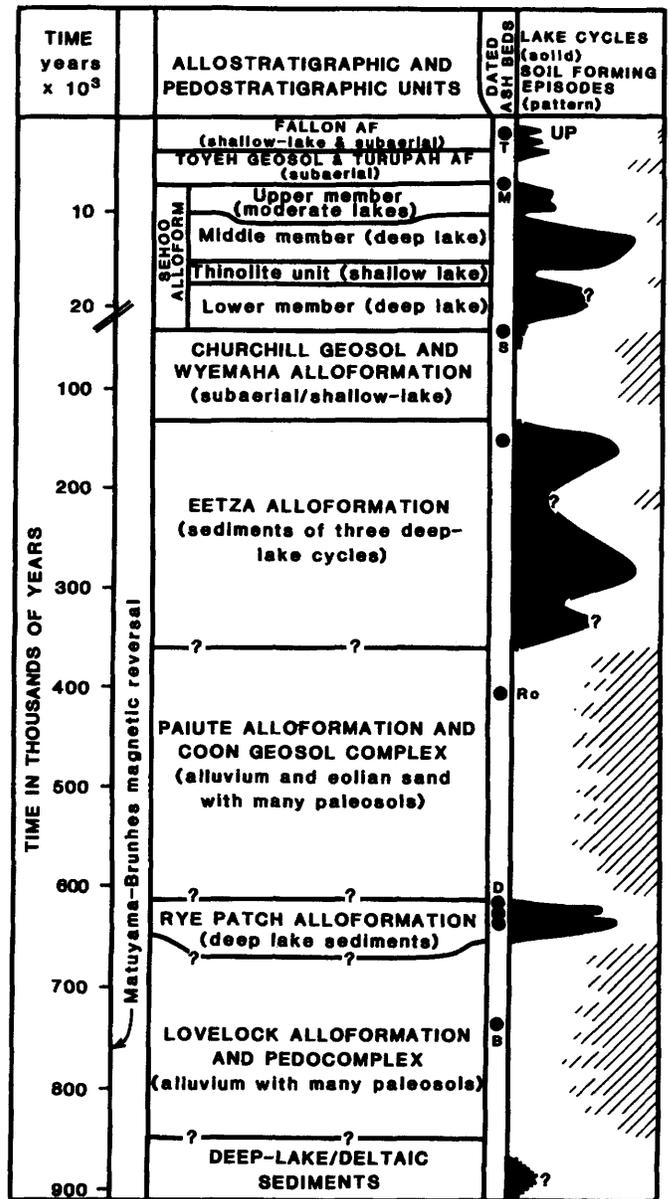


FIGURE 7.—Stratigraphic units of the Lake Lahontan pluvial system (from Morrison, 1991b, fig. 6).

angular unconformity that separates it from the unit containing the Glass Mountain G tephra layer.

Although these older lacustrine units are presumed to predate the Lovelock Formation, this formation may itself be quite old at some localities. For example, the ~0.9–1.0 My old Glass Mountain D tephra has been found in the upper part of the Lovelock Alloformation approximately 10 m below the Rye Patch Alloformation at a locality in the Humboldt River canyon (Parker, 1993, and references therein). In fact, Parker (1993) used magnetostratigraphy to show that the 25 m of sediments found below this tephra were at least ~2.0 My old. No

lacustrine sediments were observed in this section below the Rye Patch Alloformation, prompting Parker (1993) to presume that these 25 m of sediments are within the Lovelock Alloformation. If one interprets the stratigraphy depicted in Figure 7 in a strict sense, then one must conclude either that the pre-Lovelock lacustrine sediments were deposited in an areally restricted lake or that an unconformity exists in Parker's section (i.e., the pre-Lovelock lacustral units in this part of the Humboldt River canyon were eroded, and the lower part of Parker's section belongs to an older interlacustral alloformation). Additional tephrochronological and magnetostratigraphical studies in the Humboldt River canyon and Weber Reservoir badlands are required to test the continuous nature of older alloformations in the Lahontan Basin.

The two allolacustral members of the Rye Patch Alloformation contain two tephra layers in the Humboldt River canyon, namely the Rye Patch Dam bed and the Lava Creek B ash (Morrison, 1991b; Davis, 1978). Morrison (1991b) quoted ages of 630 Ky and 620 Ky for these two ashes, respectively. As discussed above, the Lava Creek B has since been redated at  $665 \pm 5$  Ka by Izett et al. (1992), which puts the Rye Patch Dam bed at a slightly older age of  $\sim 675$  Ky. These tephra layers imply a correlation of this lacustral episode with OIS 16.

The Dibekulewe tephra of Davis (1978) is found above the Lava Creek B tephra in the Humboldt River canyon (Morrison and Davis, 1984a; Negrini, Verosub, et al., 1987). Morrison (1991b) quoted an age of 610 Ky for the Dibekulewe tephra and placed it at the top of the Rye Patch Alloformation. This age estimate was probably derived from the work of Reick et al. (1992), who found this tephra bed in close proximity to the Lava Creek B ash in the Tulelake core. Although this was their preferred age, these authors acknowledged that the age could be much closer to that of the overlying Rockland ash (410 Ky) because of the likelihood of disconformities in the interval between the Lava Creek B and Rockland ashes. A more recent study on a long core from Owens Lake placed the age of the Dibekulewe tephra at approximately 510 Ky based upon constant-mass accumulation rates in this core (Sarna-Wojcicki et al., 1997). This age is more in line with an earlier estimate by Negrini, Verosub, et al. (1987:10,625) that was based upon the relative position of these three tephra in a sedimentary section near Blairsden, California. If the Dibekulewe is  $\sim 500$  Ky old, then either the Rye Patch Alloformation is younger or, alternatively, the Dibekulewe ash is within the overlying Paiute Alloformation. Indeed, the Rockland ash lies within the Paiute Alloformation in the Humboldt River canyon (Parker, 1993); thus, the upper age limit of the base of this alloformation is 410 Ky.

The Eetza Alloformation corresponds roughly to Russell's (1895) lower lacustral clay. This alloformation contains at least three major lacustral allomembers, which consist primarily of silts and clays separated by thick lenses of alluvium or colluvium. All told there are possibly as many as six to eight lake cycles recorded in exposures along the Truckee River between

Nixon and Wadsworth, Nevada (Morrison and Davis, 1984a; Morrison, 1991b). The Wadsworth tephra of Davis (1978) is found toward the top of this alloformation near Pyramid Lake. The age of this tephra was estimated to be in the range of 155–200 Ky (Morrison, 1991b; Reick et al., 1992, and references therein). Because of this age and the observation that the Rockland tephra resides below the Eetza in the Paiute Alloformation in the Humboldt River canyon, Morrison (1991b) correlated the Eetza lacustral episodes with OIS stages 10, 8, and 6. This correlation is supported by  $^{230}\text{Th}$  ages of  $290 \pm 90$  Ky and  $128 \pm 10$  Ky for samples from near the bottom and top of the Eetza, respectively (Kaufman and Broecker, 1965).

The Wyemaha Alloformation represents a long interlacustral interval from  $\sim 130$  Ka to  $\sim 35$  Ka and is characterized by eolian and alluvial coarse-grain deposits and well-developed paleosols at higher elevations and by finer-grained sediments deposited in shallow lakes in the depocenters of the major subbasins (Morrison, 1991a). Morrison proposed that the boundary between the Wyemaha Alloformation and the overlying lacustral Sehoi Alloformation should be put at the Mount St. Helens Cy tephra, now thought to have formed 45–50 Ka (see above). This is a reasonable suggestion as it would make the Wyemaha/Sehoi transition relatively easy to map. This tephra layer is thick, is widespread throughout much of the Lahontan Basin, is distinctive both petrographically and geochemically, and is commonly found at the base of lacustrine sequences associated with the Sehoi Alloformation (Davis, 1978:45). There is a trade off, however, between the mappability of this contact and its correlation with global climate transitions. The Sehoi Alloformation is commonly considered to be roughly coeval with OIS 2 and perhaps with the early Holocene (Davis, 1978; Morrison, 1991b). If the Mount St. Helens Cy tephra layer is indeed as old as it appears to be based upon recent chronometric studies (see above), then the base of the Sehoi Alloformation is pushed back to early OIS 3 time. Perhaps the 27.3  $^{14}\text{C}$  Ky B.P. Wono tephra would be a better choice for the base of the Sehoi Alloformation. It is as widespread as the Mount St. Helens Cy tephra layer in the Lahontan Basin (Davis, 1978) and has a more appropriate age. Furthermore, it was deposited in a lake of moderate depth preceding the last significant recession of Lake Lahontan, which, in turn, preceded the prominent transgressive phase correlated to the OIS 2 ice sheet advance (Benson et al., 1995, 1997). The 23.2  $^{14}\text{C}$  Ky B.P. Trego Hot Springs tephra layer is, in some sense, still a better choice as it was probably deposited in the shallow-water lakes of the recession immediately prior to the OIS 2-related transgression. The Trego Hot Springs tephra, however, is not as widespread as the Wono bed (Davis, 1978), probably because it was deposited under shallower lake conditions.

In addition to its limited application for exact correlations to global or regional climate change, the Lake Lahontan stratigraphy places only very loose constraints on the size of this pluvial lake versus time. That is, one can determine whether or not the lake existed during a given time interval but not the exact

elevation of the shoreline. To most effectively use the geologic record to determine the effects of climate change on the lake, one must determine the surface area of the lake versus time (Smith and Street-Perrot, 1983; Benson and Thompson, 1987a; Benson and Paillet, 1989). To do this, one must, of course, determine the precise elevation of the lake surface. Although this has been done exceedingly well for the time period after 30 Ka (see next section), very little has been done to determine absolute lake levels for earlier time periods. Morrison (1991b) has done this in a general way by documenting the maximum elevation occupied by lacustral alloformations. Reheis et al. (2002) also have obtained estimates of the lake size during pluvial maxima in the early and middle Pleistocene by mapping highly eroded but still discernable strandlines and near-shore deposits around the Lahontan Basin and nearby basins. In doing so, they have reconstructed an enormous lake corresponding to OIS 16 that would have covered Reno and Carson City, Nevada, and would have backed the Humboldt River at least to the town of Battle Mountain, Nevada. Lao and Benson (1988, and references therein) and Szabo et al. (1996) determined lake-level minima by dating tufa deposits with the uranium-series method. The results of the earlier study indicated that the surface of Lake Lahontan in the Walker subbasin (the first to fill up if it is fed by the Walker River) would have reached a level more or less equal to its late Pleistocene maximum of 1330 m at  $290 \pm 90$  Ka,  $\sim 200$  Ka,  $128 \pm 10$  Ka, and  $49 \pm 5$  Ka. According to the model of Benson and Thompson (1987b), Pyramid Lake, Winnemucca Dry Lake, and Smoke Creek/Black Rock Desert subbasins would have coalesced and risen to their common elevation of 1207 m at Emerson Pass. It is conceivable that all of these subbasins could have joined the Walker subbasin at its 1330 m elevation if they received sufficient spillover from the Walker subbasin through the Carson River subbasin. Szabo et al. (1996) combined dates from several studies in the Pyramid Lake subbasin near the elevation of the 1207 spillpoint into the Smoke Creek/Black Rock Desert subbasin. They found that a lake filling at least the local subbasins would have been at or above the Emerson Pass sill for much of the middle Pleistocene, especially in the time interval from 250 Ky to 170 Ky. Also, these subbasins would have filled at least twice during the time period from 65 Ka to 30 Ka.

**LAKE MODOC AND ENVIRONS.**—The longest, most continuous pluvial lake record in the northwestern Great Basin comes from the sediments of pluvial Lake Modoc (Figure 1) and nearby Buck Lake and Round Lake in south-central Oregon (Klamath County) and northernmost California (Modoc and Siskiyou Counties), respectively. Upper and Lower Klamath Lakes and Tule Lake are the remnants of pluvial Lake Modoc, which once filled the subbasins that these lakes occupy. At pluvial maximum, the surface of Lake Modoc stood at an elevation of 1292 m, approximately 63 m above the surface of modern Tule Lake (Dicken, 1980). The Lake Modoc system is not considered to be part of the Great Basin hydrologic province as

defined by Grayson (1993) because most of it presently drains into the Pacific Ocean via surface flow through the Klamath River and via groundwater flow through permeable volcanic rocks into the Klamath River and Pit River systems. Nevertheless, it is often included as a source of Great Basin paleoclimate data because it lies within the botanical Great Basin and its size has responded dramatically to climate changes in the past regardless of its connection to the Pacific Ocean (Dicken, 1980; Bradbury, 1991; Grayson, 1993). Also, as with most pluvial systems in the hydrographic Great Basin, Lake Modoc has been a site of lacustrine sedimentation for millions of years as a consequence of its presence within the Basin and Range structural province (Dicken, 1980).

Sediment cores were taken from seven sites in this system by the USGS (Adam et al., 1989; Adam, 1993; Klamath Core Study Team, 1995). At two of the sites (Tulelake, 334 m; and Butte Valley, 102 m) coring was completed into sediments older than 3 My. At three of the other sites (Wocus Marsh, 52 m; Buck Lake, 41 m; and Round Lake, 50 m) the oldest cored sediments were from 1.4 to  $\sim 1.0$  Ma. The Grass Lake core (29 m) penetrated sediments no older than  $\sim 400$  Ky, and the Caledonia Marsh cores (15.3 m) bottomed out in sediments younger than 100 Ky. The ages of all of the cores were constrained using tephrochronology (Adam et al., 1989; Reick et al., 1992). Several well-known tephra were identified, including the 1.94 My old Bear Gulch ash, the 1.45 My old Rio Dell ash, the 665 Ky old Lava Creek B ash, the 410 Ky old Rockland ash (Sarna-Wojcicki et al., 1985; Meyer et al., 1991), the 50–55 Ky old Olema ash (Sarna-Wojcicki et al., 1988), a precursor ash (the Tsoyawata bed) to the Mount Mazama eruption (Davis, 1978; Bacon, 1983), and several ashes that correlate with the collection of tephra found nearby at Summer Lake, Oregon, such as one of the Pumice Castle tephra set (Bacon, 1983; Davis, 1985; Reick et al., 1992). The ages of the Tulelake, Butte Valley, and Buck Lake cores were also constrained by magnetostratigraphy (Reick et al., 1992; Roberts et al., 1996; Rosenbaum et al., 1996). Radiocarbon dating was conducted on samples from the top of the Grass Lake, Caledonia Marsh, and Wocus Marsh cores with limited success because of inverted ages, low concentrations of carbon, and a preponderance of anomalously young ages (Bradbury, 1991; Klamath Core Study Team, 1995). Despite similar difficulties encountered with the Tulelake core, Bradbury (1991, fig. 6) (Figure 8) was able to assemble a chronology for the top of this core by using selected radiocarbon dates and tephra.

In addition to age control, several other studies have begun on the Klamath Basin cores that have generated data from which interpretations of pluvial lake conditions can be made. These include lithologic description, palynology, diatom and ostracode analyses, environmental magnetism, and geochemistry. An initial study on the Tulelake core found that two major shifts in the character of pollen type versus depth curves occurred at  $\sim 2.5$  Ma and  $\sim 1.65$  Ma (Adam et al., 1989). The 2.5 My shift is best expressed by a slight overall increase in

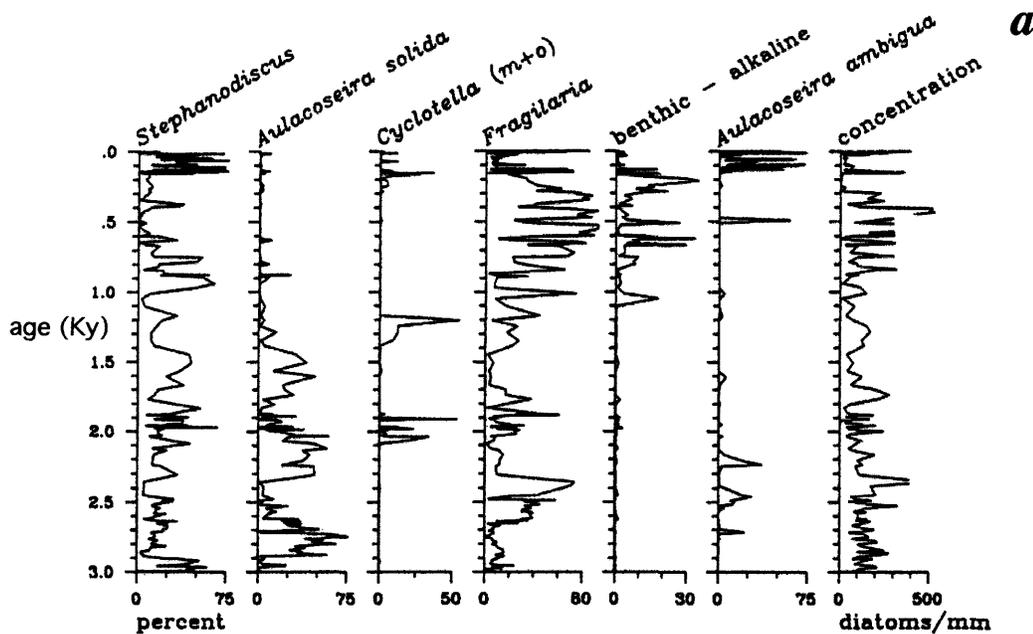
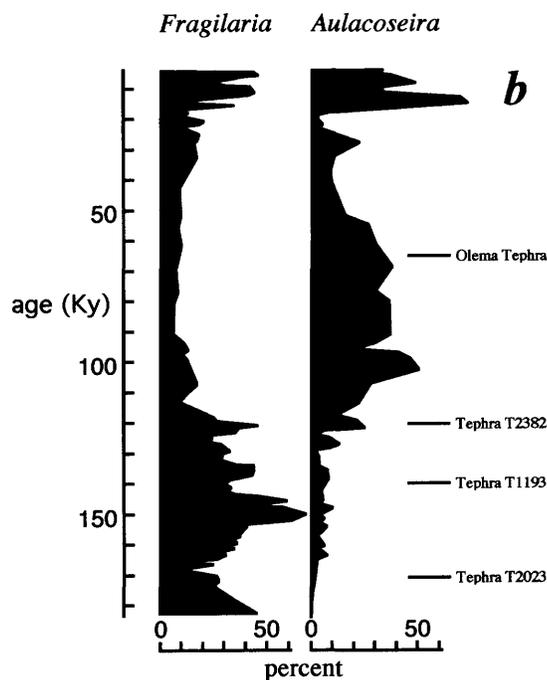


FIGURE 8.—*a*, Diatom biostratigraphy for the entire Tulelake core from Bradbury (1992, fig. 6). For detailed descriptions of all genera, groups, and species the reader is referred to Bradbury (1991, 1992). *b*, *Fragilaria* and *Aulacoseira* diatom profiles for the last 180 Ky, after Bradbury (1997, fig. 9). Note positions of key tephra layers.



*Artemisia* count and by the transition toward higher-frequency variations in both *Artemisia* and TCT (Taxodiaceae + Cupressaceae + Taxaceae, which includes Western Juniper). This older shift was correlated with the onset of continental glaciers in North America and the beginning of the Praetiglian cold period in Europe. Some researchers believe that the Plio/Pleistocene boundary should be moved back to this point in time, specifically to the Gauss/Matuyama polarity chronozone

boundary, rather than the currently accepted time, the top of the Olduvai normal-polarity subchronozone (see Morrison, 1991a, and references therein). The latter candidate for the Plio/Pleistocene boundary is also expressed in the Tulelake core. After 1.65 Ma there are common interruptions in pollen preservation, a drop in TCT amplitude, increases in the peak percentages of *Artemisia*, Chen-ams, and Poaceae (grasses), and high-amplitude oscillations in total algae, all of which were interpreted to indicate a pattern of alternating lacustrine and nonlacustrine phases (Adam et al., 1989). Two diagnostic species of diatoms, *Anomoeoneis costata* (Kützing) Husted (saline water) and *Cocconeis placentula* Ehrenberg (shallow water), were most abundant between 90 and 50 m of depth (800 to <400 Ka), indicating an overall drying of the lake and a hydrologically closed lake that was rich in solutes. These observations are consistent with well-preserved ostracodes and with high values for "factor 3," an association of geochemical entities (e.g., (carbonate), Mg, and Sr) indicative of dry lake conditions (Adam et al., 1989).

Bradbury (1991, 1992, 1997) later used a more detailed and comprehensive diatom stratigraphy to reconstruct lake conditions in the Tule Lake subbasin throughout the entire three million years represented by that core. In these reports he made several intriguing interpretations that bear on global climate-change models. First, he noted an ~40 Ky periodicity in total diatom concentration in the two densely sampled time intervals (3.0–2.5 Ma and 2.05–1.85 Ma) prior to 1.0 My. This observation is consistent with the dominance of the obliquity period in the late Pliocene and early Pleistocene observed in marine oxygen isotope records (Ruddiman et al., 1986; Ruddiman and Raymo, 1988). Second, based upon the gradual disappearance of *Aulacoseira solida* (Eulenstein) Krammer and the subse-

quent takeover by a *Fragilaria–Stephanodiscus–Cyclotella* assemblage, he noted a transition from “more equable and probably warmer Pliocene climates to more variable, more seasonal, drier, and probably colder Pleistocene climates” (Bradbury, 1992:284). Third, three broad peaks in *Aulacoseira solida* alternating with broad peaks in *Fragilaria* species oscillate with a period approximately equal to the 413 Ky eccentricity-driven insolation cycle (Ruddiman and Raymo, 1988). Fourth, from 900 to ~300 Ka, the diatom stratigraphy in the Tulelake core is characterized by several peaks in *Fragilaria* sp. concentration that are more or less in tune with glacial stages recorded by marine oxygen isotope curves (Bradbury, 1992, fig. 7). Furthermore, these peaks are terminated by increases in diatoms that prefer more saline or alkaline waters (e.g., *Anomoeoneis costata*, *Cocconeis placentula*). Bradbury interpreted these data to imply that, during glacial periods, Tule Lake was probably an open, freshwater marsh formed during cold and somewhat dry climates. During interglacials, effective moisture decreased but winter precipitation was probably significant as the presence of *Stephanodiscus* and *Aulacoseira* species in these intervals suggests at least seasonally high lake levels and dilute waters. Fifth, Bradbury (1992) noted that the more or less uniform response to glacial cycles during the 900–300 Ka time period breaks down in the latest Pleistocene. The interval from 300 to ~180 Ka is represented by *Anomoeoneis costata*, a diatom that prefers “exceptionally shallow and alkaline conditions.” Thus, the low effective moisture interval that might correspond to OIS 7 appears to begin 80 Ky too soon in the Tulelake core. The interval from ~170 to ~130 Ka contains abundant *Fragilaria*, which would be expected for a glacial interval like OIS 6 based upon its occurrence patterns in this core from 900 to 300 Ka; however, as *Fragilaria* abundance declines, the diatom concentration becomes characterized by deeper-water diatoms (e.g., *Aulacoseira ambigua* (Grunow) Simonson, *Cyclotella meneghiniana* Kutzing, *Cyclotella bodanica* Grunow) until *A. ambigua* decreases at ~50 Ka. Thus, if the 900–300 Ka diatom assemblage is a good analog for the latest Pleistocene, then it appears as if the entire interval from 170 to 50 Ka is characterized by a glacial interval; that is, the OIS 5 interglacial is not represented in the Tulelake core. Bradbury (1991:228) noted that diatoms such as *Fragilaria*, which characterized pluvial intervals in the middle Pleistocene, might also do well during a warm-dry interpluvial period like OIS 5; however, the relatively low abundances of *Fragilaria* during previous interglacials is left open for question.

Two cores from the Klamath Basin have proven to be fertile ground for the nascent field of environmental magnetism. Roberts et al. (1996) conducted sediment magnetic measurements on bulk samples and reflected light microscopy and x-ray diffraction (XRD) analysis on magnetic separates from the Butte Valley core. They found that most of the magnetism in the 3.0 My of core was carried by titanomagnetite, which was most likely derived from basalt detritus in the catchment area.

Greigite ( $\text{Fe}_3\text{S}_4$ ), an authigenic magnetic mineral, was found in several horizons in the age interval from 3.0 to ~1.0 Ma. Because the formation of greigite depends upon the availability of dissolved sulfate, Roberts et al. (1996) tentatively concluded that greater residence time of lake water may have caused the slightly anoxic conditions under which the availability of dissolved sulfate would have been enhanced. Thus, lake conditions were significantly different, at least in intervals, for the periods before and after ~1.0 Ma. Notably, a nine-fold increase in sedimentation rate also occurred at ~1.0 Ma, supporting a major change in the environment of deposition at this time.

Climate change during the middle Pleistocene (~400 Ka to ~300–200 Ka) also was interpreted with the help of an environmental magnetism record from Buck Lake, 15 km west of Klamath Basin (Rosenbaum et al., 1996). Variations in magnetic properties were found to correlate strongly with changes in climate, as indicated by pollen type. In particular, zones of high magnetic susceptibility, hence, high concentrations of magnetite, coincide with cold and dry climate zones, and zones characterized by low susceptibilities were identified with warm climate zones. The magnetic variations preceded the changes in pollen, an observation that prompted Rosenbaum et al. (1996) to propose that Buck Lake magnetic properties responded more quickly to climate change than did vegetation. High hematite concentrations, inferred from two ratios (HIRM and the S parameter) calculated from measurements of isothermal remnant magnetization (Thompson and Oldfield, 1986), were found to be in phase with high magnetite concentrations. The overall content of heavy minerals, as indicated by the concentrations of Ti and Zr (immobile elements mainly held in heavy minerals), was also found to be in phase with increases in magnetic-mineral content; however, because the magnetic-mineral concentrations varied by two orders of magnitude between cold and warm climates and, in contrast, the heavy-mineral concentration varied only by a factor of three, Rosenbaum et al. (1996) concluded that the low amount of magnetic minerals during warm climates relative to other heavy minerals was caused by sourcing from soil and highly weathered rock in the catchment. In contrast, during pluvials, greater runoff would have brought in a greater concentration of relatively fresh detritus derived from basaltic bedrock.

**LAKE CHEWAUCAN.**—Four subbasins (Summer Lake, Upper and Lower Chewaucan Marshes, and Lake Abert) combined during pluvial maxima to become pluvial Lake Chewaucan in south-central Oregon (Figure 1). At its maximum, the lake was 113 m deep, and its surface stood at an elevation of 1328 m. The climate prehistory of this pluvial lake (Allison, 1945) was made well known when Antevs (1948) used it as a constraint for his Neothermal climate model. Although this prehistory proved to be wrong in light of the application of more modern chronological techniques (see earlier discussion under “Other Models for Holocene Climate Change”), pluvial Lake Chewaucan has continued to be the focus of climate-change research

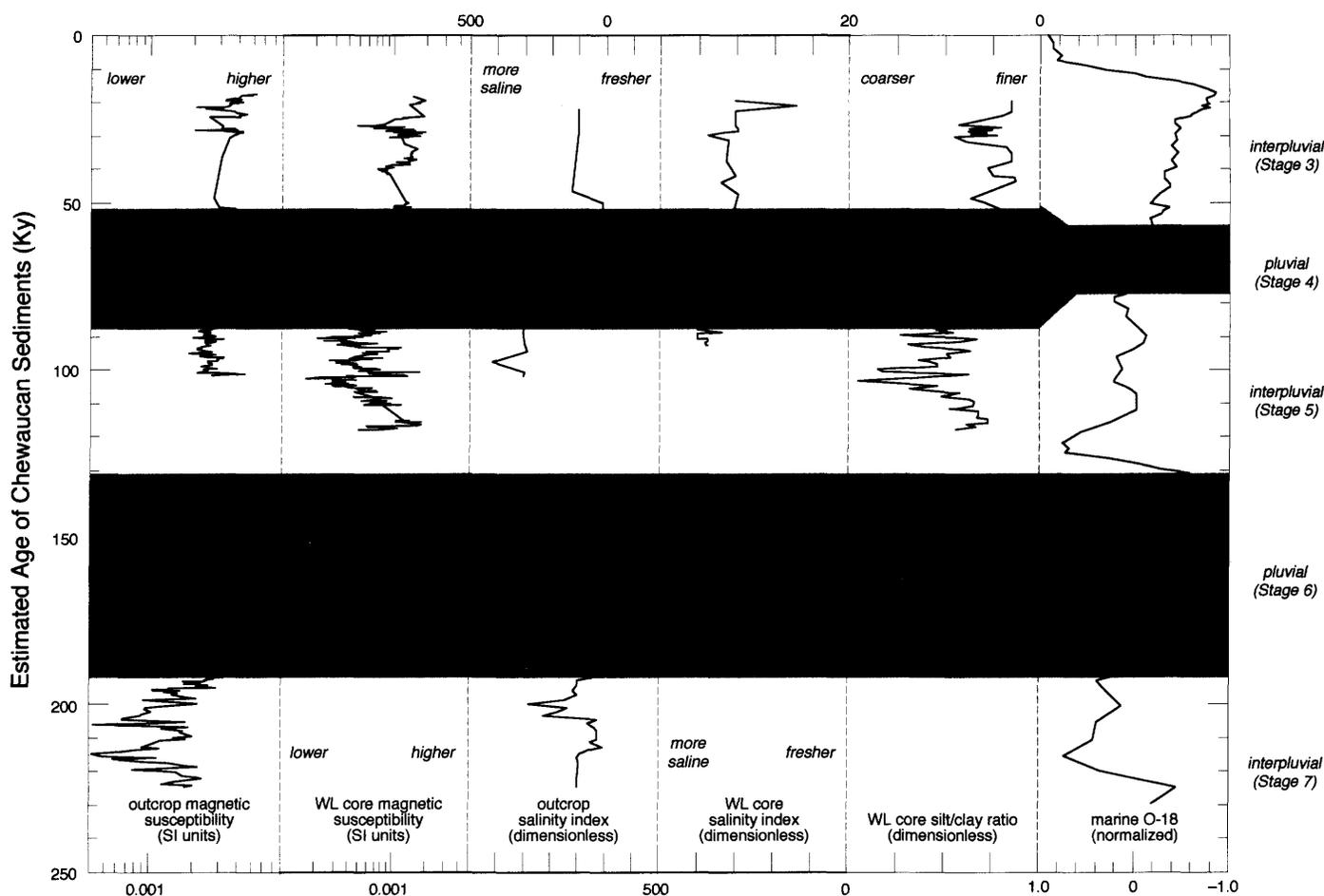


FIGURE 9.—Lake-size proxies for Summer Lake subbasin of pluvial Lake Chewaucan compared with a marine oxygen isotope proxy for ice-sheet extent (Martinson et al., 1987, fig. 18). Magnetic susceptibility has been shown to correlate with other lake-level proxies by Erbes (1996). The salinity index is a weighted ratio of salinophile ostracode faunal counts over counts of ostracodes that prefer fresh water (Palacios-Fest et al., 1993). The outcrop samples are from the Ana River canyon near the northern margin of the subbasin. The WL core samples are from a locality closer to the depocenter, near the northern edge of the modern playa lake.

owing to the combination of excellent exposures of pluvial lake sediments, abundant tephra layers, climate-controlled geomorphology, and well-preserved records of fossil biota and magnetism (e.g., Allison, 1982; Grayson, 1993). Furthermore, in the last 50 years many studies on archeology, climate modeling, geochemistry, geomorphology, fossil magnetism, hydrology, mineralogy, paleontology, sedimentology, structural geology, and tephrochronology have set the stage for continuing paleoclimate and related research in this basin (Conrad, 1953; Brown, 1957; Phillips and Van Denburgh, 1971; Van Denburgh, 1975; Allison, 1982; Negrini et al., 1984; Davis, 1985; Negrini et al., 1988; Simpson, 1990; Banfield et al., 1991a, 1991b; Berger and Davis, 1992; Gobalet and Negrini, 1992; Negrini and Davis, 1992; Freidel, 1993; Palacios-Fest et al., 1993; Pezzopanne, 1993; Negrini et al., 1994; Oetting, 1994; Roberts et al., 1994; Wigand et al., 1995; Erbes, 1996; Wigand and Rhode, 2002).

The lake-level history for the Chewaucan system during the last 200–300 Ky has been estimated from several proxy indicators derived from the analysis of bottom sediments exposed in outcrops and sampled from cores (Figure 9). The correlation of cores with outcrops and the age control of the resulting composite section (Figure 3) are based upon a variety of methods, including lithostratigraphy, tephrochronology, sediment magnetism, paleomagnetic secular variation, radiometric methods, and thermoluminescence (Davis, 1985; Berger and Davis, 1992; Negrini et al. 1994; Erbes, 1996). Notably, this chronology was constructed completely independent from *a priori* assumptions regarding correlations to climate-change events. Variations in lithology type, sediment grain size, and the concentration of magnetite grains, as indicated by magnetic susceptibility, all indicate that the environment of deposition changed systematically through time more or less in tune with the marine OIS signal (Figure 9). Complementary variations

through time in the paleosalinity of the lake, as estimated by the faunal distribution and geochemistry of fossil ostracodes, and in the shallowness of the lake, as estimated by the noisiness of the trace-element concentration of the same ostracodes, strongly suggest that the changes in the depositional environment were caused by increases in lake size as the ice sheets advanced and vice-versa (Figure 9; Palacios-Fest et al., 1993; Erbes, 1996). Thus, both the nature of the variations of climate proxies in the Chewaucan sediment and their timing indicate that, to a first order, the lake-level history of pluvial Lake Chewaucan supports Antevs' jet stream migration model.

Marine OIS 4 is well resolved in the Summer Lake record (Figure 9). In fact, the freshest water, hence the deepest lake, appears to have occurred in OIS 4 rather than in OIS 6 or 2. There are two explanations for this observation. First, because the signatures and durations of OIS 4 are either subdued, shortened, or nonexistent in lake-level proxies from southern Great Basin lakes (e.g., Bradbury, 1997; Lowenstein, 2002), it may be that the southernmost position of the jet stream occupied a more northerly latitude (i.e., over Summer Lake) than it did during the OIS 2 glacial maximum (Lowenstein, pers. comm., 1997). More specifically, if the jet stream remained for a while at its southernmost point over southern Oregon during OIS 4, this lesser glacial stage would have had a very profound effect on Lake Chewaucan. In contrast, if the jet stream moved quickly through Oregon on its way south and back during the OIS 2 event, then the pluvial episode seen at Summer Lake during OIS 2 may have been relatively minor. A second and equally plausible explanation is the following. Lake Chewaucan could have been deeper and fresher during OIS 6 and 2 than it was during OIS 4, but the records of the freshest lakes were erased by deflation during the subsequent interpluvial maxima. The latter explanation is supported by the gap in sedimentation shown in Figure 9 from ~160 to 115 Ka and also by the fact that the sediments at the surface of the modern Summer Lake playa are no younger than 23 <sup>14</sup>C Ky B.P. (Negrini et al., 1993). Note that without good independent age control one would never realize that cold/wet and hot/dry extrema corresponding to both sides of glacial terminations had been erased by deflation. Thus, the Summer Lake example serves as a warning to those drawing conclusions regarding climate extrema from poorly dated paleoclimate records associated with deflation-prone desert basins.

In addition to climate variations, drainage diversions also could have affected the surface level of Summer Lake. In fact, the Chewaucan River, the main stream entering the Chewaucan system, is currently diverted from the Summer Lake subbasin by its own fan-delta complex (Allison, 1982; Davis, 1985). It is unlikely, however, that such diversions would have resulted in a lake-level history that matches the OIS signal so well (Figure 9). Thus, climate variation is probably the major influence on lake level in this subbasin. A similar study of the Lake Abert subbasin could provide a test for this hypothesis.

In an early study of the paleomagnetism at this locality, Milankovitch-like periodicities were reported in spectra of the magnetic vector time series (Negrini and Verosub, 1987; Negrini, Darke, et al., 1987; Negrini et al., 1988). This was certainly a provocative result but has since proven to be incorrect by improvements in the chronology (e.g., Negrini et al., 1994). Even though the PSV time series are no longer considered to be related to climate change, they still have potential as tools for high-resolution correlation of other climate records with the Chewaucan record (see above).

*Comparison of Lake Chewaucan and Lake Modoc Records:* The Lake Modoc climate record, as described in a preceding section, contrasts greatly with the Chewaucan record. Specifically, OIS 4 is a major feature in the Chewaucan record but is barely noticed in the Tulelake record. Furthermore, the OIS 5 interglacial episode at Lake Modoc is characterized by continuous deposition in an environment similar to that of glacial episodes earlier in the Pleistocene. Most of the discrepancies between these records can be explained by differing interpretation of chronologies rather than by radically different climates in regions that are in close proximity. Figure 10 presents a comparison of the two records after the Lake Modoc chronology has been reinterpreted by aligning the records using four tephra layers common to both records. The age scale assumes that the chronology for the Lake Chewaucan record is accurate, but because the comparison is based upon the relative position of the four tephra layers, the comparison would still hold up if the Chewaucan chronology changes with improved age control.

With the reinterpreted chronology, the two records now have much in common with each other and with the marine OIS signal (Figure 10). In particular, the interval of time from ~190 to ~160 Ka is characterized in both records by more pluvial conditions, and a strong OIS 4 signal is now observed in both records. Note also that the reinterpretation forces a major OIS 5 unconformity on the Lake Modoc record. This is not entirely unreasonable considering that such an unconformity occurs in the Chewaucan record.

**PLUVIAL LAKE MALHEUR.**—A large region (2400 km<sup>2</sup>) of very low relief (<10 m) in eastern Oregon presently contains Malheur, Mud, Harney, and Silver Lakes (Figure 1). Presently, all except Malheur are ephemeral lakes. In 1986, after a series of abnormally wet years, Malheur overflowed through a sill called The Narrows into Mud Lake and then into Harney Lake (Hostetler and Bartlein, 1990). At its peak, this combined lake reached a depth of only 4.4 m, and its surface stood at an elevation of 1250.5 m. Had the effective moisture level increased so that the lake rose another one meter or so, then the combined lake also would have overflowed into the Silver Lake basin. If the lake deepened yet another three meters to a surface elevation of ~1254 m, it would have overflowed into the Columbia River system.

One of the tephra layers from the ~70 Ky old Pumice Castle set was identified in lacustrine sediments at an elevation of 1247 m near the base of two trenches associated with archeological

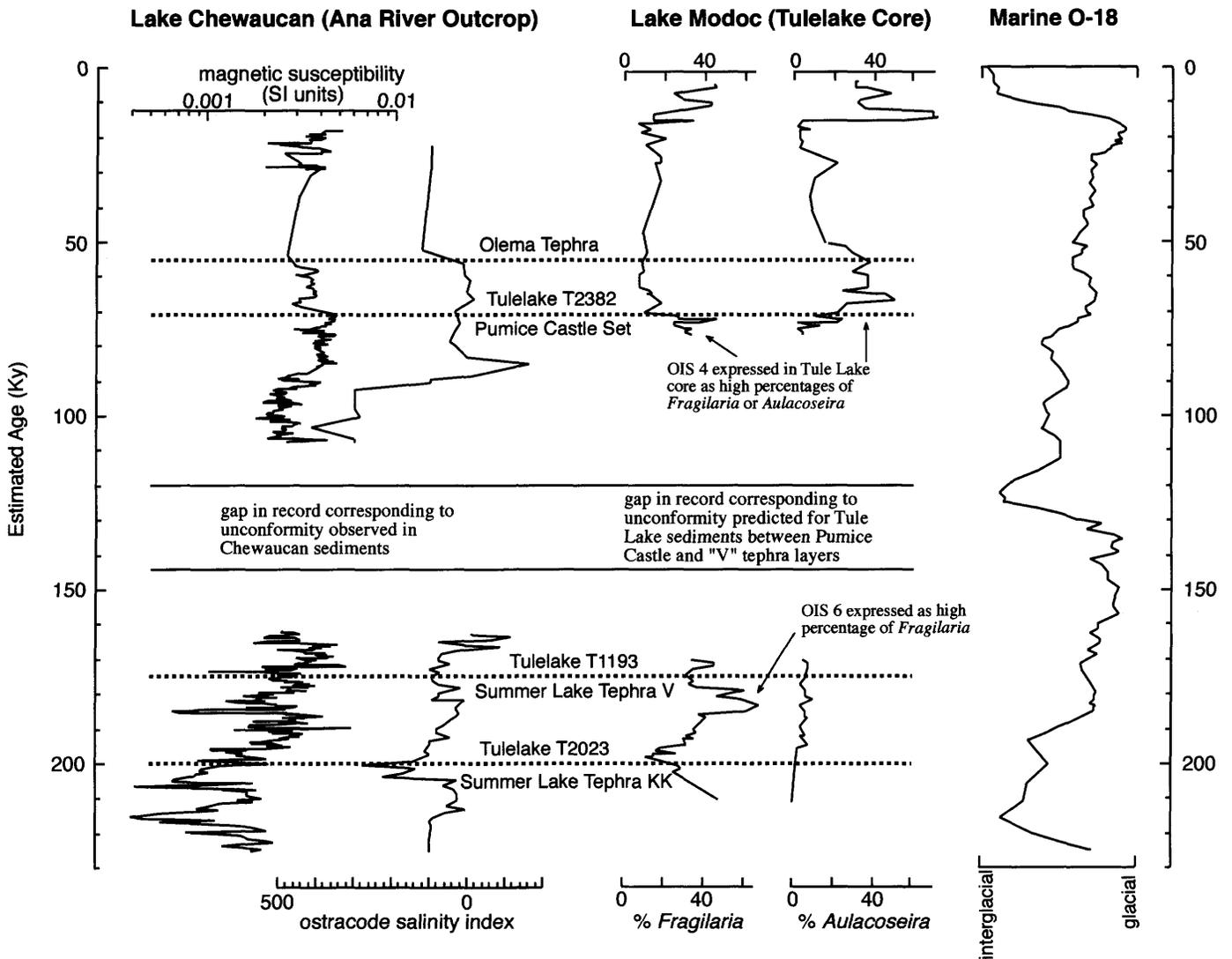


FIGURE 10.—Comparison of Lake Chewaucan and Lake Modoc/Tulelake core (from Figure 8) paleolake environments. Pluvial conditions increase to the right in all diagrams. Relative age-control is anchored by four common ash layers, as per Reick et al. (1992). The absolute chronology of the Lake Modoc record is reinterpreted in terms of preferred ages for the tephra layers, as discussed in the text. The positions of these tephra layers in the original Tulelake chronology are shown in Figure 8b. The new chronology for the Lake Modoc record resolves the anomalous occurrence of *Fragilaria* sp. in the OIS 5 interpluvial, which was noted by Bradbury (1991, 1992), by placing this occurrence in OIS 6 and OIS 4. This chronology also indicates a major gap in the Tulelake record between the Pumice Castle tephra and the Summer Lake V tephra layers.

investigations near the southern margins of modern Malheur Lake (Elston, 1992; Botkin and Carembelas, 1992a, 1992b). In one of the trenches, the ash is a continuous layer found near the base of at least one meter of stratified lacustrine sandy clays. Thus, for approximately 70 Ky, during the middle of OIS 4, pluvial Lake Malheur had enough water in it to deposit more than one meter of sediments on a lake bottom at 1248 m, which is two meters above the present-day lake surface. If the OIS 4 lake had a depth of at least 2 m, then pluvial Lake Malheur would have been at least as large as it was in 1986.

Pluvial Lake Malheur also appears to have included all of the four major subbasins at ~32 <sup>14</sup>C Ky B.P., as evidenced by a radiocarbon date on mollusk shells collected on the "lakeside face of a gravel beach ridge" (Gehr, 1980:167). The elevation of this ridge is 1251 m.

#### Latest Pleistocene (30 to ~10 Ka)

LAKE LAHONTAN.—The late-Pleistocene pluvial history of Lake Lahontan has been the subject of several reviews published

in the last 50 years (e.g., Morrison, 1965; Mifflin and Wheat, 1979; Davis, 1982; Smith and Street-Perrot, 1983; Benson and Thompson, 1987a, 1987b; Dansie et al., 1988; Benson et al., 1990; Morrison, 1991b; Grayson, 1993). This current review draws heavily on those earlier reviews and adds supplemental material from subsequent research.

Extensive radiocarbon dating associated with tufas, organic materials from packrat middens and other terrestrial animals, tephra, wood, shells, bulk sediments, fishing cordage, etc., have allowed a detailed and coherent picture to emerge for the past 30,000 years (especially the last 25,000 years) of lake-level prehistory for the Lahontan Basin. The pioneering radiometric studies in the Lake Lahontan area were done on carbonates by Broecker and Orr (1958) and Broecker and Kaufman (1965). Many of these dates have been contested by Benson (1978), particularly those indicating an unexpectedly young age (11.5–9.5  $^{14}\text{C}$  Ky B.P.) for the last 1330 m Lahontan highstand, because they were found to be inconsistent with the stratigraphic framework as reviewed in Morrison and Frye (1965). Since the work of Broecker's group, more than 100 radiocarbon dates have been done on Lahontan Basin materials, most of them by L. Benson and colleagues (e.g., Benson, 1978, 1994; Benson et al., 1995). This group has demonstrated that dense, lithoid tufas and aragonitic gastropods yield consistent dates, whereas massive forms of tufa (e.g., dendritic tufa) yield significantly younger ages. Through careful petrographic analysis, Benson (1978) demonstrated that the latter type of tufa contains abundant evidence for the introduction of secondary carbon (e.g., shell fragments in pores and precipitated acicular carbonate) well after the initial formation of the tufa. Thus, massive tufa is usually not an appropriate material for radiocarbon dating. After careful selection of dateable materials from his petrographic analysis and from previous radiocarbon analyses on deltaic wood from Born (1972), Benson (1978) published a new prehistory of the Lake Lahontan surface level through time and, on its basis, pushed the highstand date back to 13.6–11.1  $^{14}\text{C}$  Ky B.P.

The next major advance came with the addition to the database of several radiocarbon dates on organic material from primarily packrat middens, which in contrast to carbonates deposited under water, constrained the maximum depth of the water. When combined with the previous analyses and the addition of new tufa dates, these complementary data led to an even clearer prehistory (Thompson et al., 1986; Benson and Thompson, 1987b; Benson et al., 1990). An exhaustive review on the formation history of the several types of tufas in the Lake Lahontan area, additional tufa dates, and new dates and lake-level context for two critical chronostratigraphic horizons, namely the Wono and Trego Hot Springs tephra beds, refined this prehistory even further (Benson, 1994; Benson et al., 1995; Benson et al., 1997).

The current state of the late Pleistocene Lake Lahontan prehistory is represented by the surface level of Lake Lahontan in the Pyramid subbasin, as shown in Figure 11. Although the

lake level of the Pyramid Lake subbasin is not a precise proxy for the surface area (the parameter most directly affected by climate) of Lake Lahontan as a whole, modeling by Benson and Paillet (1989, fig. 8) showed that the overall shapes of both quantities over time are quite similar.

According to radiocarbon dates on tufas, tufa-coated wood, and organic remains of a camel (see below), low to moderate lake levels were present in this subbasin from ~35 to 23–22  $^{14}\text{C}$  Ky B.P., although Lake Lahontan was high enough (1172 m in elevation) for Pyramid Lake to spill over into Winnemucca Lake for a few thousand years ~30  $^{14}\text{C}$  Ky B.P. (Figure 11). The lake was low enough for a camel to become stuck in the mud near the modern (post-irrigation) shoreline during the "Wizard's Beach Recession" (Dansie et al., 1988), which lasted perhaps as long as 4 Ky from ~26 to ~22  $^{14}\text{C}$  Ky B.P. Further support for this lowstand is provided by coarse-grained alluvial deposits underlying the Trego Hot Springs tephra in the Black Rock Desert (Ewing, 1996; F. Nials, pers. comm., 1996) and by high values of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  measured in tufa of that approximate age (Benson et al., 1996).

After the Wizard's Beach recession, abundant data summarized in Benson et al. (1990) indicate that the lake rose very quickly at ~23–22  $^{14}\text{C}$  Ky B.P. to a level high enough to connect all of the major subbasins except for Walker Lake (Figure 11). The lake remained stable near this elevation until ~16.0  $^{14}\text{C}$  Ky B.P. when it underwent a series of high-amplitude oscillations ending with the terminal recession to below the Emerson Pass sill (1207 m) at ~9.5  $^{14}\text{C}$  Ky B.P. The high-amplitude oscillations included a spike-like, major transgression to the maximum highstand centered somewhere between 14.0 and 13.5  $^{14}\text{C}$  Ky B.P. and a return to levels high enough for Pyramid Lake to spill into the Smoke Creek and Black Rock Desert basins at just before 10  $^{14}\text{C}$  Ky B.P. This last transgression is supported by dates on shells, tufa, and marl from the Carson Desert subbasin at similar elevations (Elston et al., 1988; Currey, 1990; Benson et al., 1992).

The overall changes in the size of Lake Lahontan, as represented in Figure 11, also are recorded in the stable isotope signatures of tufas from the Pyramid Lake subbasin (Benson et al., 1996). Benson et al. (1996) found that when Pyramid Lake is a closed lake the values of  $\delta^{18}\text{O}$  are dependent upon the balance between input through river discharge, which decreases  $\delta^{18}\text{O}$ , and evaporation, which increases  $\delta^{18}\text{O}$ . When Pyramid Lake is open  $\delta^{18}\text{O}$  is dependent mostly upon the fraction of water input lost to spillover into the next basin;  $\delta^{13}\text{C}$  was found to depend upon lake volume indirectly through its affect on the photosynthesis–respiration balance. Regarding the lake-level prehistory shown in Figure 11, the major lake-level minima at 26, 15.5, and 12  $^{14}\text{C}$  Ky B.P. were found to be associated with relatively heavy  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values, and the opposite was found to be true for the major maxima at 14 and 10.5  $^{14}\text{C}$  Ky B.P. (Benson et al., 1996). Buoyed by these results, Benson et al. (unpublished) derived an even higher-resolution record of change in the level of Pyramid Lake with  $\delta^{18}\text{O}$  measurements of the total

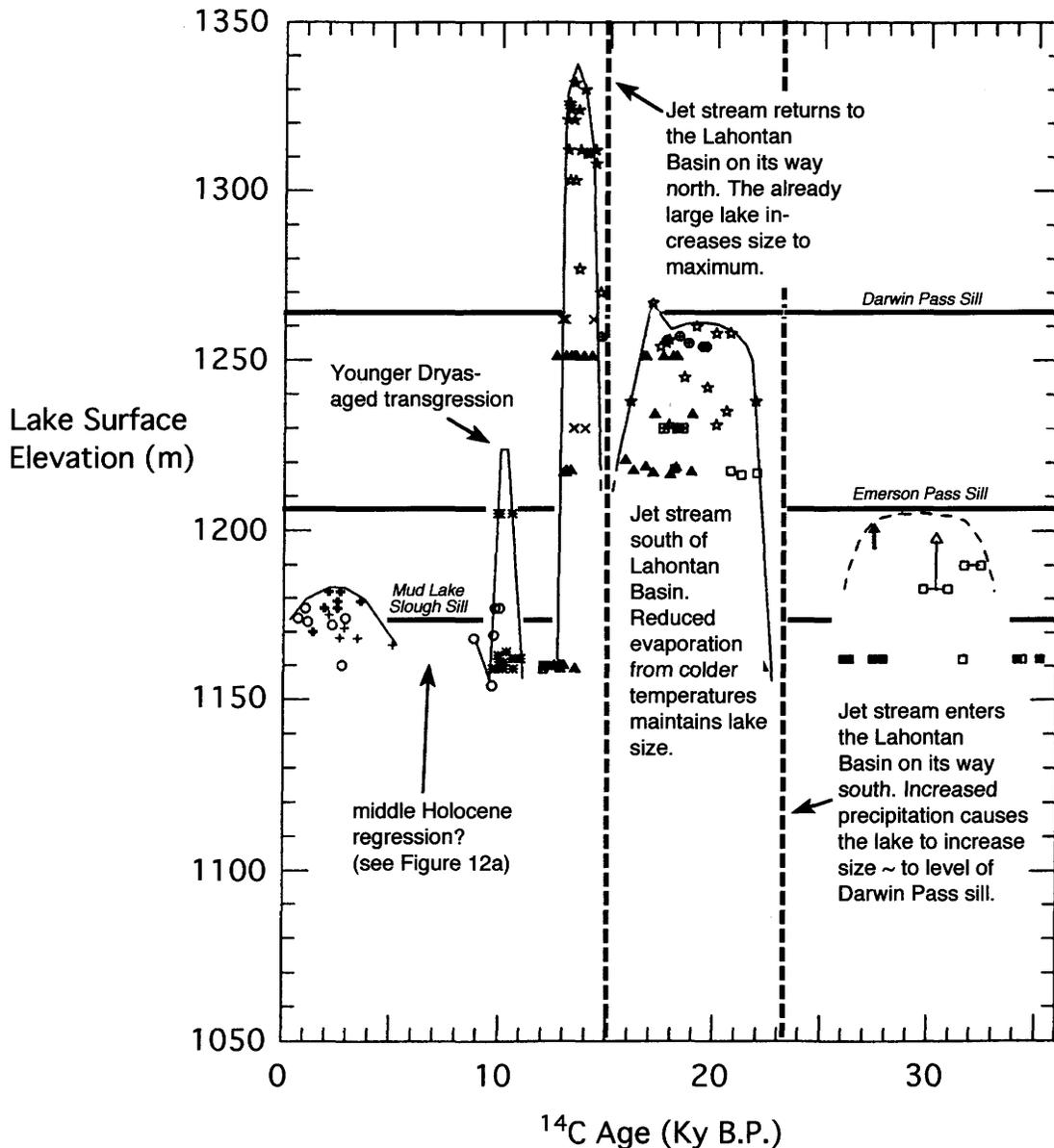


FIGURE 11.—High-resolution lake-level prehistory of the Pyramid Lake subbasin for the latest Pleistocene and Holocene after Benson et al. (1995, fig. 11). The various symbols denote the type of subaqueous materials dated. See Benson et al. (1995) for detailed explanation. Abundant, unplots terrestrial dates, mostly from packrat middens, constrain the maximum lake level from 13  $^{14}\text{C}$  Ky B.P. to present. Interpretation of data in terms of supporting Antevs' jet stream model is after Benson and Thompson (1987a, 1987b) and Benson et al. (1995).

inorganic carbon (TIC) fraction from a sediment core sampled at about 200-year intervals. These data, in conjunction with measurements of total organic carbon (TOC), were found to vary through time in high-frequency oscillations with square-wave morphologies that can be correlated in a general way to D-O cycles and Heinrich events (Benson et al., unpublished).

*Timing of the Last Lake Lahontan Highstand:* The only major point of contention during the last 20 years with the

22–9.5  $^{14}\text{C}$  Ky B.P. lake-level record for Lake Lahontan has been the timing of the maximum highstand (Bradbury et al., 1989; Benson, 1991; Grayson, 1993:96). Bradbury et al. (1989) argued that a Lake Lahontan that was high enough to incorporate the Walker Lake subbasin could not have occurred after 23  $^{14}\text{C}$  Ky B.P. because a well-dated sequence of sediments from Walker Lake shows this lake to have been a saline lake or a playa for the entire interval from 23 to 5  $^{14}\text{C}$  Ky B.P. Further-

more, evidence for a deep lake during this highstand interval is missing from the lake-bottom sediments at a coring location in the Black Rock Desert (Ewing, 1996), although this latter record does indicate a spike-like interval of freshwater conditions at the slightly older age of 14.5  $^{14}\text{C}$  Ky B.P.

An attempt to resolve this controversy with a core from the Carson Sink proved to be inconclusive because of inconsistent radiocarbon dates (Thompson et al., 1990). Benson (1991), in an article that focused on replying to Bradbury et al. (1989), made a strong case for deflation as a means to remove the one meter or less thickness of lacustrine sediment he estimated to have been deposited in the Walker Lake subbasin during the approximately 200-year duration of the Lake Lahontan highstand in this location. Although the Black Rock Desert would have had highstand water in it for a few hundred more years, deflation also could have removed the record of the highstand from the sediments studied by Ewing (1996).

The lack of evidence from lake-bottom sediments from only two locations can be explained by deflation or even, perhaps, by erosion from underwater currents or slumping; however, if a highstand lake did indeed exist at this time, then there must be a lake-bottom sediment record preserved somewhere in the Lahontan subbasins. Recent studies in the Carson Desert subbasin by graduate students from the University of Nevada, Reno (UNR), appear to have found exactly this type of evidence. One of these students (Cupp, 1998) found evidence for a surface elevation of the lake at  $\sim 1280$  m and dated it at 12.8  $^{14}\text{C}$  Ky B.P. The dated materials were gastropods sampled from well-bedded lacustrine sands interpreted to be a near-shore deposit. When the Carson Desert subbasin is filled to 1280 m the effective wetness of the entire Lahontan system is approximately 80 percent of maximum (Benson and Paillet, 1989). Although this is not high enough for the lake to reach the Adrian Pass spill point (1302 m) into Walker Lake, the lake only reached this elevation during the highstand interval. The work of K. Adams, the other UNR student, provided even more direct evidence for the highstand during the time indicated by Benson and others. Working in the Jessup embayment at the north margin of the Carson Desert subbasin, Adams (1998) and Adams and Wesnousky (1998) dated three shorelines, two with gastropod shells and the third with a camel bone preserved in these lakeshore deposits. The older dates,  $13.28 \pm 0.11$   $^{14}\text{C}$  Ky B.P. and  $13.11 \pm 0.11$   $^{14}\text{C}$  Ky B.P., were on the shells found in shoreline deposits at elevations of 1327 m and 1331 m, respectively. The youngest date,  $13.07 \pm 0.06$   $^{14}\text{C}$  Ky B.P., was on the camel bone found in shoreline deposits at an elevation of 1338.5 m. These dates and elevations provide strong, independent support for the 14–12.8  $^{14}\text{C}$  Ky B.P. highstand of Benson et al. (1995). Incidentally, further evidence for this highstand is provided by the low values of  $\delta^{18}\text{O}$  found by Benson et al. (1996; unpublished) in tufas and lake-bottom sediments with ages of  $\sim 14$   $^{14}\text{C}$  Ky B.P.

*Testing Paleoclimate Records with the Late Pleistocene Lake Lahontan Record:* The high-resolution Lahontan lake-level

record from the Pyramid Lake subbasin has been used to test models of late Pleistocene climate change. Benson et al. (1995: 25–26) demonstrated that, in response to the deflection of the jet stream during the last glacial advance, “Lake Lahontan should have experienced two lake-level maxima corresponding to the pre- and post-maximum glacial passages of the jet stream core over the Lahontan basin.” The timing of these lake-level maxima are indicated by the dashed vertical lines in Figure 11. The corresponding glacial maximum was at  $\sim 20$ – $18$   $^{14}\text{C}$  Ky B.P., at which time the jet stream would have been deflected to its southernmost position. In this scenario, the lake would have maintained a high level while the jet stream was south of the Lahontan area because of reduced evaporation associated with lower temperatures and the probable occurrence of ice cover during the winter. This is consistent with the modeling results of Benson (1986), Hostetler and Benson (1990), and Hostetler (1991). The larger pluvial maximum occurred as the jet stream returned north after the glacial maximum because the initial size of the lake was larger than it was when the jet stream passed through the Lahontan area on its way south (Benson et al., 1995). Thus, to a first order, the size of Lake Lahontan through time supports Antevs’ jet stream migration model.

The Lake Lahontan record is sufficiently detailed that it also has been used to test higher-resolution models of climate change. For example, Benson et al. (1992) used the abrupt transgression at  $\sim 10$   $^{14}\text{C}$  Ky B.P. as evidence in support of the Younger Dryas climatic interval as a global climate event. Furthermore, Benson et al. (unpublished) used the higher-resolution  $\delta^{18}\text{O}$  record from the Pyramid Lake core to show that relatively dry periods coincided with the H1, H2, and possibly H3 Heinrich events. This observation supports the descriptive model that Heinrich events represent global climate change.

**LAKE MODOC.**—The latest Pleistocene age control in the Tulelake core is provided by the  $23.2 \pm 0.3$   $^{14}\text{C}$  Ky B.P. Trego Hot Springs tephra (Bradbury, 1991; Reick et al., 1992; Benson et al., 1997) and a complementary date of  $25.06 \pm 0.32$   $^{14}\text{C}$  Ky B.P. from slightly lower in the section. Above the Trego Hot Springs tephra is a several meter gap and then sediments containing a series of three precise but inverted radiocarbon dates in the age range from 14.9 to 9.4  $^{14}\text{C}$  Ky B.P. (Bradbury, 1991).

From  $\sim 40$  Ka to a few meters above the Trego Hot Springs bed, the Tulelake core is characterized by diatoms that are indicative of “somewhat shallower and more alkaline conditions” (Bradbury, 1991:231). Because the Trego Hot Springs bed is exposed in littoral sediments in an outcrop 15 m higher than the position of that tephra in the Tulelake core, the lake must have been  $\sim 15$  m deep at that time, 5 m deeper than the historical maximum (Bradbury, 1991). After that time, presumably during a time interval corresponding to OIS 2, the climate in the Lake Modoc region was dry overall but was punctuated with rapid and large fluctuations in moisture.

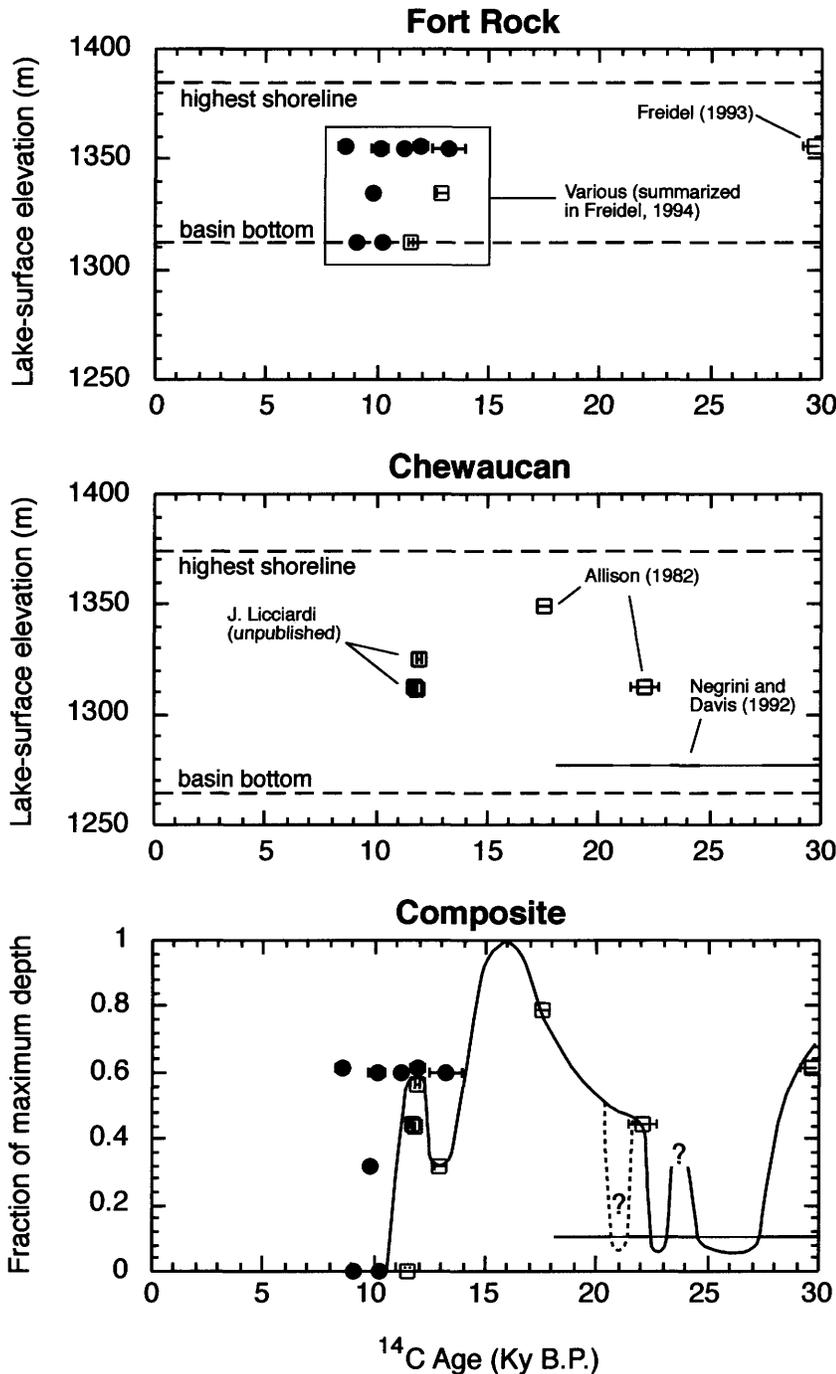


FIGURE 12.—Lake-level prehistories of pluvial Lakes Fort Rock and Chewaucan for the latest Pleistocene (after Negrini and Davis, 1992; Freidel, 1993, 1994). Solid circles denote ages from archeological sites and from other terrestrial materials formed above lake level. Open squares represent materials formed below lake level. In the Chewaucan record from ~30 to 18  $^{14}\text{C}$  Ky B.P. at an elevation of 1276 m, the bold line alternating between black and grey indicates lake levels above and below, respectively, the Ana River outcrop sampled by Negrini and Davis (1992). The ages of these transitions have been changed slightly to conform to the new ages for the Wono and Trego Hot Springs tephra layers (Benson et al., 1997). Unpublished radiocarbon shell dates from near-shore sediments were provided by J. Licciardi. In the composite record, the question mark (?) at ~24  $^{14}\text{C}$  Ky B.P. indicates a lack of data constraining the maximum lake depth. A question mark (?) also is placed at ~21  $^{14}\text{C}$  Ky B.P. because the gap in the bottom sediment record at this time interval is represented by a slight angular unconformity. This could be caused by either a lowering of the lake or a post-depositional deformation.

PLUVIAL LAKES CHEWAUCAN, FORT ROCK, AND ALKALI.—The latest Pleistocene/early Holocene lake-level prehistory of pluvial Lake Chewaucan and nearby pluvial Lake Fort Rock and Lake Alkali (Figure 1) have been summarized by Allison (1966b, 1979, 1982) and Freidel (1993, 1994). Lake levels through time are constrained in these basins by the age of bottom sediments (Allison, 1982; Davis, 1985; Negrini and Davis, 1992), fossils from ancient shorelines (Allison, 1982; Freidel, 1993), and dates associated with archeological sites (Ferguson

and Libby, 1962; Bedwell, 1973; Allison, 1979; McDowell and Benjamin, 1991; Freidel, 1994). The individual data for the Lake Fort Rock and Lake Chewaucan basins and a composite lake-level history are presented in Figure 12.

The oldest radiocarbon date shown is from gastropod shells collected in beach deposits exposed in Fandango Canyon at the southern margin of Lake Fort Rock (Freidel, 1993). X-ray diffraction analysis demonstrated that the shells were made of 100% aragonite, i.e., no secondary calcite was detected. More

details of the predating treatment of the shells were given in Freidel (1993). The shells were collected from two exposures of beach deposits. The oldest date of  $\sim 34$   $^{14}\text{C}$  Ky B.P. corresponds to samples collected at an elevation of 1361 m; the youngest date of  $30 \pm 0.6$   $^{14}\text{C}$  Ky B.P. was from 1353 m. These dates and elevations imply that Lake Fort Rock was at  $\sim 65\%$  maximum depth twice between  $\sim 34$  and  $30$   $^{14}\text{C}$  Ky B.P.

Paleomagnetic secular variation dating of Lake Chewaucan bottom sediments showed that the lake had water at least to the level of the Ana River section ( $\sim 13\%$  of maximum) for the time interval containing the Mono Lake geomagnetic excursion. This excursion is dated  $\sim 28$   $^{14}\text{C}$  Ky B.P. at Mono Lake, California (e.g., Lund et al., 1988). Approximately 4 Ky of deposits are missing above the excursion level, probably because the lake level was below the level of the Ana River canyon outcrop (Figure 12). The lake dropped below the level of the Ana River section sometime during this time interval, as evidenced by the incorporation of the  $27.3 \pm 0.3$   $^{14}\text{C}$  Ky B.P. Wono tephra layer (Negrini and Davis, 1992; Benson et al., 1997) in a beach-lag deposit. The Summer Lake subbasin of Lake Chewaucan held at least some water during this entire time interval because the PSV record from a basin-bottom core is complete for several thousands of years after the Mono Lake excursion (Figure 5b). Lake Chewaucan rose to approximately 50% of its maximum level at  $23\text{--}22 \pm \sim 0.7$   $^{14}\text{C}$  Ky B.P. This age is based upon two pieces of evidence. First, Allison (1982) collected and dated gastropod shells ( $22.1 \pm 0.7$   $^{14}\text{C}$  Ky B.P.) in a baymouth bar deposit at an elevation of 1312 m. This date and elevation is supported by the presence of the Trego Hot Springs tephra ( $23.2 \pm 0.3$   $^{14}\text{C}$  Ky B.P.) in the lacustrine sediments of the Ana River canyon (Negrini and Davis, 1992; Benson et al., 1997). A 2 Ky hiatus in the PSV record from the Ana River section and an associated cross-bedded sand deposit are consistent with the lake again dropping below 13% of its maximum depth sometime after the deposition of the Trego Hot Springs tephra and before the deposition of the  $20.5 \pm \sim 0.5$   $^{14}\text{C}$  Ky B.P. Mount St. Helens Mp tephra bed (Negrini and Davis, 1992). After that, the lacustrine sediments at Ana River were deposited more or less continually until at least  $16.7 \pm \sim 0.5$   $^{14}\text{C}$  Ky B.P. This latter date marks the top of the lake sediments at an unconformity over which lie eolian sands containing the Mount Mazama tephra (Davis, 1985). The extent of deflation or other post-depositional erosion of overlying lacustrine sediments is unknown. Another shell date of  $17.5 \pm 0.3$   $^{14}\text{C}$  Ky B.P. from a basalt pebble conglomerate collected at 1349 m by Allison (1982) indicates that the long-lived lake implied by the interpretations of Negrini and Davis (1992) rose to at least 75% of its maximum elevation during this time. This long-lived lake probably represents the pluvial maximum at Lake Chewaucan. Lake levels between the highstand and its terminal Pleistocene recession (Figure 12) are constrained by unpublished radiocarbon dates on shells from near-shore sediments (J. Licciardi, pers. comm., 1995).

Evidence for the timing of the termination of the pluvial maximum in these Oregon lakes also is available from the Lake Fort Rock basin (Bedwell, 1973; Freidel, 1993, 1994). Subaqueous dates on gastropod and ostracode shells (Bedwell, 1973; McDowell and Benjamin, 1991) constrain the lake level to no lower than 1335 m and 1312 m at  $12.9 \pm 0.23$   $^{14}\text{C}$  Ky B.P. and  $11.5 \pm 0.09$   $^{14}\text{C}$  Ky B.P., respectively. Thus, pluvial Lake Fort Rock probably dropped through elevations corresponding to 36% and  $\sim 2\%$ – $3\%$  of its maximum elevation in this  $\sim 1.5$  Ky interval. This timing is well supported by several dates on archeological materials that must have been above lake level, including charcoal, camel bone, and a sandal (Figure 12; Bedwell, 1973; Freidel, 1993; McDowell and Dugas, 1993). Further support is lent by similar evidence for extremely shallow lakes in the nearby Alkali Lake basin by  $\sim 11$   $^{14}\text{C}$  Ky B.P. (Freidel, 1993, and references therein; McDowell and Dugas, 1993).

LATE PLEISTOCENE PALEOCLIMATE MODELS AND RECORDS FROM OREGON AND CALIFORNIA LAKES.—Without better age control it is difficult to use the Tulelake record as a test for late Pleistocene climate models. One can, however, compare the overall character of the latest Pleistocene climate data from the Tulelake core with the well-dated record from Lake Lahontan during the same time interval. For example, the hydroclimate data implied by the Tulelake core for the time of and before the Trego Hot Springs tephra layer (relatively shallow and alkaline) are consistent with the low to moderate levels of Lake Lahontan during late OIS 3 times (Bradbury, 1991). Also, the rapid and large fluctuations in Tulelake-area hydroclimate after the Trego Hot Springs tephra and before the onset of the Holocene (Bradbury, 1991) are in character with many of the rapid fluctuations seen at Lake Lahontan.

Lack of data is the main problem with the latest Pleistocene record from the Oregon lakes. Again, the record compares with the coeval Lake Lahontan record in a general sense. The predominance of shallow lakes from  $\sim 27$  to  $23$   $^{14}\text{C}$  Ky B.P. following a moderately deep lake is quite similar to Lake Lahontan prehistory in that same time interval (Figures 11, 12). After that, both systems were characterized by long time intervals with very large lakes until the Holocene, perhaps interrupted only by short-term recessions. The paucity of data in the records for Oregon lakes, especially in the important time interval between 17 and 12  $^{14}\text{C}$  Ky B.P., makes a more detailed comparison futile at this time.

### *Holocene*

Several previous reviews focussed heavily on Holocene paleoenvironments, principally because of their importance to the archeological sciences (Baumhoff and Heitzer, 1965; Mehlinger, 1977, 1986; Davis, 1982; Aikens, 1983; Dansie et al., 1988; Grayson, 1993; Hattori and Tuohy, 1993; McDowell and Dugas, 1993; Aikens and Jenkins, 1994; Madsen, 2002).

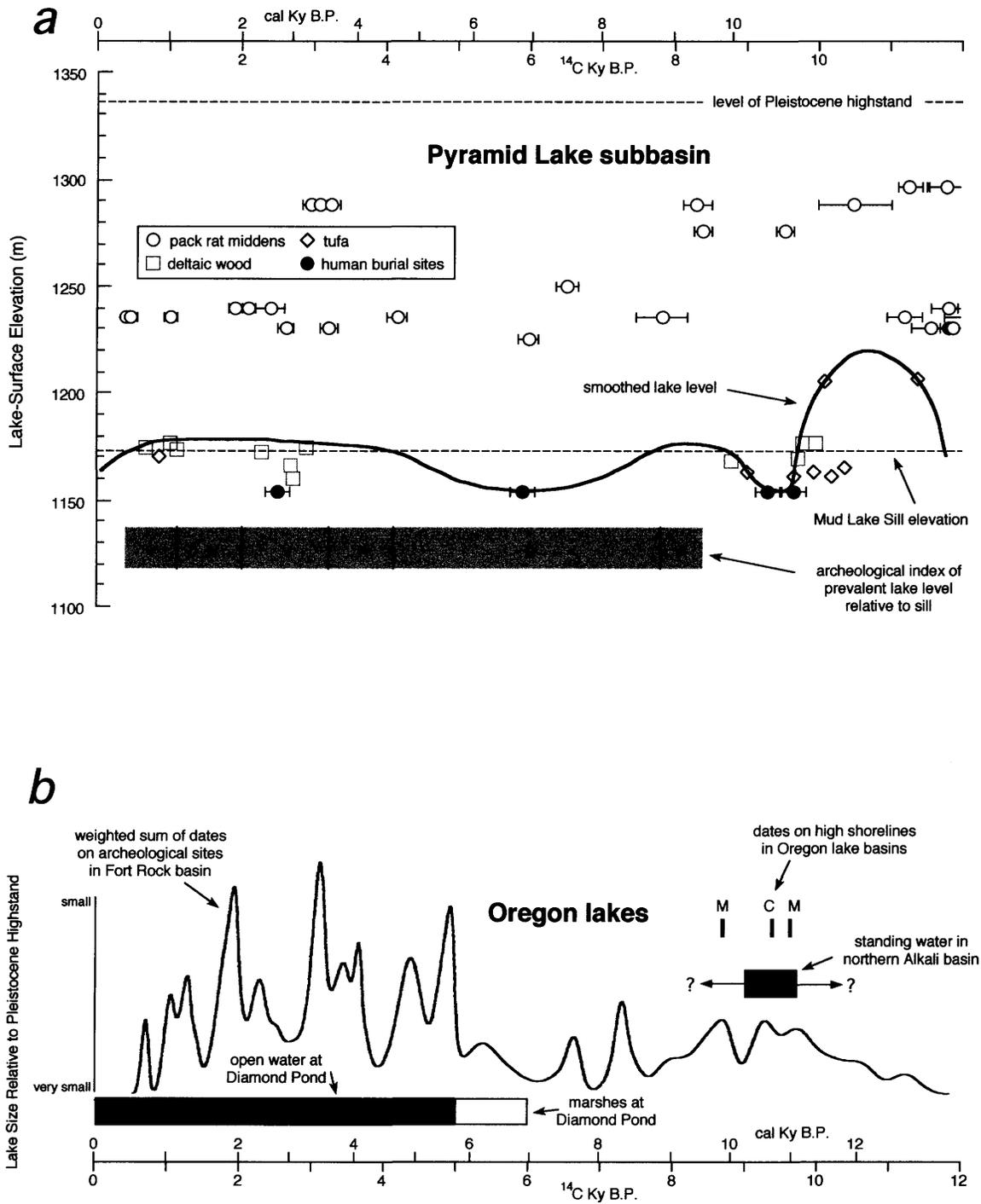


FIGURE 13.—*a*, Holocene lake-level prehistory for the Pyramid Lake subbasin of the Lahontan pluvial system. Published data are from Born (1972), Benson and Thompson (1987b), Benson et al. (1990), Hattori and Tuohy (1993), Benson et al. (1995), and Tuohy and Dansie (1997). Evidence for the middle Holocene 1153 m lowstand is provided by a recent radiocarbon date ( $5.91 \pm 0.125$  <sup>14</sup>C Ky B.P.) on a nearly complete human skeleton with a partial cranium coated in tufa (A. Dansie and D. Tuohy, in litt., 1998). The archeological index corresponds to a qualitative estimate of lake level by Hattori and Tuohy (1993), which was based upon the frequency of occupation in the Winnemucca Caves. These caves would have been abandoned except when lake levels were above

the mud lake sill and, thus, Winnemucca Lake held water. A = lake levels above the sill, B = below, and V = variable. *b*, Holocene lake-level prehistory for Oregon pluvial lakes. C = the date on a shoreline corresponding to a relatively high early Holocene Lake Chewaucan (S. Robinson, pers. comm. to Gehr, 1980); M = dates of a relatively high Lake Malheur (Gehr, 1980). Relevant data for early Holocene standing water in the northern Alkali basin is from Willig (1988) and Pinson (MS.). An index of relative availability of water on the surface of Lake Fort Rock basin is indicated by the weighted sum of radiocarbon dates published by Mehringer and Cannon (1994). Diamond Pond interpretation is from Wigand (1987).

Selected data for Holocene lake levels in the northwestern Great Basin are summarized in Figure 13.

**LAKE LAHONTAN.**—Because Holocene lake-level changes were too small in magnitude to reach most of the sills between major subbasins, the case for each basin is presented separately. Holocene lake-level minima in the Pyramid Lake subbasin are constrained by radiocarbon dates on deltaic wood and tufas; maxima are constrained by organic materials from packrat middens and archeological sites (Figure 13a). The lake-level curve shown in Figure 13a is considered to be smoothed because it reflects general trends in lake levels as indicated by, for example, the occupation of archeological sites. The reader should bear in mind that there are several excursions within these general trends to higher or lower lakes that probably represent higher-frequency lake-level changes. For a related discussion, see Hattori and Tuohy (1993) and Mehringer and Cannon (1994).

The Holocene record in the Pyramid Lake subbasin begins with the recession that terminated the relative highstand associated with the Younger Dryas stade (Benson et al., 1992; Benson et al., 1995). The lowest lake level during this recession (~1153 m) is indicated by two radiocarbon dates. One of these ( $9.66 \pm 0.13$   $^{14}\text{C}$  Ky B.P.) was on a piece of fishing line made from sagebrush bark found at an archeological site on the northwestern shoreline of Pyramid Lake (Tuohy, 1988). The other ( $9.5\text{--}9.1$   $^{14}\text{C}$  Ky B.P.) was on a partial human skeleton found at approximately the same elevation at the north end of Pyramid Lake (Tuohy and Dansie, 1997). Thereafter, the lake probably rose to a level above 1168 m, as indicated by an age of  $8.80 \pm 0.09$   $^{14}\text{C}$  Ky B.P. on a piece of wood from sediments interpreted to have been deposited on a delta slope (Born, 1972). The occupation of Winnemucca Caves from ~8.4 to 7.8  $^{14}\text{C}$  Ky B.P. indicates that water levels high enough for Pyramid Lake to spill into Winnemucca Lake were probably sustained, at least intermittently, until ~8  $^{14}\text{C}$  Ky B.P. (Hattori, 1982; Hattori and Tuohy, 1993).

Except for a few radiocarbon dates from the Winnemucca Caves (Hattori and Tuohy, 1993), no evidence has been found for a long-lived lake above historical levels for the time interval between ~8 and 5  $^{14}\text{C}$  Ky B.P. Davis (1982) and Benson and Thompson (1987b) argued that such lack of radiocarbon evidence does not indicate a desiccation of Pyramid Lake. They noted that elevations of the lake far below the historical (before modern agricultural water diversion) lowstand level of ~1177 m would have killed two species of endemic fish, the cui-ui (*Chasmistes cujus* Cope) and the Lahontan cutthroat trout (*Oncorhynchus clarki henshawi* Richardson). This argument is supported by the failure of these fish to survive during the present century without help from hatcheries after the lake was lowered artificially to below 1160 m by irrigation-related diversion of the Truckee River. The lowest possible level for the survival of these fish is, of course, constrained by the 1153 m regression at  $9.66$   $^{14}\text{C}$  Ky B.P., as discussed in the previous paragraph. The lake reached this low level at least one other

occasion, in the middle Holocene. Evidence for this 1153 m lowstand is provided by a recent radiocarbon date ( $5.91 \pm 0.125$   $^{14}\text{C}$  Ky B.P.) on a nearly complete human skeleton with a partial cranium coated in tufa found at Wizard's Beach at Pyramid Lake (A. Dansie and D. Tuohy, in litt., 1998). A rise to levels as high as 1185 m during the late Holocene is indicated by abundant dates for inorganic carbonates and wood deposited near lake-surface level in a fluvio-deltaic environment (Born, 1972; Benson et al., 1995).

The only direct information on Holocene lake levels with quantitative age control in the Carson Sink area is provided by the tephrochronology of Davis (1978). A Mazama-age lake level was inferred by the identification of the Mazama tephra ( $6.845 \pm 0.05$   $^{14}\text{C}$  Ky B.P.) and its precursor, the Tsoyawata bed ( $7.015 \pm 0.045$   $^{14}\text{C}$  Ky B.P.), at two localities in this subbasin. The two tephra were found in the alluvium in the West Humboldt Range at an elevation of 1204 m. They were also identified in the shallow lake or marsh sediments described by Morrison as Section 22a (Morrison, 1964:128) east of Fallon, Nevada, near the Stillwater Reservoir at an elevation of ~1193 m, which is only one or two meters above the modern low point in the entire Carson Sink subbasin (Davis, 1978; Elston et al., 1988). Thus, in the few hundred years of time spanned by the volcanic eruptions associated with these two tephra, the lake in the Carson Desert subbasin was less than 10 m deep (Davis, 1982). In contrast, sometime after the eruption that created the Tarupah Flat bed (1500–600 years old), the lake had risen to a level of 1207 m, as evidenced by the wave-cut platforms crosscutting this ash layer at two locations near Salt Wells, Nevada (Davis, 1978).

Walker Lake was interpreted to have been an ephemeral playa lake during the early Holocene (Bradbury et al., 1989; Benson et al., 1991). This interpretation was based upon the assemblage of microfossils (diatoms, ostracodes, aquatic pollen), lithology, and an abrupt change in sedimentation rates. After ~5.0–4.5  $^{14}\text{C}$  Ky B.P. the lake quickly filled to a depth as great as 90 m. This rapid transgression has been attributed to the diversion of the Walker River into the Walker Lake subbasin from its previous destination, the Carson Desert subbasin (King, 1978, 1993; Davis, 1982; Morrison and Davis, 1984a, 1984b; Bradbury et al., 1989; Benson et al., 1991). Based upon similar evidence to that mentioned above and also on the stable isotope analyses of Benson et al. (1991), a coherent lake-level prehistory of this subbasin has been determined for the latest Holocene. The coherence of this prehistory with that of nearby Mono Lake (Stine, 1990) gives confidence that late Holocene lake levels in the Walker Lake subbasin accurately reflect climate change (Bradbury et al., 1989; Benson et al., 1991).

There is some controversy as to whether an extreme lowstand of the lake from ~2.5 to 2.0  $^{14}\text{C}$  Ky B.P. was caused by climate change or by another diversion of the Walker River. Bradbury et al. (1989) contended that climate change is the more likely cause because the very existence of even a shallow lake would have required some recharge from the Walker River

into the basin, where evaporation greatly exceeded precipitation, and because climate records from nearby localities in the Great Basin also indicate drier climates during this time interval. They further noted that Walker Lake filled more slowly after 2.0  $^{14}\text{C}$  Ky B.P., as evidenced by step-like increases in key ostracode and diatom taxa, than it did after the previous desiccation. Such a slow transgression is more consistent with climate change than with the sudden diversion of a major river, like the Walker River, back into this subbasin.

Benson et al. (1991), on the other hand, preferred river diversion over climate change as a cause for this near-desiccation event because (1) the usually coherent discharge of the Truckee and Walker Rivers would not have allowed flow in the Walker River to almost cease while the Truckee was flowing enough to keep Pyramid Lake above the level required for the spawning of cui-ui and emerald trout, (2) the Walker River must have continued to flow somewhere to have allowed the survival of the cutthroat trout while the lake-dwelling cui-ui population was wiped out as Walker Lake nearly dried out, and (3) currently, discharge from local streams is sufficient to maintain Walker Lake at very shallow levels (<1 m) even in the absence of the Walker River.

**LAKE MODOC.**—Despite the poor age control in the Holocene part of the Tulelake core, Bradbury (1991:233) asserted convincingly that “the strong fluctuations between planktonic and benthic diatoms reflect real lake level changes that are important for resolving paleoclimatic and archaeological questions.” Clearly, this record will become a valuable one with improved age control. Even as it stands, it provides important information surrounding the Tsoyawata tephra ( $7.015 \pm 0.045$   $^{14}\text{C}$  Ky B.P.), which was identified in the Tulelake core (Reick et al., 1992). Two complementary  $^{14}\text{C}$  dates were obtained within ~1 m below this tephra in the correct stratigraphic order, thereby confirming the ash correlation. The dominance of *Aulacoseira ambigua* in the vicinity of the Tsoyawata tephra bed suggests the presence of a relatively deep lake at this time, perhaps the 20 m lake suggested by an archeological study at Nightfire Island (Sampson, 1985; Bradbury, 1991). Above the Tsoyawata tephra, *A. ambigua* is replaced by *Fragilaria* sp. This indicates a lower lake in the middle Holocene. The return of *A. ambigua* at the top of the core marks a deepening lake at a poorly constrained time, perhaps by ~3 Ka (Bradbury, 1991).

**OTHER OREGON LAKES.**—Most of the evidence for Holocene lake-level changes in Oregon lakes has been reviewed by Freidel (1993, 1994), McDowell (1992), Grayson (1993), McDowell and Dugas (1993), and Aikens and Jenkins (1994). A summary of these reviews with a minor amount of supplemental material follows.

The early Holocene appears to have been characterized by pervasive shallow lakes throughout the Oregon portion of the Great Basin (Figure 13*b*). Four very shallow lakes were reported to have come and gone during the early Holocene

within the confines of pluvial Lake Alkali (Figure 1). The first of these lakes would have been ~0.5 m deep in the Dietz subbasin, located in the northern part of the Alkali Lake basin. The shore of this lake, named Lake Koko, was occupied by a Clovis-age culture. This conclusion was based upon fluted-point assemblages that were found distributed along a linear trend, which was interpreted to be a shoreline (Fagan, 1988; Willig, 1988; Willig and Aikens, 1988). Another assemblage of artifacts, which was characterized by large, stemmed, shouldered, and lanceolate points, was found distributed around a slightly higher shoreline and has been attributed (by Willig, 1988) to the Western Stemmed Point culture. Willig (1988) interpreted this association as a later culture that occupied the shores of the younger, slightly deeper (~2 m) Sand Ridge Lake. Thus, she concluded that Lake Koko existed sometime during the time interval attributed to the Clovis-age culture (11.5–11.0  $^{14}\text{C}$  Ky B.P.) and that Sand Ridge Lake existed during the time interval attributed to Western Stemmed Point tradition (10.8–7.0  $^{14}\text{C}$  Ky B.P.). Although the overlap in age of these two cultures may be larger than implied herein (e.g., Beck and Jones, 1997:196–197), the observation of Lake Koko shorelines covered by Sand Ridge Lake sediments strongly supports an older age for Lake Koko. Charcoal fragments associated with Sand Ridge Lake were radiocarbon-dated (Willig, 1988) at  $9.61 \pm 0.1$   $^{14}\text{C}$  Ky B.P., providing further support for the occupation of Sand Ridge Lake by a Western Stemmed Point culture. Willig (1988) postulated the existence of two younger lakes, an intermediate-sized Lake Delainie and a deeper (~4 m) Big Cut Lake, based upon the superposition of shorelines and lake sediments. The ages of these two younger lakes are not constrained.

The Dietz site lake-level history has since been reinterpreted by Pinson (MS.). In this later study, the stratigraphy was interpreted to consist of deep-lake sediments covered by an eolian deposit, which in turn was covered by a clay-silt layer that was interpreted to have been deposited in a marsh, based upon its internal distribution of gastropods and organic material. Over this last unit is another eolian deposit from which Willig's charcoal date was obtained. A second charcoal date of  $9.43 \pm 0.08$   $^{14}\text{C}$  Ky B.P. from this horizon confirmed Willig's date (Pinson (MS.)). This eolian unit is also the one from which most of the buried, early Holocene archeological materials were derived. Notably, the top of this unit appears to have a nascent soil horizon directly over which lies the Mazama pumice. Pinson (MS.) argued convincingly that this stratigraphy can be interpreted as the drying up of the terminal, deep Pleistocene lake at ~10  $^{14}\text{C}$  Ky B.P. and that thereafter only a shallow marsh existed. This marsh, in turn, dried completely by ~9  $^{14}\text{C}$  Ky B.P., and there has been no standing water in the Dietz subbasin since that time.

Fort Rock Basin has been the location of several important late Pleistocene and early Holocene archeological sites (Bedwell, 1973; Grayson, 1993; Aikens and Jenkins, 1994; Beck and

Jones, 1997), some of which reveal a great deal about paleolake levels (e.g., Figure 13*b*). Early interpretations, based upon evidence from the Connley Caves excavation, pointed to continuous human occupation for the time from ~11 to 3 <sup>14</sup>C Ky B.P., with the notable exception of the interval from 7.2 to 4.4 <sup>14</sup>C Ky B.P. (Bedwell, 1973). The apparent disappearance of human occupation was initially interpreted, at least in part, to have been the result of a catastrophic impact on the population caused by the eruption of Mount Mazama (Bedwell, 1973); however, it was later attributed to the shrinkage of large, nearby bodies of water, as evidenced by the near disappearance of waterfowl remains in the archeological middens of these caves (Grayson, 1979, 1993).

Since the work at Connley Caves, Aikens and Jenkins (1994) conducted a new, basin-wide project. They concluded that when more sites are considered the hypothesis for the middle Holocene abandonment of the Fort Rock Basin begins to fall apart. For example, Mehringer and Cannon's (1994) investigation of "Kelly's Site" in the Fort Rock Basin indicated that people not only occupied the basin on occasion during that time interval, but they were eating waterfowl. Analyses of radiocarbon dates from several additional studies done as part of this basin-wide project, however, revealed shorter-term intervals of relatively lower population density at the bottom of Fort Rock Basin that were presumably related to shorter intervals of lower lake levels and dried-up marshes (Figure 13*b*). These periods are roughly 7–5 <sup>14</sup>C Ky B.P. (Jenkins, 1994; Mehringer and Cannon, 1994) and 3–2 <sup>14</sup>C Ky B.P. (Jenkins, 1994). Although much more work has to be done to precisely define these dry/wet intervals, it is interesting to note that the onset of wetter conditions at ~5 <sup>14</sup>C Ky B.P. implied by the above chronology coincides almost exactly with the transition from ephemeral marshes to open water at Diamond Pond/Malheur Maar in eastern Oregon south of pluvial Lake Malheur (Wigand, 1987).

In addition to dispelling the notion of a 3000-year long middle Holocene abandonment in the Fort Rock Basin (Bedwell, 1973), new work by P. McDowell and J. Benjamin suggests that the Neopluvial (post-altithermal) lake postulated by Allison (1979) also did not exist in the Fort Rock basin. Their conclusions were based upon observations of "extensive dunes with elevations low enough and dates early enough that they would have been destroyed or badly eroded had they been inundated by a basin-wide Neopluvial lake" (Greenspan, 1994: 488; P. McDowell, pers. comm. with Greenspan, 1994).

The subbasin remnants of Lake Chewaucan also appear to have been significantly higher during the early Holocene than during modern times. The evidence for this includes a personal communication cited in Gehr (1980) from S. Robinson of the USGS in which Robinson reported a radiocarbon age of  $9.39 \pm 0.045$  <sup>14</sup>C Ky B.P. on a tufa-coated beach gravel found 20–22 m above the modern level of Lake Abert. Summer Lake rose in the late Holocene, as evidenced by a shoreline 12 m above the

bottom of the Summer Lake basin. This shoreline cuts across sand dunes consisting of pumice from the Mount Mazama eruption (Allison, 1982). There is no age control constraining the minimum age of this feature. There is also evidence that Lake Abert rose again, probably in the late Holocene. This evidence consists of a higher shoreline (18 m above the modern lake) that truncates presumably young colluvium (Allison, 1982). This feature has not been dated.

Pluvial Lake Malheur rose to levels high enough to join all of the subbasins into one lake and perhaps to overflow into the Columbia River system at least three times during the early Holocene (Figure 13*b*). Two of these episodes are dated at  $9.62 \pm 0.05$  <sup>14</sup>C Ky B.P. and  $8.68 \pm 0.55$  <sup>14</sup>C Ky B.P. (Gehr, 1980). No record for the surface levels of this lake exists for the remainder of the Holocene.

TESTING HOLOCENE PALEOCLIMATE MODELS WITH NORTH-WESTERN GREAT BASIN PLUVIAL RECORDS.—The balance of evidence from Figure 13 indicates that pluvial lake levels were slightly higher in the northwestern Great Basin during the early and late Holocene than they were in the middle Holocene. This set of observations, at first glance, appears to support Antevs' Neothermal climate model (Figure 2*a*), although the observations call for a slightly older Altithermal age than was anticipated by Antevs (Grayson, 1993). As more evidence has accumulated, however, it has become increasingly apparent that exceptions to the rule are abundant and that data must be spatially and temporally averaged to conform to the Neothermal model (Grayson, 1993; Mehringer and Cannon, 1994). In particular, the Holocene appears to be characterized by short-period fluctuations in climate of significant magnitude superimposed on the long-term averages (e.g., Benson et al., 1991; Mehringer and Cannon, 1994). Such variability is consistent with the high-frequency variations in solar luminosity inferred by cosmogenic isotope concentrations (Figure 2); however, there is no obvious correlation between the observed climate change presented in Figure 13 and those predicted by the luminosity proxies shown in Figure 2*d*. In addition, there is no evidence in northwestern Great Basin pluvial records, as of yet, for the early Holocene "cooling event" at 8.4–8.0 cal Ky B.P. (Figure 2*c*).

The lack of correlation between northwestern Great Basin pluvial records and the predictions of Holocene climate models probably results from deficiencies in the collective data set and the lack of specific climate changes inferred from the models. The sampling of Holocene paleoclimate data from individual pluvial lake basins in the northwestern Great Basin is usually too sparse for the detection of high-frequency climate change. Furthermore, little modeling has been done to predict the effects of low-amplitude changes in Holocene climate on pluvial lake levels in this region. For example, one recent study on the geochemistry of Great Barrier Reef corals (Gagan et al., 1998) has demonstrated that tropical oceans in the Pacific were ~1° C warmer ~5.35 cal Ky B.P. than they are today and that they

were enriched in  $^{18}\text{O}$ , implying increased levels of evapotranspiration. This intriguing result is consistent with intensified El Niño events during the middle Holocene, which in turn could explain the apparent increased variability in lake levels during this time (e.g., Grayson, 1993; Mehringer and Cannon, 1994). Before such a hypothesis can be anything more than speculative, atmospheric circulation models with the ability to predict the resulting low-amplitude changes in lake levels need to be constructed, and extremely high-resolution pluvial lake records need to be available to test the applicability of this idea to the northwestern Great Basin.

## Summary and Future Trends

### SUMMARY OF MAJOR RESULTS

Since the time of Antevs, many contributions have been made toward the understanding of climate change from studies of pluvial lakes in the northwestern Great Basin. The following list is a sample of these contributions.

1. Both of the global climate events proposed for the Plio/Pleistocene boundary at  $\sim 2.5$  Ma and  $\sim 1.65$  Ma have been observed in several paleoclimate indicators from the Tulelake core (Adam et al., 1989).

2. Variations in the diatom stratigraphy of the Tulelake core, which have been interpreted to represent cycles between glacial and interglacial climates, change frequency in accordance with the evolution through time of the spectral character of marine oxygen isotope curves and other marine paleoclimate proxies (Bradbury, 1991, 1992). Specifically, periods of 400 Ky and 41 Ky appear to dominate the climate variations prior to  $\sim 900$  Ka; thereafter, 100 Ky variations dominate.

3. Evidence for an extremely large lake in the Lahontan and surrounding basins during the largest excursion toward glacial oxygen isotope values in the Quaternary (OIS 16) supports a connection between the sizes of ice sheets and the sizes of pluvial lakes in the northwestern Great Basin (Reheis, 2002).

4. Milankovitch-like periodicities were reported in the spectrum of a middle to late Pleistocene PSV record for Lake Chewaucan (Negrini and Verosub, 1987; Negrini et al., 1988). Subsequent improvements on the age control of the Chewaucan sediments have disproved Milankovitch-like periodicities as the origin of these PSVs (Negrini et al., 1994).

5. Several lake-level proxies in a 250–20 Ka paleoclimate record from Lake Chewaucan support an in-phase relationship between increases/decreases in lake levels and advances/retreats of the North American ice sheet as inferred from marine OIS 7–3 (Davis, 1985; Berger and Davis, 1992; Negrini et al., 1994; Erbes, 1996). This represents a significant test of Antevs' jet stream migration model because the age control of the Lake Chewaucan record is entirely independent of *a priori* assumptions of correlations with climate change.

6. Bradbury (1991, 1992) explained the unusual occurrence of a pluvial diatom assemblage during OIS 5 as being the result

of a tectonic or geomorphologic change that affected the local Tule Lake subbasin. In this review paper, late Pleistocene Tulelake stratigraphy has been reinterpreted, resulting in a significantly younger age for the Pumice Castle tephra (Figure 10). Thus, the diatom assemblage is determined to be a likely expression of OIS 4.

7. OIS 4 is expressed strongly in the northwestern Great Basin by the presence of Pumice Castle set tephra layers in pluvial-lake sediments from three lake basins (Lake Modoc, Lake Chewaucan, Lake Malheur).

8. An exceptionally precise and accurate lake-level prehistory for Lake Lahontan during the latest Pleistocene is consistent with increases in lake size both when the jet stream passes by the Lake Lahontan area on its way south during OIS 2 ice sheet advance and also when it passes by on its way north during ice sheet retreat (Benson and Thompson, 1987a, 1987b; Benson et al., 1995).

9. Higher-frequency climate-change events inferred by stable isotope and total organic carbon analyses of Pyramid Lake bottom sediments have the same square-wave type morphology and duration as the D-O cycles and Heinrich events observed in paleoclimate records from marine sediments and ice cores (Benson et al., unpublished).

10. The observation by Allison (1945) of several meters of Lake Chewaucan sediments above the Mount Mazama ash was a key piece of data that inspired Antevs' theory of a moist Anathermal age. Improvements in tephrochronology and absolute-age dating demonstrated that this ash was, instead, the much older Mount St. Helens Cy tephra (Allison, 1966a; Davis, 1985).

11. Bedwell (1973) noted the lack of middle Holocene archeological remains in the Connley Caves of the Lake Fort Rock basin. An analysis of the associated archeofauna revealed the near disappearance of waterfowl remains in the area, prompting Grayson (1979, 1993) to hypothesize a middle Holocene human abandonment of this basin because of lowered water levels in a nearby lake/marsh complex. Subsequent work on dune sites in the area demonstrated that Lake Fort Rock basin was indeed occupied during the middle Holocene and that the presence of "fish and waterfowl remains ... challenge notions of a long uninterrupted mid-Holocene drought" (Mehringer and Cannon, 1994:321).

12. As more records of Holocene lake-level changes have accumulated, it is becoming more and more apparent that high-frequency change characterized this entire period of time, as suggested by Mehringer and Cannon (1994). Against this background, some long-term trends have emerged (e.g., lower lake levels during the middle Holocene) that loosely fit Antevs' Neothermal age divisions. Neither the long-term changes nor the high-frequency changes appear to correlate unambiguously with newer models of Holocene climate change, such as variability in solar luminosity.

### REMAINING PROBLEMS

Despite the progress that has been made during the last 50 years, the potential for understanding climate change from northwestern Great Basin pluvial lake records has hardly been tapped. For example, long-term records from pluvial lakes other than Lake Modoc need to be obtained to determine if the climate record from the Tulelake core is representative of the rest of the northwestern Great Basin, considering its proximity to the Pacific Ocean and the fact that Lake Modoc drained into the Pacific after reaching only modest depths.

The source vents and correlative proximal volcanic rocks have yet to be identified for many of the water-lain tephra beds in the northwestern Great Basin. Further work of this nature will improve the overall chronology of the region because it is inevitably easier to apply radiometric- and radiogenic-age methods to proximal volcanic rocks than to water-lain ashes. In addition, promising dating techniques, such as luminescence methods, should be used more frequently on the water-lain ashes.

The only well-constrained pluvial lake-size record in the northwestern Great Basin is that of the Pyramid Lake subbasin of Lake Lahontan for the time interval from ~30 to 9 <sup>14</sup>C Ky B.P.; the Walker Lake subbasin may be well-constrained for the late Holocene. The provocative results from these prehistories need to be tested with records of similar resolution and accuracy from other basins.

The present state of the composite Holocene record does not allow accurate testing of models for global climate change during the Holocene. This problem can only be alleviated with well-dated, high-resolution, continuous Holocene records from several basins within the northwestern Great Basin.

### THE NEED FOR COMPREHENSIVE CORING PROGRAMS

Most of the problems mentioned above could be solved with a comprehensive program of coring bottom sediments throughout the northwestern Great Basin. Although core studies can never completely replace field-based surface studies, at this stage in the study of the northwestern Great Basin an extensive coring program would most efficiently provide a wealth of hypotheses. These hypotheses could be tested later by well-focused studies on the extensive exposures of lake deposits in this region, which represent much of the Quaternary period.

There are several indicators that point to the success of such an extensive coring program, many of which are discussed in this review. The work of Benson and others (see "Latest Pleistocene," above) has demonstrated that geochemical climate proxies in cores provide estimates of lake sizes through time that are consistent with independently derived lake-size prehistories from surface materials and that these proxies can be ac-

quired relatively rapidly with high resolution. The consistency of paleoclimate results from geochemical measurements with other bottom-sediment proxies, such as the distribution of faunal and floral taxa, lithostratigraphy, granulometry, and environmental magnetism, points to a variety of useful techniques that may be applicable for each core.

Unprecedented age control for terrestrial records can be provided by an already rich, tephrochronological database, which will only improve through iteration as results from additional cores are added to a composite data set. Under ideal conditions, the promising and complementary application of paleomagnetic secular variation often can provide nearly continuous relative age control, which conceivably can be tied directly to marine paleoclimate records. This method, too, will grow in usefulness as a reference PSV record continues to develop. Advances in luminescence and radiocarbon methods have contributed greatly to our understanding of northwestern Great Basin pluvial lakes and will continue to do so in the future.

Coring programs should be preceded by careful consideration of coring sites optimally selected on the basis of sound sedimentological models and geophysical studies. Several localities around most basins should be cored in order to sample and compare the many varieties of depositional environments observed within each basin. At least two cores should be taken at each coring site to guard against localized synsedimentary deformations, loss of core samples during withdrawal, etc. Cores should be oriented azimuthally whenever possible to enable the accurate measurement of magnetic declination for use in PSV studies. Finally, and perhaps most important, a full array of lithological, paleontological, geochemical, tephrochronological, and magnetic studies should be done on these cores in a timely fashion and with careful management of data and archival of core splits.

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# Pliocene to Middle Pleistocene Lakes in the Western Great Basin: Ages and Connections

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## ABSTRACT

During the Pliocene to middle Pleistocene, pluvial lakes in the western Great Basin repeatedly rose to levels much higher than those well-documented levels of the late Pleistocene. Sedimentologic, geomorphic, and chronologic evidence indicates that Lakes Lahontan and Columbus-Rennie were as much as 70 m higher at about 650 thousand years ago (Ka) than during their late Pleistocene highstands. At its former altitude of 1400 m, Lake Lahontan submerged present-day Reno, Carson City, and Battle Mountain in Nevada and flooded other now-dry basins. To the east, Lakes Jonathan (new name), Diamond, Newark, and Hubbs reached highstands during the early-middle(?) Pleistocene that were 25–40 m above their late Pleistocene shorelines; at these very high levels, the lakes became temporary or permanent tributaries to the Humboldt River and, hence, to Lake Lahontan. This scenario presents a startling vision of a western Great Basin in which climatic and tectonic effects conspired to integrate presently isolated basins into one enormous drainage system during at least one brief period during the Quaternary. Such a temporary connection could have permitted fish to migrate from the Humboldt River southward into the presently isolated Newark Valley and from Lake Lahontan into Fairview Valley. The timing of drainage integration provides suggested maximum ages for fish to populate the basins of Lake Diamond and Lake Jonathan.

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The Walker Lake subbasin of Lake Lahontan held deep lakes at least four times during the early Pleistocene; these were at least 15–25 m above the Sehoos highstand. One site on the Humboldt River in the northeastern Lahontan Basin displays exposed, faulted lake sediments of early Pleistocene age that are now 40–55 m above the Sehoos limit. These sediments suggest that the northern and Walker Lake subbasins were contiguous parts of Lake Lahontan by about one million years ago (Ma), but fish fossils indicate that drainage connections existed before 1 Ma. For example, high beach deposits suggest that Lake Russell, now a tributary to the Owens River, previously overflowed to the Walker River, potentially providing a migration route for fish southward along the east side of the Sierra Nevada into the Owens River system. Deposits of Pliocene lakes suggest connections existed among proto-Lakes Lahontan, Columbus-Rennie, Clayton, and possibly Tonopah. Tephrochronologic ages of these Pliocene lakes provide constraints on the availability of aquatic migration routes at different times.

Reconstructing and dating these lake levels also has important implications for paleoclimate, tectonics, and drainage evolution in the western Great Basin. For example, shorelines in several basins form a stair-step sequence downward with time from the highest levels, thought to have formed at about 650 Ka, to the lowest, formed during the late Pleistocene. This descending sequence indicates progressive drying of pluvial periods, possibly caused by uplift of the Sierra Nevada and other western ranges relative to the western Great Basin. These effects, however, cannot account for the extremely high lake levels during the early-middle Pleistocene; rather, these high levels were probably caused by a combination of increased effective moisture and changes in the size of the Lake Lahontan drainage basin.

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## Introduction

Pluvial lakes in the western Great Basin have been the focus of many classic studies on paleoclimate and on biogeographic distributions of aquatic species, such as fish and snails. Until recently, these studies have focused on sedimentary records of the late Pleistocene and on the distributions of modern species (especially fish), because few pre-late Pleistocene deposits of

pluvial lakes were known and because fossil localities were scarce and commonly not well dated. In their seminal work, Hubbs and Miller (1948) argued for relatively rapid evolution of fish in now-isolated drainage basins on the assumption that, in most cases, the last aquatic connections between the fish-bearing basins were during the last pluvial period, now known to have ended about 12 thousand years ago (Ka). They recognized that in some cases modern sills between basins were far too high to have been exceeded by late Pleistocene lake levels; they called upon transfers by interdivide stream diversions or "pre-pluvial" connections to explain these fish distributions. As more fossil localities were identified and dated, research in the last 20 years has shown that many modern species of fish and springsnails are very similar to ancestral species that were widely distributed in the western Great Basin and areas to the north and south during the Pliocene (Miller and Smith, 1981; Taylor and Smith, 1981; Taylor, 1985; Minckley et al., 1986; Gobalet and Negrini, 1992; papers in this volume). As a result, less credence has been placed in rapid evolution, and modern aquatic-species distributions are more commonly attributed to inheritance from widespread Tertiary populations followed by extinctions and intermittent population-mixing caused by wet-dry climatic cycles and tectonic disruptions during the Pleistocene.

The possibility that modern species-distributions could be produced in part by aquatic migration routes older than late Pleistocene in age but younger than Tertiary in age has been given little consideration in biogeographic studies for the very good reason that such intermediate-age migration routes were largely unknown. This paper documents connections among several large lakes in the western Great Basin during part of the early or middle Pleistocene but that probably have been severed for the past one-half million years or more. Arguments for the evolution of modern species from widely distributed ancestral ones that suggested rapid evolutionary changes took place during the last few thousand years (e.g., Hubbs and Miller, 1948) have been challenged recently (Smith et al., 2002) as being not representative of the much slower rates observed in the fossil record during the past several million years. We suggest that if the observed divergence between some species can be averaged over a half a million years rather than over a few thousand, the apparent discrepancy in evolutionary rates may be greatly reduced. This new information at least provides alternative hypotheses about rates of evolution from independent evidence, as urged by Smith et al. (2002). In some cases, these older Pleistocene lakes may require revision of previous interpretations about ages and relations among fossil fish (e.g., Miller and Smith, 1981) that were based on incorrect age assignments.

In addition to far-reaching implications for biogeographic studies, the new lacustrine records hold significance for studies of paleoclimate, tectonics, and drainage evolution in the western Great Basin. The existence of enormously expanded lakes at about 650 Ka and earlier imply that much wetter conditions prevailed at that time than are indicated in global climate records, such as oxygen-isotope data from marine cores; however, sudden and dramatic integrations of previously discon-

nected basins with the Lahontan Basin may help to account for the large size of Lake Lahontan in the early-middle Pleistocene. Progressively shrinking lake highstands from the middle to late Pleistocene indicate different regional climatic conditions. Some Pliocene and younger basins were probably isolated by tectonic processes, such as compressional folding and extensional faulting along the Walker Lane tectonic belt (Stewart, 1988).

This paper focuses on pluvial lakes in the Lahontan Basin and the basins of Columbus Salt Marsh and Fish Lake Valley, where most of the field work in the western Great Basin has been concentrated. Detailed descriptions of the stratigraphy, chronology, geomorphology, and geology of pre-late Pleistocene lacustrine deposits in the Lahontan Basin are presented first, followed by a correlation of the deposits from sampled localities. Next, data from reconnaissance field work for this study and from previously published studies are discussed briefly for Lake Russell (Mono Basin) in western Nevada and for lakes in central Nevada, including those in the basins of Kobeh (Lake Jonathan)–Diamond, Long (Lake Hubbs), Newark, and Pine Valleys. These lakes are described in chronologic order, beginning with Pliocene localities. A discussion of the ages of the pre-late Pleistocene lakes in the study area is followed by an examination of the possible causes of these very large lakes. The paper concludes by discussing the implications of very high lake stands and prior connections among drainage basins on the migration of aquatic species.

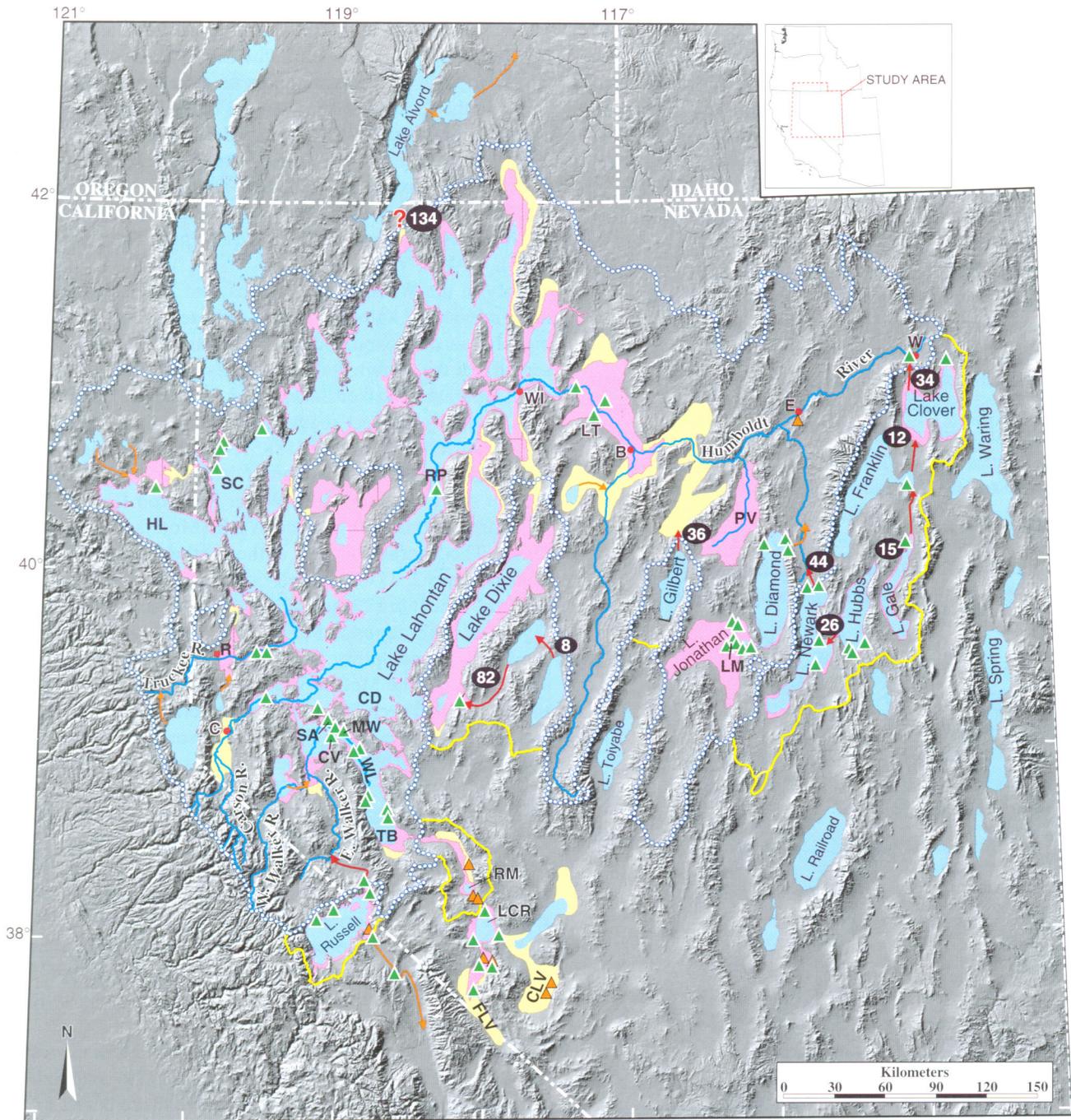
#### PREVIOUS WORK

During its well-studied late-middle (Eetza) and late Pleistocene (Sehoo) highstands, Lake Lahontan reached a maximum altitude of about 1330 m and extended more than 350 km, from the Nevada–Oregon border to beyond the southern end of Walker Lake (Figure 1; Russell, 1885; Benson et al., 1990; Morrison, 1991). Many smaller, isolated lakes also occupied other basins in the western Great Basin (Mifflin and Wheat, 1979), but their late Pleistocene highstands are generally not well dated, and little information has been available on older pluvial lakes and their high shorelines.

Previous workers have observed that the Eetza (~180–130 Ka, but possibly in part as old as 300 Ka; Morrison, 1991) and Sehoo (~35–12 Ka; Benson et al., 1990) shorelines in un-

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FIGURE 1 (opposite).—Regional map showing pluvial lakes of northern Nevada and vicinity, late Pleistocene shorelines, and areas of maximum middle Pleistocene (where known) and late Pleistocene lakes. See Table 1 for shoreline altitudes. Triangles show study sites (data for selected sites is in Table 1); arrows on drainages show possible links between basins during highest lake stands. Localities: CD = Carson Desert, CLV = Clayton Valley, CV = Campbell Valley, FLV = Fish Lake Valley, HL = Honey Lake, LCR = Lake Columbus-Rennie, LM = Lone Mountain, LT = Lone Tree Hill, MW = McGee Wash, PV = Pine Valley, RM = Rhodes Salt Marsh, RP = Rye Patch Dam, SA = Sunshine Amphitheater, SC = Smoke Creek Desert, TB = Thorne Bar, WL = Walker Lake. Towns: B = Battle Mountain, C = Carson City, E = Elko, R = Reno, W = Wells, WI = Winnemucca.



faulted positions throughout the Lahontan Basin lie at about  $1330 \pm 12$  m (Mifflin and Wheat, 1979; Benson, 1978). Isostatic rebound has caused shoreline altitudes to range from about 1318 m at the northeastern margin of the lake to as much as 1341 m in the Carson Desert (Adams, 1996, 1997). The highest vertical faulting rates of late Pleistocene shorelines are along the Wassuk fault, which bounds the west side of the Walker Lake subbasin (Figures 1, 2). Demsey (1987) estimated a Holocene slip rate of 0.4–0.5 mm/yr and total offset of 6–7 m of the Seho shoreline along this fault.

Morrison (1991) summarized the previously known ages and altitudes of early-middle and early Pleistocene nearshore and deltaic deposits of Lake Lahontan. Four sites were in outcrops below the Seho shoreline where incision exposed older deposits buried by Seho- and Eetza-aged sediment. The fifth site, Thorne Bar, is described below. The pre-Eetza lake cycles identified by Morrison (1991) are the Rye Patch Alloformation, from about 700 to 600 Ka, and two sets of unnamed deposits containing and underlying the Glass Mountain tephra, which were erupted about one million years ago (Ma) (only found in the Walker Lake subbasin). He believed that the 0.76 My old Bishop ash bed was deposited during a long period of alluvial

and eolian sedimentation (the Lovelock Alloformation) during which no deep lakes existed in the Lahontan Basin; however, the Bishop ash bed is contained within lacustrine deposits in basins to the south, including pluvial Lakes Rennie (Fish Lake Valley; Reheis et al., 1993), Owens (Smith et al., 1997), Tecopa (Sarna-Wojcicki et al., 1987), and Manley (Death Valley; Knott et al., 1996). Also, an ash bed with Bishop-like chemical composition was identified in beach gravel exposed in a fault scarp below the Seho shoreline south of Schurz, Nevada (Davis, 1978).

Only in the Walker Lake subbasin of Lake Lahontan are there previously known outcrops of beach gravel at altitudes higher than the Seho and Eetza shorelines. W.J. McGee observed that the eastern end of the “crest of the gravel embankment separating Walker Lake Valley from the ... Walker River ... is now fully 200 feet above its original position” (that is, the Seho shoreline) (Russell, 1885:142, pl. 28). This locality, which apparently had not been revisited until the time of the present study, is southeast of Weber Reservoir (Figure 2) and is informally named McGee Wash (Morrison and Davis, 1984). The Thorne Bar site, at the southeast edge of Walker Lake (Figures 2, 3) was first reported by King (1978) and Mifflin and Wheat (1979) to have pre-Eetza “shore gravel with layers of lake-deposited carbonate, preserved in a much-eroded V-bar complex ... up to 1443 m altitude” (Morrison, 1991:296). At the McGee Wash site, Russell (1885) thought the gravels had been folded into an anticline; mapping for this study (see Figure 7) and that of Morrison and Davis (1984) confirms the presence of numerous faults and tilted strata. The beach ridge at Thorne Bar has been attributed either to faulting (King, 1978:67–68) or to northward tilting of the entire Lahontan Basin (Mifflin and Wheat, 1979; Mifflin, 1984; Morrison, 1991). Detailed leveling surveys by Demsey (1987), however, revealed no evidence of Quaternary faults or deformation either at Thorne Bar or northward along the Gillis Range, in contrast to several localities of super-elevated beach gravel along the footwall block of the Wassuk Range fault (King, 1978; R. Bucknam, U.S. Geological Survey, in litt. to M.C.R., 1996).

Little work has been done on other pluvial lakes in western Nevada (Figure 1). Mifflin and Wheat (1979) mapped late Pleistocene shorelines for all of the pluvial lake basins of Nevada. These authors also briefly noted higher, older shoreline features of Lakes Diamond, Newark, and Hubbs; Mifflin (1984) thought that these features supported his hypothesis of the northward tilting of northwestern Nevada. Tackman (1993) obtained ages on the late Pleistocene shorelines of Lake Diamond. He also located many pre-late Pleistocene shorelines and discussed Lake Diamond's history as controlled by overflow from Kobeh Valley (Lake Jonathan) and the incision of sills. Davis (1981) investigated Tertiary lacustrine deposits in Clayton Valley. Gilbert et al. (1968) mapped Pliocene lacustrine deposits interbedded with basalt and rhyolite flows on the

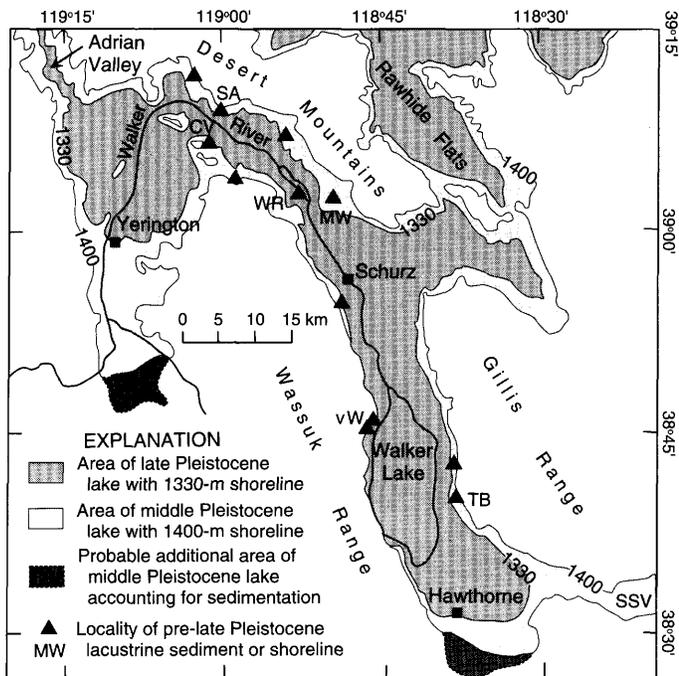
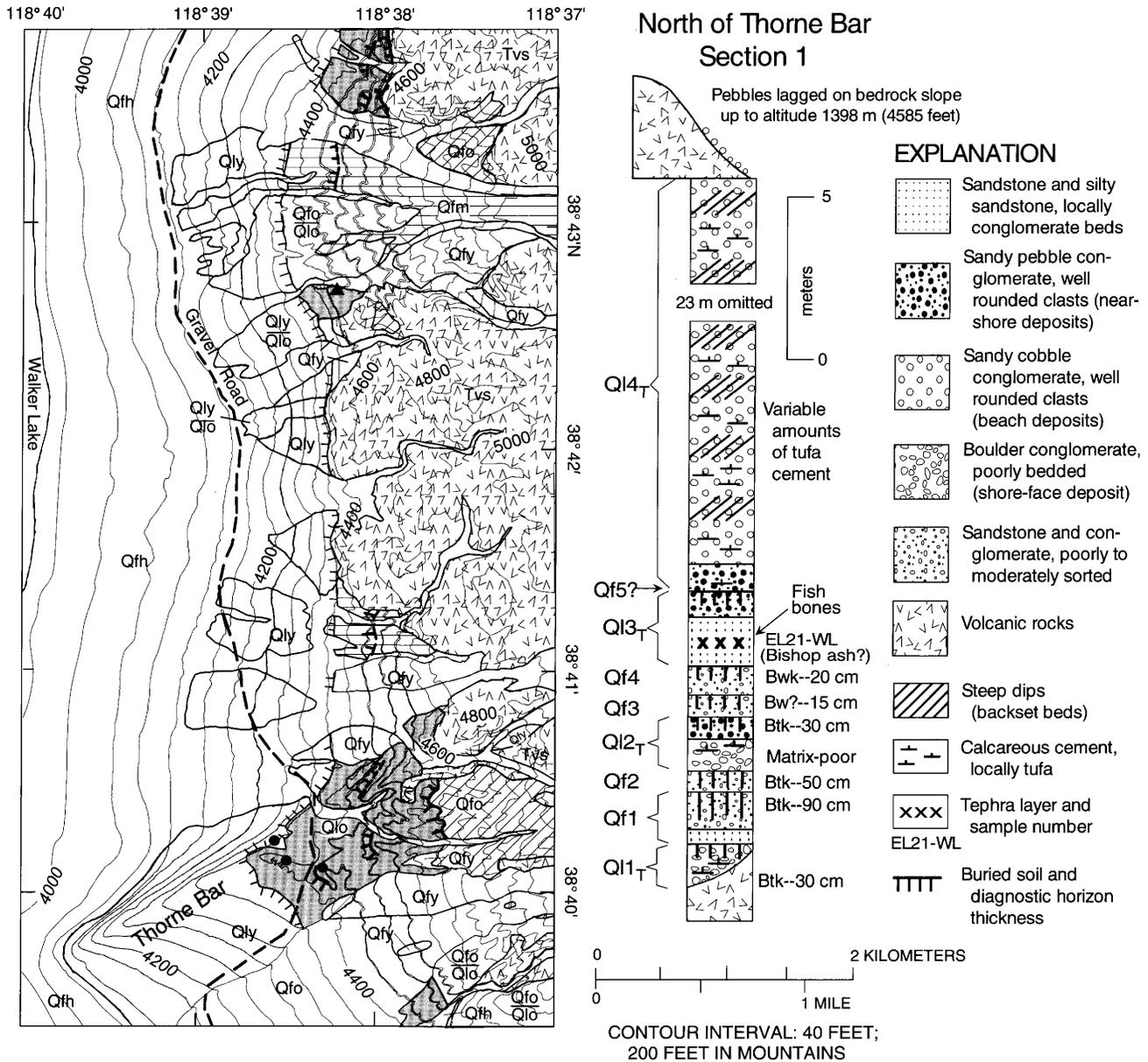


FIGURE 2.—Map of Walker Lake basin and southernmost Carson Desert (Rawhide Flats) showing study sites and lake areas. Area of lake at 1400 m is drawn using modern topography, acknowledging that this is only an approximation of the topography in the middle Pleistocene because of subsequent isostatic rebound, faulting, erosion, and sedimentation. From north to south, letters indicate the following: SA = Sunshine Amphitheater, CV = Campbell Valley, WR = Weber Reservoir, MW = McGee Wash, TW = Twentymile Beach, TB = Thorne Bar, SSV = Soda Springs Valley.



**MAP EXPLANATION**

Qfh	Fan deposits (Holocene); includes some Holocene lake deposits	Qlo	Nearshore deposits and beach gravel of middle to early Pleistocene lakes (units Q11 <sub>T</sub> to Q16 <sub>T</sub> )
Qfy	Fan deposits (late Pleistocene)	Tvs	Volcanic and sedimentary rocks (Pliocene and Miocene)
Qly	Deposits of late Pleistocene (Sehoo) lake (unit Q17 <sub>T</sub> )	TTTT	Late Pleistocene shoreline
Qlm	Fan deposits (middle Pleistocene)	- - - -	Middle Pleistocene shorelines; dashed where inferred
Qfo	Fan deposits (middle and early? Pleistocene)	▲	Tephra locality and measured section
		●	Soil pit (Adams and Wesnousky, 1999)

FIGURE 3.—Geologic map of area around Thorne Bar (Figure 2, Table 1) and measured section north of Thorne Bar (triangle in northern map area).

TABLE 1.—Information for representative sites (see Figure 1; within each basin, sites are in order beginning in the south and proceeding clockwise or northward).

Site	General location	Latitude (N)	Longitude (W)	Altitude range of nearshore features (m)	Type of deposit or shoreline feature
Lake Lahontan (late Pleistocene shoreline, 1330 ± 12 m)					
US-95 roadcut	Rhodes Salt Marsh	38°14.7'	118°03.3'	1402–1423	Nearshore and sublacustrine deltaic deposits
Thorne Bar area	Southeastern Walker Lake valley	38°39'–44'	118°37.3'–39'	1360–1400, 1350–1365, 1330–1350	Tufa-cemented beach gravel and sand; 3 shoreline levels, 6 ages of deposits
20-Mile Beach	West-central Walker Lake valley	38°46.6' 38°45.1'	118°45.4' 118°46.5'	Depends on footwall location; <1475	Tufa-cemented beach gravel and sand; 2 shoreline levels, 2–4 ages of deposits
McGee Wash	Northern Walker Lake valley	39°01'–03.5'	118°47.5'–50.7'	1420–1433, 1393–1402, 1347–1365	Lake mud, silt, sand, and gravel; 3 shoreline levels, 5 ages of deposits
Campbell Valley	Northern Walker Lake valley	39°04–07'	118°59'–119°01.2'	1378–1390, 1356–1378	Lake mud, silt, sand, and gravel; shoreline angle; 2 shoreline levels, 3 ages of deposits
Sunshine Amphitheater	Northern Walker Lake valley	39°08.6'–09.4'	118°59.5'–119°00.7'	1341–1426	Lake mud, silt, sand, and gravel; 3 shoreline levels, 5 ages of deposits
Clifton site	Carson River canyon	39°18.1'–18.4'	119°27.4'–28.0'	1333–1380	Beach or fluvial gravel lag on bedrock
I-80 roadcut (?)	Truckee River canyon	39°30.8'	119°38.7'	1360	Deltaic(?) and fluvial deposits
Secret Valley cutoff	North of Honey Lake valley	40°25.0'	120°16.9'	1370–1372	Large botryoidal tufa heads, locally attached to well-rounded clasts; scattered patches of well-rounded pebbles and cobbles
Burro Mountain	Smoke Creek Desert	40°32.5'	119°50.6'–51.4'	1396–1402, 1373	Beach gravel lag and tufa; 2 different levels
Freds Field	Smoke Creek Desert	40°44.7'–45'	119°31.4'–32.2'	1378–1400, 1350–1370	Rounded, water-polished gravel; 2 different levels
Iron Point	Humboldt River	40°56.6'–59.5'	117°17.2'–19.5'	1353–1368	Beach or fluvial gravel lag
Treaty Hill area	Humboldt River	40°50.3'–58.0'	117°04'–12'	1344–1362, 1390–1414	Sand and gravel in extensive delta plain to north; upper level is berm on Treaty Hill
Lone Tree Hill	Humboldt River	40°49.4'–50.5'	117°12.0'–12.7'	1326–1414	Lake mud, silt, sand, and gravel; 1 shoreline level, 3 or 4 ages of deposits
Drumm Summit	Fairview Valley	39°18'–18.5'	118°07.9'	1355–1384	Lake mud and silt (Pliocene?) overlain by beach(?) gravel of uncertain age
Lake Columbus-Rennie (late Pleistocene shoreline, 1402 m)					
Sinter mound	Fish Lake Valley	37°51.1'	118°00'	1442–1460	Sinter-cemented silt and sand; Bishop ash (Reheis et al., 1993)
Borrow pit	Southern Columbus Salt Marsh	38°00'–00.9'	118°01.2'–02.2'	1442–1452, 1426–1433, 1417	Lake silt, sand, and gravel; shoreline angle; 3 shoreline levels, 4 ages of deposits
Rock Hill	Northern Columbus Salt Marsh	38°08.4'–09'	118°56.9–57.8'	1390–1417	Beach sand and gravel in moderately preserved berm; pit exposes buried lacustrine deposits containing Bishop ash
Coaldale Junction	Southeastern Columbus Salt Marsh	38°00.7'–01.5'	117°52.6'–53.8'	1422–1430	Beach sand and gravel in eroded berms
Lake Russell (Mono Basin) (late Pleistocene shoreline, 2155 m)					
Southern outlet area	Eastern Mono Basin	38°00'–04'	118°44'–47.5'	2207–2277	Lake silt, sand, gravel, and beach rock; at least 2 ages of deposits, oldest is late Pliocene; upper limit defined by beach gravel lagged on bedrock
Rancheria Gulch	Northern Mono Basin	38°05.5'–06'	119°05'–06'	<2268, 2195–2225	Beach gravel; 2 shoreline levels, lower marked by berm
Kirkwood Spring	Northern Mono Basin	38°08.7'–09'	118°58'–59'	2205–2252	Scattered beach cobbles lagged on bedrock
Andesite sill	Northeastern Mono Basin	38°18.5'	118°46.7'	2237	Bedrock sill bearing scattered rounded clasts
Lake Jonathan (Kobeh Valley) (no late Pleistocene lake)					
US-50 site	Eastern Kobeh Valley	39°34.1'–35.3'	116°11.7'–13.3'	1871–1920	Lake silt, sand, and gravel; 2 ages of deposits
Slough Creek	Southwestern side Lone Mountain	39°33.5'–34'	116°16.6'–17.4'	1856–1890	Lake clay, silt, sand, and gravel; 3 ages of deposits
Borrow pit on county road	Northeastern Kobeh Valley	39°42.0'	116°15.2'	1914–1925	Lake sand and gravel; 3 ages of deposits separated by paleosols; well-preserved berms in vicinity

TABLE 1.—Continued.

Site	General location	Latitude (N)	Longitude (W)	Altitude range of nearshore features (m)	Type of deposit or shoreline feature
Lake Newark (late Pleistocene shoreline, 1847 m)					
Pancake Summit	Southern Newark Valley	39°27'–27.4'	115°39.6'–40.6'	1856–1859, 1850–1855	Beach sand and gravel; 2 shoreline levels, more eroded upward
West of Beck Pass	Eastern Newark Valley	39°36'	115°39.0'	1850–1855	Beach sand and gravel in moderately preserved berm
Stage Road	Northern Newark Valley	39°52.7'–53.5'	115°39.2'–40.4'	1887–1890, 1868–1875, 1856–1859, 1850–1855	Beach gravel in berms and as lag on bedrock; 3 or 4 shoreline levels (possibly one repeated by fault), more eroded upward
Lake Hubbs (Long Valley) (late Pleistocene shoreline, 1920 m)					
Maple Syrup well	Southern Long Valley	39°32.2'–34'	115°25'–28'	1935–1940, 1920–1927, 1907–1912	Beach sand and gravel; 3 different shoreline levels, more eroded upward
Long Valley Canyon	Eastern Long Valley	39°35.3'	115°20.8'	1930–1940?, 1920–1927	Beach gravel in moderately preserved berm; lag gravel above
Lake Gale (late Pleistocene shoreline, 1915 m—revised from 1905 m as stated by Mifflin and Wheat, 1979)					
Elko–White Pine County line	Northeastern Butte Valley	40°03.5'–07.5'	115°01'–04'	1917–1922	Beach sand and gravel in subdued berms above well-defined late Pleistocene shoreline features
Lake Clover (late Pleistocene shoreline, 1730 m)					
Independence interchange	Independence Valley	41°05.5'–06.3'	114°42.2'–43'	1754–1763	Beach(?) gravel exposed in I-80 borrow pits
Wells	Humboldt River headwaters	41°06.4'–07.4'	114°58.5'–59.1'	1737–1750	North-dipping delta foreset beds of gravel, sand, and silt; locally tufa-cemented; locally overlain by marl beds
Pliocene localities					
Angel Island	Eastern Clayton Valley	37°40'–44'	117°32'–35'	1340–1440	Indurated lake clay, silt, sand, and gravel; at least 2 ages of deposits, many tephra layers; Pliocene (Davis, 1981)
Emigrant Pass section	Northeastern Fish Lake Valley	117°55'	37°53.4'	1475–1560	Indurated lake clay, silt, and sand; at least 2 ages of deposits, many tephra layers; Pliocene (Reheis et al., 1993)
The Gap	Columbus–Fish Lake sill	37°54.5'–57'	117°57'–59'	1432–1463	Indurated lake clay, silt, and sand; at least 2 ages of deposits, many tephra layers; Pliocene
Redlich Summit	Rhodes–Columbus divide area	38°12.5'–14.5'	117°59'–118°01.5'	1450–1585	Indurated lake clay, silt, sand, and gravel; at least 2 ages of deposits, many tephra layers; Miocene to late Pliocene

east side of Mono Lake. Reheis et al. (1993) documented several Pliocene to middle Pleistocene cycles of pluvial Lake Rennie in Fish Lake Valley (Figure 1) and proposed that Lake Rennie merged with Lake Columbus to the north about 760 Ka at a shoreline altitude of about 1460 m.

#### METHODS

The vastness of the Lahontan Basin and the large number of other pluvial lakes in Nevada precluded a systematic search for shorelines older and higher than those of late Pleistocene age. This search relied heavily upon (1) extrapolation from known localities in the Walker Lake subbasin and in Newark, Long, and Diamond Valleys (Figure 1), (2) Mifflin's recollections of

possible shoreline localities from field work in the 1970s, and (3) observation from roads. Geologic maps were searched for outcrops of late Tertiary or Quaternary fine-grained deposits; several sites in the northern Walker Lake subbasin, for example, had been mapped as Miocene to Pliocene sedimentary rocks (Greene et al., 1991) but in fact are Quaternary lacustrine deposits. Potential sites were examined on 1:24,000-scale topographic maps and (or) aerial photographs for relatively flat benches above late Pleistocene shorelines. Dozens of potential sites were checked in the field, but only those with evidence of lacustrine deposition are listed in Table 1.

The altitudes and ages of shorelines (Table 1) were estimated from shoreline features and from sedimentologic evidence. Classic shoreline morphologies, such as wave-cut cliffs and

beach berms, become increasingly difficult to discern with age and are rarely preserved after half a million years or more of erosion. Thus, the highest altitude of beach-gravel beds or lag on bedrock slopes was taken as a minimum shoreline altitude. Where beach morphology was discernible, the preservation of berm features and the degree of development of relict soils permitted assignment of relative ages. Fine-grained beds and even some gravels locally contained tephra layers; these were identified by chemical correlation with tephra of known age by the United States Geological Survey (USGS) Tephrochronology Laboratory. Ages of some units also were constrained by magnetostratigraphy and by vertebrate biostratigraphy.

Glass shards from tephra layers found within lacustrine sequences during mapping were analyzed by electron microprobe for major-oxide composition (Table 2) using methods described by Sarna-Wojcicki et al. (1984) and Sarna-Wojcicki (2000). Sample compositions were compared with compositions in a data base of previously analyzed tephra layers using statistical programs (Table 3). Correlations were based on similarity in chemical composition, petrographic characteristics (such as shard morphology, phenocryst mineralogy), and stratigraphic data. Values for glass compositions in Tables 2 and 3 were normalized to 100 percent to correct for the variable amounts of hydration of the volcanic glass, as reflected by the original totals. In addition to hydration, some postdepositional alkali exchange had occurred in many of the samples. Variability in sodium and potassium contents was particularly apparent for the older tephra layers.

Samples used for paleomagnetic directions were collected as large (typically 500–1000 cm<sup>3</sup>) blocks of sediment that were oriented in the outcrop using a magnetic compass and a level to mark the horizontal plane. Many samples were sufficiently indurated to carve from the outcrop; some friable samples were hardened using sodium silicate before extraction. In the laboratory, smaller samples were shaped from block samples to fit into plastic cubes (3.2 cm<sup>3</sup> volume). We estimate that the final orientation of each sample was within  $\pm 10^\circ$  of the magnetic field declination and within  $10^\circ$  of the original horizontal attitude. Such orientation is adequate for polarity determinations at these sites. We corrected for tectonic tilting when bedding dips exceeded  $5^\circ$ . The natural remanent magnetization of the oriented samples was measured using a 90 Hz spinner magnetometer having a sensitivity better than  $10^{-5}$  amperes per meter (A/m). Samples were demagnetized by alternating-field (AF) demagnetization with peak fields of 5, 10, 20, 40, 60, and 80 milliteslas (mT). We evaluated the paleomagnetic reliability of each sample from an examination of orthogonal demagnetization diagrams that show the change in remanent direction and magnitude in response to each demagnetization step (Zijderveld, 1967). Samples that showed unstable behavior (lack of systematic decay in magnitude and direction toward the origin of the diagram over most of the demagnetization range) were not considered further and are represented by a question mark

on the diagrams of stratigraphic sections. Polarity was determined for stably magnetized samples: normal, when the remanent vector was northward (clockwise between  $60^\circ$  and  $300^\circ$ ) with a moderate to steep, positive inclination (between  $20^\circ$  and  $80^\circ$ ); reversed, when the remanent vector was southward (clockwise between  $120^\circ$  and  $240^\circ$ ) with a moderate to steep, negative inclination. The expected inclination for the latitude of  $39^\circ\text{N}$  through the study region is about  $58^\circ$ . Several samples exhibited magnetic behavior that reflected the removal of a normal polarity overprint in response to low AF inductions to isolate a reversed component of magnetization. Although inclinations in these samples may not stabilize in moderately steep angles, the magnetization clearly is reversed. Such samples are listed as having a reversed component (R comp; see Figure 11C for sample P10). Samples that showed stable magnetization are listed as questionably normal (“N?”) or questionably reversed (“R?”) if they had moderate to steep positive or negative inclination, respectively, with a declination beyond ranges for a clearly defined polarity.

#### ACKNOWLEDGMENTS

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### Evidence for Old Pluvial Lakes in the Western Great Basin

We have adopted several conventions for ordering the information presented and for naming the lacustrine units so as to accommodate the complex geographic, stratigraphic, and chronological relationships among the many sites discussed in this paper. Because most of the work to date has focused upon the Lahontan Basin and upon the Walker Lake subbasin in particular, we begin by describing these primary study sites from south to north, followed by evidence from supporting localities, also from south to north. Other pluvial-lake records in western and central Nevada are described in chronological order by lake basin, working roughly from southwest to northeast. At each study site, the lacustrine units were numbered in order from oldest to youngest, followed by a subscript letter designating the site: for example, the youngest lake unit at Thorne Bar is Q17<sub>T</sub>. As a result of differential deposition and preservation, this convention can produce same-numbered units of different ages at different study sites; however, it avoids bias in the nomenclature and in the correlation of some lake units that are undated or whose ages are only relative. Based upon current evidence and best judgment, we then correlate the units from site to site and assign names to deposits of similar age; names were chosen for localities where a unit is well exposed. For example, deposits associated with the 1400 m highstand of Lake Lahontan were named "lake deposits of McGee," for the well-preserved arcuate beach ridge above McGee Wash that was deposited during this highstand.

#### THE LAHONTAN BASIN

The Lahontan Basin consists of a sprawling complex of subbasins (Figure 1), many of which have independent hydrographic histories (Davis, 1982; Reheis and Morrison, 1997) controlled not only by climate but also by interbasin river diversions and changes in threshold altitudes. Of the four principal rivers—the Truckee, Carson, and Walker, draining the Sierra Nevada, and the Humboldt, draining northern and eastern Nevada—all but the Carson River have been diverted among different subbasins, some more than once. Thus, lake levels recorded in some subbasins may not apply to other subbasins, especially at moderate to low water levels.

**EVIDENCE FROM THE WALKER LAKE SUBBASIN.**—The Walker Lake subbasin (Figures 1, 2) contains much of the stratigraphic evidence of early and middle Pleistocene lakes with high shorelines in the Lahontan Basin. This evidence must be interpreted with caution because the area is tectonically active. The Walker Lake subbasin is bounded on the west by the Wassuk Range and the active Wassuk normal fault and is bounded on the east by the Gillis Range. At the north end of the Gillis Range, faults of the strike-slip Walker Lane belt (Stewart, 1988) intersect the basin. The Thorne Bar area lies in a tectonically quiescent area of the basin (Demsey, 1987), but other sites discussed below have been affected by faulting. The

Walker River, the only major source of water, arises in the Sierra Nevada and presently feeds Walker Lake. At times in the past, however, the Walker River flowed north into the Carson Desert via Adrian Valley (Morrison and Davis, 1984; Bradbury et al., 1989; King, 1993).

**Thorne Bar Area:** The beach ridge, or bar, at Thorne Bar is a large, V-shaped barrier complex of shore gravel built at the mouth of a large canyon that drains the Gillis Range (Figures 2, 3). The part of this complex above the Seho shoreline was previously described as pre-Seho lacustrine gravel that was elevated by northward tilting of the Lahontan Basin (King, 1978; Mifflin and Wheat, 1979; Morrison, 1991). Detailed leveling studies by Demsey (1987) and interpretation (this study) of aerial photographs revealed no evidence of Quaternary deformation on this side of the Walker Lake subbasin. We interpret the altitudes of the bar and its morphologic subdivisions to represent essentially undeformed shorelines.

The bar consists mainly of pebble- to cobble-sized gravel that is locally tufa-cemented; the bedding ranges from horizontal to angled at 25° or more. The bar can be divided into four morphologic units (Figures 3, 4A). The lowest and youngest unit is the group of historic shorelines below 1250 m in altitude, formed during the last 100 years; this unit is not separately numbered. The next higher group of shorelines is distinguished by sharp, well-preserved barriers (unit Q17<sub>T</sub>) that are marked at the top by the Seho highstand shoreline at an altitude of about 1330 m (~4360 ft; Figure 3). A small loop bar bears a soil profile with a thin vesicular A horizon and a slightly oxidized Bw horizon with a few thin clay films and little pedogenic CaCO<sub>3</sub> (Table 3, profile WL-5c of Adams and Wesnousky, 1999). This degree of development is typical of Seho-aged or younger soils (Chadwick and Davis, 1990).

Between 1330 m and about 1370 m (4360–4500 ft), the bar complex consists of two nested, eroded V-shaped barriers; the lower (unit Q16<sub>T</sub>, marked by vehicles in Figure 4A) is better preserved than the upper (unit Q15<sub>T</sub>). Soil pits on the eroded surfaces of these barriers show increasing thicknesses of Av and Bw horizons and increasing cementation by pedogenic CaCO<sub>3</sub> and silica of subsurface horizons relative to barrier altitude and to the Seho-aged soil, although clay and silt content remain low (Adams and Wesnousky, 1999). These soil features indicate that the barriers increase in age upward and are older than the Seho highstand (Chadwick and Davis, 1990), but the soils are not adequately preserved for a more accurate age assessment. Between 1370 m and 1402 m (4500–4600 ft) the complex has no preserved morphology, but deep arroyos have exposed well-bedded, cemented shore gravel of unit Q14<sub>T</sub>, and beach pebbles locally occur as lag on basalt outcrops.

In summary, the degree of morphologic preservation and the degree of soil development in three reconnaissance soil pits (Adams and Wesnousky, 1999) indicate the presence of at least four lacustrine units above the historic limit at 1250 m: the Seho-aged bar, unit Q17<sub>T</sub>, extending upward from the historic limit to

TABLE 2.—Results of electron-microprobe analysis of volcanic glass shards separated from tephra layers. Shards were analyzed using the JEOL8900\* instrument, except for sample EL-2-M, which was analyzed using the SEMQ\* instrument. n = number of shards analyzed for each sample;  $\pm s$  = standard deviation calculated using individual analyses of shards, except for EL-2-RM, for which the standard deviations were calculated from variations in peak intensity values. Total (O) = original total on analysis; Total (R) = total recalculated to a 100% fluid-free basis. Analyses were performed by C.E. Meyer, U.S. Geological Survey, Menlo Park, California, during 1993–1998.

Sample no.	Study site	Latitude (N)	Longitude (W)	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (O)	Total (R)
EL-2-RM n=18; $\pm s$	South of Rhodes Salt Marsh	38°14.7'	118°03.3'	77.54	12.72	0.55	0.03	0.06	0.44	0.06	3.94	4.65	95.43	99.99
EL-3-FL n=18; $\pm s$	The Gap, Fish Lake Valley	37°56.1'	117°58.7'	66.64	12.88	0.62	0.04	0.03	0.02	0.04	0.11	0.07	94.64	100.00
EL-4-FL n=16; $\pm s$	The Gap, Fish Lake Valley	37°55.6'	117°58.6'	66.21	13.14	0.56	0.04	0.07	0.59	0.06	3.50	5.83	93.97	100.00
EL-5-WD n=15; $\pm s$	McGee Wash, Walker Lake basin (WD = Weber Dam)	39°02.6'	118°50.2'	71.98	14.97	2.31	0.25	0.04	1.49	0.20	5.29	3.47	93.17	100.00
EL-15-CA n=18; $\pm s$	Campbell Valley, Walker Lake basin	39°05.7'	119°00.6'	66.55	12.83	0.76	0.03	0.05	0.44	0.06	4.14	5.14	94.09	100.00
EL-19-WD n=10; $\pm s$	McGee Wash, Walker Lake basin	39°03.3'	118°48.0'	75.88	12.23	2.02	0.09	0.03	0.70	0.25	3.36	5.42	92.54	99.98
EL-20-WD n=19; $\pm s$	McGee Wash, Walker Lake basin	39°02.5'	118°49.9'	66.78	12.88	0.78	0.03	0.04	0.44	0.06	4.31	4.68	92.67	100.00
EL-21-WL n=4; $\pm s$	North of Thorne Bar, Walker Lake basin	38°42.7'	118°38.3'	66.52	13.08	0.73	0.03	0.03	0.42	0.06	4.44	4.69	94.88	100.00
EL-24-M n=20; $\pm s$	East of Mina, Soda Springs Valley	38°25.5'	118°04.2'	75.58	12.56	1.77	0.06	0.03	0.59	0.17	3.17	6.09	93.05	100.02
EL-26-RM n=18; $\pm s$	South of Rhodes Salt Marsh	38°14.7'	118°03.3'	66.29	12.98	0.56	0.03	0.11	0.32	0.06	4.82	4.84	93.40	100.01
EL-29-RM n=16; $\pm s$	Redlich Summit	38°13.9'	117°59.7'	66.61	12.81	0.64	0.05	0.02	0.03	0.09	3.68	5.60	93.27	100.01
EL-34-RM n=18; $\pm s$	Redlich Summit	38°13.5'	118°01.1'	73.84	13.52	1.24	0.09	0.10	0.39	0.15	3.87	6.80	91.20	100.00
EL-35A-MS n=19; $\pm s$	Mud Spring Canyon, North of Mono Basin	38°21.5'	118°45.4'	77.37	12.59	0.63	0.05	0.05	0.53	0.06	2.25	6.37	89.49	99.90
EL-35B-MS n=19; $\pm s$	Mud Spring Canyon, North of Mono Basin	38°21.5'	118°45.4'	76.90	12.93	0.58	0.04	0.04	0.48	0.06	3.34	5.61	91.19	99.98
EL-36-MS n=7; $\pm s$	Mud Spring Canyon, North of Mono Basin	38°21.5'	118°45.4'	77.31	12.71	0.59	0.05	0.06	0.48	0.07	3.53	5.20	92.18	100.00
EL-42-CV #1 n=19; $\pm s$	Clayton Valley	37°42.9'	117°32.2'	66.88	13.08	0.68	0.05	0.03	0.01	0.01	0.22	0.36	94.77	100.01
EL-42-CV #2 n=3; $\pm s$	Clayton Valley	37°42.9'	117°32.2'	71.48	14.53	2.73	0.26	0.09	0.92	0.36	5.06	4.57	94.82	100.00
EL-43-CV n=17; $\pm s$	Clayton Valley	37°42.8'	117°32.2'	66.61	12.17	1.97	0.01	0.03	0.05	0.04	0.24	0.29	94.67	100.00
EL-44-FL n=18; $\pm s$	The Gap, Fish Lake Valley	37°56.1'	117°58.7'	66.63	13.04	0.58	0.03	0.12	0.32	0.07	3.43	5.77	95.73	99.99
EL-50-RM n=20; $\pm s$	Rhodes Salt Marsh	38°13.8'	117°59.4'	74.03	13.93	2.05	0.32	0.05	1.43	0.28	4.30	3.61	93.89	100.00
EL-53-ML #1 n=11; $\pm s$	Southeast corner of Mono Basin	38°02.7'	118°44.6'	77.27	12.69	0.57	0.04	0.06	0.45	0.08	3.63	5.22	94.73	100.01
				0.51	0.17	0.06	0.02	0.01	0.04	0.02	0.33	0.37		

TABLE 2.—Continued.

Sample no.	Study site	Latitude (N)	Longitude (W)	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (O)	Total (R)
EL-53-ML #2 n=5; ±s	Southeast corner of Mono Basin	38°02.7'	118°44.6'	76.86	12.60	0.58	0.04	0.07	0.43	0.09	2.47	6.85	94.25	99.99
EL-54A-ML n=17; ±s	Southeast corner of Mono Basin	38°02.7'	118°44.6'	0.56	0.15	0.20	0.01	0.02	0.02	0.03	0.25	0.26	94.81	100.02
EL-54B-ML n=6; ±s	Southeast corner of Mono Basin	38°02.7'	118°44.6'	0.66	0.17	0.08	0.02	0.03	0.08	0.03	0.21	0.31	94.10	100.01
EL-57-WD n=16; ±s	McGee Wash, Walker Lake basin	39°02.5'	118°50.0'	0.34	0.15	0.05	0.01	0.02	0.01	0.01	0.18	0.28	93.78	100.01
EL-58-WD #1 n=18; ±s	McGee Wash, Walker Lake basin	39°02.4'	118°50.0'	76.73	12.97	0.69	0.05	0.07	0.43	0.09	3.65	5.33	94.12	100.00
EL-58-WD #2 n=20; ±s	McGee Wash, Walker Lake basin	39°02.4'	118°50.0'	0.62	0.23	0.04	0.01	0.03	0.04	0.03	0.12	0.18	93.53	99.99
EL-59-FV #1 n=14; ±s	Drumm Summit, Fairview Valley	39°17.9'	118°07.9'	0.29	0.16	0.06	0.01	0.03	0.02	0.03	0.06	0.08	93.96	100.01
EL-59-FV #2 n=19; ±s	Drumm Summit, Fairview Valley	39°17.9'	118°07.9'	76.52	11.99	1.88	0.04	0.03	0.58	0.17	2.73	6.06	94.31	100.00
EL-60-TC n=14; ±s	I-80 roadcut, Truckee River canyon	39°30.8'	119°38.7'	0.32	0.12	0.10	0.01	0.02	0.03	0.04	0.10	0.21	91.91	100.01
EL-61-TC n=14; ±s	I-80 roadcut, Truckee River canyon	39°30.8'	119°38.7'	77.35	13.29	0.83	0.15	0.08	0.69	0.13	2.47	5.02	92.26	100.00
EL-66-FV n=20; ±s	Drumm Summit, Fairview Valley	39°33.8'	116°17.1'	0.39	0.12	0.07	0.02	0.03	0.04	0.03	0.24	0.16	93.53	100.01
EL-69-KV n=16; ±s	East side of Lone Mountain, Kobeh Valley	39°35.2'	116°12.5'	0.44	0.11	0.06	0.01	0.02	0.03	0.05	0.20	0.61	94.15	100.00
EL-72-KV #1 n=10; ±s	Southwest Lone Mountain, Kobeh Valley	39°33.8'	116°17.1'	76.28	12.22	1.86	0.04	0.02	0.60	0.18	2.94	5.87	94.99	99.99
EL-72-KV #2 n=4; ±s	Southwest Lone Mountain, Kobeh Valley	39°33.8'	116°17.1'	0.67	0.29	0.19	0.13	0.03	0.31	0.07	0.27	0.14	99.77	100.00
EL-76A-LT n=24; ±s	Roadcut section, Lone Tree Mine	40°49.7'	117°12.3'	0.13	0.15	0.18	0.09	0.04	0.24	0.11	0.22	0.06	95.00	99.99
EL-78-LT n=23; ±s	Roadcut section, Lone Tree Mine	40°49.7'	117°12.3'	77.18	12.97	0.69	0.03	0.05	0.49	0.07	3.59	4.92	94.38	99.99
EL-80-KV n=28; ±s	East side of Lone Mountain, Kobeh Valley	39°35.1'	116°12.6'	0.66	0.21	0.05	0.02	0.02	0.03	0.04	0.22	0.26	93.91	100.00
EL-81-KV n=37; ±s	Southwest Lone Mountain, Kobeh Valley	39°33.9'	116°17.2'	0.72	0.18	0.05	0.01	0.02	0.03	0.04	0.12	0.12	93.60	99.99
EL-92-LT n=7; ±s	Core hole, Lone Tree Mine	~40°49.6'	~117°12'	0.54	0.10	0.13	0.01	0.02	0.03	0.04	0.12	0.10	94.23	100.01
D77-2D† n=10-15; ±s	Drill hole cuttings Clayton Valley	~37°47'	~117°33'	0.54	0.16	0.13	0.01	0.02	0.04	0.02	0.48	0.21	94.50	100.00
29068501‡ n=17; ±s	Large pit, Columbus Salt Marsh	38°09.0'	117°56.9'	nd	nd	nd	nd	nd	nd	nd	nd	nd	95.18	99.99
AA-04/ n=15; ±s	US-50 site, Kobeh Valley	39°34.1'	116°11.7'	0.65	0.38	0.04	0.02	0.02	0.02	0.03	0.11	0.07	94.13	99.98

\* Use of trade names in this report does not represent endorsement by the U.S. Geological Survey.

† Sample collected and submitted by Davis (1981).

‡ Sample collected and submitted by P. Glancy and J. Whitney (U.S. Geological Survey) in 1985.

/ Sample analyzed by Davis (1987).

TABLE 3.—List of tephra layers analyzed in this study and their compositionally closest matches, based on electron-microprobe analysis of volcanic glass shards. All samples were from lacustrine deposits unless otherwise noted; localities are given in Table 2. Analyses and methods are given in Table 2. Closest matches are based on calculations of similarity coefficients using oxides of the elements Si, Al, Fe, Ca, Na, and K, except as noted below, and data not used in the calculations are shaded in gray. Closely matched samples that did not provide age constraints or stratigraphic context were omitted from the table.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer in roadcut south of Rhodes Salt Marsh (1). Closest matches are with the Teels Lake tephra sequence (2–4, 11), the tephra layers in lake sediments of the Mono Basin (7, 9; 2.3 Ma; R. Fleck, in litt. to A.S.-W., 1997), and the tephra layer at Willow Wash, Nevada (8; <2.57 Ma, >2.22 Ma; Sarna-Wojcicki et al., In review).												
1	EL-2-RM	77.54	12.72	0.55	0.03	0.06	0.44	0.06	3.94	4.65	99.99	1.0000
2	TLN-1	77.28	12.76	0.56	0.04	0.08	0.44	0.08	4.09	4.69	100.02	0.9884
3	TLN-3	77.20	12.87	0.54	0.04	0.09	0.43	0.09	4.03	4.70	99.99	0.9850
4	TLN-4	77.26	12.83	0.58	0.04	0.08	0.45	0.08	3.95	4.74	100.01	0.9821
7	EL-54A-ML	77.38	12.76	0.55	0.04	0.07	0.40	0.08	3.83	4.91	100.02	0.9705
8	FLV-36-WW	77.47	12.83	0.58	0.05	0.09	0.43	0.11	3.66	4.76	99.98	0.9703
9	EL-54B-ML	77.53	12.64	0.53	0.03	0.07	0.41	0.07	3.82	4.91	100.01	0.9676
11	TLN-2	77.06	12.96	0.58	0.05	0.09	0.42	0.09	4.22	4.54	100.01	0.9647
Tephra layer at The Gap (1). Closest matches are with the tuff of Taylor Canyon tephra layers and related units (2–6, 8–10; Sarna-Wojcicki et al., In review).												
1	EL-3-FL	76.66	12.88	0.62	0.04	0.08	0.33	0.07	4.13	5.19	100.00	1.0000
2	FLV-150-CS	77.26	12.71	0.61	0.03	0.09	0.34	0.05	3.96	4.96	100.01	0.9747
3	PC-C	76.76	13.14	0.60	0.03	0.08	0.32	0.07	3.90	5.10	100.00	0.9739
4	WAC-6	77.20	12.74	0.60	0.04	0.06	0.34	0.09	3.98	4.94	99.99	0.9727
5	CH88004	76.67	13.20	0.64	0.05	0.09	0.34	0.08	3.80	5.13	100.00	0.9706
6	FLV-151-CS	77.34	12.70	0.60	0.04	0.09	0.34	0.05	4.09	4.74	99.99	0.9699
8	TTC-6	77.20	12.93	0.58	0.05	0.09	0.33	0.09	4.08	4.64	99.99	0.9678
9	TTC-19 (2)	77.54	12.57	0.59	0.05	0.07	0.33	0.06	3.91	4.89	100.01	0.9675
10	DG-4	76.96	13.03	0.56	0.04	0.09	0.33	0.08	4.00	4.92	100.01	0.9674
Tephra layer at The Gap (1). Closest matches are with the tuff near Mount Jackson (5), the tuff (surface) in Clayton Valley (4), and the tephra layers in Mud Spring Canyon north of Mono Basin (this study; 6, 9).												
1	EL-4-FL	76.21	13.14	0.56	0.04	0.07	0.59	0.06	3.50	5.83	100.00	1.0000
4	D77-27B	77.05	13.00	0.58	0.04	0.04	0.53	0.09	3.45	5.22	100.00	0.9539
5	MJ-1A	76.95	13.05	0.56	0.04	0.07	0.50	0.08	3.26	5.49	100.00	0.9507
6	EL-37-MS	76.17	13.64	0.60	0.05	0.05	0.52	0.10	3.47	5.40	100.00	0.9492
9	EL-35B-MS	76.90	12.93	0.58	0.04	0.04	0.48	0.06	3.34	5.61	99.98	0.9451
Tephra layer in alluvial deposits at McGee Wash (1). The only reasonably close match is to the tephra layer at Weber Reservoir, in Lovelock Formation(?) (2; J.O. Davis, unpublished data); possibly the same sample locality. Note: 8-element comparison, excludes Mn.												
1	EL-5-WD	71.98	14.97	2.31	0.25	0.04	1.49	0.20	5.29	3.47	100.00	1.0000
2	DR-96	72.64	14.93	2.33	0.24	0.05	1.46	0.24	4.71	3.41	100.01	0.9532
Tephra layer at Campbell Valley (1). Closest matches are with the Bishop ash bed in Owens Lake core OL-92 (3, 5, 9, 10), at Lake Tecopa, California (7), and in Adobe Valley (6); and with the ~1 Ma Glass Mountain tephra at McGee Wash (8).												
1	EL-15-CA	76.55	12.83	0.76	0.03	0.05	0.44	0.06	4.14	5.14	100.00	1.0000
3	OL92-1030	76.94	12.91	0.74	0.04	0.03	0.44	0.07	3.90	4.93	100.00	0.9773
5	OL-92-2 (97)	76.88	13.05	0.73	0.03	0.04	0.44	0.02	4.12	4.70	100.01	0.9748
6	EL-38-AV	76.69	13.23	0.76	0.03	0.05	0.44	0.07	3.81	4.93	100.01	0.9746
7	TECO-28B	77.00	12.89	0.75	0.04	0.03	0.43	0.06	3.80	5.00	100.00	0.9740
8	EL-20-WD	76.78	12.88	0.78	0.03	0.04	0.44	0.06	4.31	4.68	100.00	0.9731
9	OL92-1022	76.95	12.95	0.74	0.03	0.03	0.45	0.07	3.99	4.79	100.00	0.9721
10	OL92-1028 (major)	76.89	12.97	0.73	0.04	0.04	0.45	0.06	3.97	4.85	100.00	0.9709
Tephra layer in alluvial deposits at McGee Wash (1). Closest matches are with the upper Miocene tephra layers (3–5; 11.81 ± 0.03 Ma correlated age; A.M. Sarna-Wojcicki, unpublished correlated age to date in Perkins et al., 1995). Note: 7-element comparison, includes Ti.												
1	EL-19-WD	75.88	12.23	2.02	0.09	0.03	0.70	0.25	3.36	5.42	99.98	1.0000
3	DSDP173-21-4 (27–28 cm)	76.40	12.16	2.14	0.06	0.03	0.69	0.26	3.12	5.14	100.00	0.9651
4	ALVES-1	76.33	12.12	2.08	0.05	0.03	0.65	0.23	3.24	5.28	100.01	0.9633
5	DSDP173-21-4 (32–35 cm)	76.47	12.08	2.08	0.06	0.05	0.69	0.23	2.99	5.36	100.01	0.9622

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer at McGee Wash (1). Closest matches are with the Bishop ash bed (11, 12, 14), with the younger tephra layers of Glass Mountain (7; 1.2–0.8 Ma), and with the tephra layers near the Thorne Bar (9) and in Campbell Valley (10).												
1	EL-20-WD	76.78	12.88	0.78	0.03	0.04	0.44	0.06	4.31	4.68	100.00	1.0000
7	PICO-73	77.29	12.83	0.79	0.03	0.04	0.45	0.06	4.03	4.48	100.00	0.9745
9	EL-21-WL	76.52	13.08	0.73	0.03	0.03	0.42	0.06	4.44	4.69	100.00	0.9734
10	EL-15-CA	76.55	12.83	0.76	0.03	0.05	0.44	0.06	4.14	5.14	100.00	0.9731
11	OL92-1019	77.20	12.83	0.76	0.04	0.08	0.42	0.06	4.20	4.42	100.01	0.9731
12	OL92-1027 (minor)	76.52	12.90	0.80	0.04	0.05	0.44	0.06	4.10	5.11	100.02	0.9729
14	JC-239	77.40	12.81	0.74	0.03	0.04	0.44	0.06	4.20	4.27	99.99	0.9704
Tephra layer at site north of Thorne Bar (1). Closest matches are with the Bishop ash bed (2, 6, 10, 14), with the younger tephra layers of Glass Mountain (5; 1.2–0.8 Ma), and with the tephra layer at McGee Wash (3).												
1	EL-21-WL	76.52	13.08	0.73	0.03	0.03	0.42	0.06	4.44	4.69	100.00	1.0000
2	OL-92-2 (97)	76.88	13.05	0.73	0.03	0.04	0.44	0.02	4.12	4.70	100.01	0.9789
3	EL-20-WD	76.78	12.88	0.78	0.03	0.04	0.44	0.06	4.31	4.68	100.00	0.9734
5	PICO-78 (2) (100–200 cm)	76.33	12.93	0.73	0.03	0.04	0.41	0.06	4.24	4.24	99.01	0.9702
6	OL92-1019	77.20	12.83	0.76	0.04	0.08	0.42	0.06	4.20	4.42	100.01	0.9702
10	OL92-1029	76.92	13.06	0.71	0.03	0.04	0.42	0.05	3.92	4.85	100.00	0.9693
14	OL92-1028 (minor)	76.73	13.16	0.71	0.04	0.01	0.45	0.07	4.08	4.75	100.00	0.9672
Tephra layer east of Mina (1). No good specific matches. Generally similar to upper Miocene and lower Pliocene tephra layers of the Snake River Plain eruptive source areas, Idaho (2), and with the tephra layers at Drumm Summit (3, 4).												
1	EL-24-M	75.58	12.56	1.77	0.06	0.03	0.59	0.17	3.17	6.09	100.02	1.0000
2	F8-90-G21 (39–41 cm) (high Fe, low Na)	76.32	12.37	1.67	0.07	0.04	0.59	0.17	2.71	6.06	100.00	0.9669
3	EL-66-FV	76.28	12.22	1.86	0.04	0.02	0.60	0.18	2.94	5.87	100.01	0.9621
4	EL-59-FV (2)	76.52	11.99	1.88	0.04	0.03	0.58	0.17	2.73	6.06	100.00	0.9604
Tephra layer in roadcut south of Rhodes Salt Marsh (overlies EL-2-RM) (1). Closest matches are with the tuff of the Taylor Canyon tephra layers (3, 5, 9–14; 2.22–2.14 Ma; Sarna-Wojcicki et al., In review).												
1	EL-26-RM	76.29	12.98	0.56	0.03	0.11	0.32	0.06	4.82	4.84	100.01	1.0000
3	DG-4	76.96	13.03	0.56	0.04	0.09	0.33	0.08	4.00	4.92	100.01	0.9618
5	FLV-SP-11	77.07	13.07	0.56	0.03	0.09	0.33	0.07	3.89	4.89	100.00	0.9583
9	DG-3A	76.88	12.92	0.63	0.02	0.09	0.31	0.05	4.45	4.63	99.98	0.9542
10	TTC-6	77.20	12.93	0.58	0.05	0.09	0.33	0.09	4.08	4.64	99.99	0.9541
11	FLV-43-WW	78.00	12.32	0.56	0.03	0.08	0.32	0.06	3.79	4.84	100.00	0.9523
12	P-169Q	77.59	12.55	0.58	0.04	0.10	0.33	0.06	3.87	4.87	99.99	0.9470
13	PC-C	76.76	13.14	0.60	0.03	0.08	0.32	0.07	3.90	5.10	100.00	0.9455
14	TTC-19 (2)	77.54	12.57	0.59	0.05	0.07	0.33	0.06	3.91	4.89	100.01	0.9454
Tephra layer at Redlich Summit (1). Closest matches are with the older Glass Mountain tephra layers (3, 11; ~1.95–1.79 Ma; Sarna-Wojcicki et al., In review).												
1	EL-29-RM	76.61	12.81	0.76	0.05	0.08	0.33	0.09	3.68	5.60	100.01	1.0000
3	CH88014	76.84	12.91	0.76	0.02	0.07	0.32	0.06	3.71	5.31	100.00	0.9832
11	TTC-23	77.58	12.62	0.71	0.03	0.03	0.32	0.03	3.58	5.10	100.00	0.9600
Tephra layer at Redlich Summit, dated 5.9 Ma (1). Closest matches are with the tuffs in Horsethief Canyon (2, 3), the tephra at Willow Wash, California (6; Reheis et al., 1991), and the overlying tephra layer at Redlich Summit (4).												
1	EL-34-RM	73.84	13.52	1.24	0.09	0.10	0.39	0.15	3.87	6.80	100.00	1.0000
2	FLV-83-HT	74.11	13.89	1.19	0.10	0.09	0.37	0.19	3.84	6.21	99.99	0.9639
3	FLV-80-HT	74.55	13.45	1.17	0.07	0.10	0.37	0.19	3.58	6.52	100.00	0.9602
4	EL-65-RM	73.50	14.26	1.11	0.09	0.10	0.38	0.19	3.71	6.66	100.00	0.9585
6	FLV-105-WW	74.57	13.81	1.21	0.09	0.10	0.38	0.20	4.35	5.28	99.99	0.9309
Tephra layer in alluvial deposits at Mud Spring Canyon (1). Closest matches are with the tephra layers at Willow Wash (6, 8, 12, 13; <2.83, >2.57 Ma; Sarna-Wojcicki et al., In review).												
1	EL-35A-MS	77.37	12.59	0.63	0.05	0.05	0.53	0.06	2.25	6.37	99.90	1.0000
6	FLV-34-WW	76.85	12.93	0.62	0.08	0.06	0.62	0.10	2.52	6.22	100.00	0.9459
8	FLV-121-WW	76.61	12.95	0.65	0.04	0.06	0.57	0.07	2.85	6.20	100.00	0.9374
12	FLV-33-WW	76.87	12.95	0.64	0.07	0.07	0.62	0.12	2.69	5.96	99.99	0.9295
13	FLV-25-WW	77.60	12.45	0.61	0.07	0.07	0.56	0.10	2.89	5.66	100.01	0.9279

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer in alluvial deposits at Mud Spring Canyon (1). Closest matches are with the tuffs near Mount Jackson (2, 5; 2.9 ± 0.16 Ma, S. Weiss, in litt. to M.C.R., 1993), an overlying tephra layer (3), and the tuff (surface) in Clayton Valley, Nevada (7).												
1	EL-35B-MS	76.90	12.93	0.58	0.04	0.04	0.48	0.06	3.34	5.61	99.98	1.0000
2	MJ-1A	76.95	13.05	0.56	0.04	0.07	0.50	0.08	3.26	5.49	100.00	0.9784
3	EL-36-MS	77.31	12.71	0.59	0.05	0.06	0.48	0.07	3.53	5.20	100.00	0.9723
5	MJ-1B	76.90	13.00	0.59	0.04	0.08	0.49	0.07	3.62	5.20	99.99	0.9678
7	D77-27B	77.05	13.00	0.58	0.04	0.04	0.53	0.09	3.45	5.22	100.00	0.9662
Tephra layer in alluvial deposits at Mud Spring Canyon (1). Closest matches are with the tuff near Mount Jackson (2; see reference above), an underlying tephra layer (3), in southeastern Mono Basin (6); with the tuff in Clayton Valley, Nevada (4), a similar tuff at Willow Wash (5; 11.3 Ma; Reheis and Sawyer, 1997), and with the tephra layer at Willow Wash (10), ~2.57 Ma (Sarna-Wojcicki et al., In review).												
1	EL-36-MS	77.31	12.71	0.59	0.05	0.06	0.48	0.07	3.53	5.20	100.00	1.0000
2	MJ-1B	76.90	13.00	0.59	0.04	0.08	0.49	0.07	3.62	5.20	99.99	0.9879
3	EL-53-ML	77.27	12.69	0.57	0.04	0.06	0.45	0.08	3.63	5.22	100.01	0.9784
4	D77-27B	77.05	13.00	0.58	0.04	0.04	0.53	0.09	3.45	5.22	100.00	0.9728
5	FL-KA-3	77.54	12.27	0.62	0.07	0.04	0.47	0.09	3.47	5.43	100.00	0.9723
6	EL-35B-MS	76.90	12.93	0.58	0.04	0.04	0.48	0.06	3.34	5.61	99.98	0.9723
10	FLV-35-WW	77.58	12.69	0.60	0.06	0.07	0.49	0.10	3.76	4.65	100.00	0.9652
Tephra layer at Clayton Valley (1). Closest matches are with the ash flow at Mount Adams, Washington (2, 3; ~510 Ka, W. Hildreth, unpub. data), with the tuff above Huckleberry Ridge ash bed at Confidence Hills, Death Valley, California (4, 5; ~2.04 Ma, Sarna-Wojcicki et al., In review), and with the tuff in Burmeister core, Great Salt Lake, Utah (6, 10; ~3 Ma., Williams, 1993).												
1	EL-42-CV #2 (high K)	71.48	14.53	2.73	0.26	0.09	0.92	0.36	5.06	4.57	100.00	1.0000
2	MA-360 (A)	71.49	14.44	2.72	0.19	0.07	0.87	0.33	5.12	4.77	100.00	0.9803
3	MA-360 (B)	71.62	14.48	2.86	0.20	0.08	0.91	0.32	4.80	4.73	100.00	0.9755
4	CH88008	70.92	15.64	2.71	0.28	0.09	0.96	0.29	5.06	4.06	100.01	0.9601
5	TL88001	70.94	15.62	2.67	0.27	0.09	0.96	0.30	5.01	4.15	100.01	0.9595
6	BUR-915 (high Fe)	73.05	14.13	2.75	0.25	0.10	0.86	0.32	4.52	4.01	99.99	0.9415
Tephra layer at Clayton Valley (1). Closest matches are with the La Salida tuff (2, 4, 5, 6), the tephra layer from the Burmeister core in the Great Salt Lake, Utah (7; 3.06 Ma; Williams, 1993), and the tephra layer in Willow Wash, California (8).												
1	EL-42-CV #1 (major)	72.20	14.67	2.67	0.27	0.13	0.89	0.31	5.65	3.22	100.01	1.0000
2	SSP-2	72.25	14.56	2.66	0.24	0.08	0.90	0.32	5.68	3.30	99.99	0.9912
4	C-83-6A	72.50	14.47	2.73	0.27	0.11	0.89	0.29	5.39	3.36	100.01	0.9788
5	ASW-61384-27	72.98	14.17	2.66	0.26	0.12	0.92	0.33	5.40	3.17	100.01	0.9765
6	ASW-61286-14	73.51	13.59	2.60	0.27	0.08	0.89	0.29	5.53	3.24	100.00	0.9758
7	BUR-915	72.02	14.46	2.67	0.26	0.11	0.87	0.33	5.66	3.63	100.01	0.9743
8	FLV-WW-52	72.48	13.92	2.70	0.27	0.10	0.92	0.32	6.10	3.19	100.00	0.9697
Tephra layer at Clayton Valley (1). Closest matches are with the Spearhead Member of Stonewall Flat tuff (2; 7.61 ± 0.03 Ma; and 3; 4.02 ± 0.08 Ma) as well as with similar tuffs in southern Fish Lake Valley (4, 5; Reheis and Sawyer, 1997), but Fe and K are slightly different. Also similar to the tephra in Willow Wash (6; <2.81, >2.57 Ma).												
1	EL-43-CV	76.61	12.17	1.97	0.01	0.06	0.31	0.14	4.24	4.49	100.00	1.0000
2	61990-1	76.42	12.05	1.85	0.01	0.07	0.31	0.12	4.24	4.94	100.01	0.9726
3	B85-195-A	76.07	12.35	1.86	0.00	0.07	0.32	0.11	4.24	4.98	100.00	0.9655
4	FLV-50-CM	76.86	11.75	1.87	0.00	0.08	0.31	0.09	3.95	5.10	100.01	0.9539
5	FLV-5-CC	76.56	11.89	1.91	0.00	0.07	0.31	0.10	3.91	5.25	100.00	0.9539
6	FLV-31-WW	77.47	12.02	2.01	0.02	0.05	0.35	0.15	3.42	4.51	100.00	0.9408
Tephra layer at The Gap (1); underlies EL-3-FL. Closest matches are with the tuff of Taylor Canyon, 2.22–2.14 Ma (Sarna-Wojcicki et al., In review), from Emigrant Pass area, Nevada (3, 8), from Waucoba lake beds (11), and from Cowan Pumice Mine, California (9, 13).												
1	EL-44-FL	76.63	13.04	0.58	0.03	0.12	0.32	0.07	3.43	5.77	99.99	1.0000
3	FLV-183-EP	77.20	12.70	0.56	0.05	0.11	0.31	0.07	3.23	5.78	100.01	0.9735
8	FLV-180-EP	77.14	12.89	0.59	0.04	0.11	0.32	0.10	2.99	5.82	100.00	0.9713
9	TTC-20	77.70	12.58	0.58	0.05	0.06	0.31	0.05	3.38	5.29	100.00	0.9703
11	W2A	77.35	12.48	0.60	0.03	0.08	0.34	0.08	3.30	5.74	100.00	0.9687
13	TTC-21	77.68	12.57	0.60	0.05	0.07	0.32	0.06	3.33	5.32	100.00	0.9683

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer at Redlich Summit (1). Closest matches are the Wono ash bed of Davis (1978) (27.2 Ka) (Benson et al., 1997), from a core off the Oregon coast (6), and from Nixon, Nevada (9, 12, 17, 18).												
1	EL-50-RM	74.03	13.93	2.05	0.32	0.05	1.43	0.28	4.30	3.61	100.00	1.0000
6	F8-90-G21 (37–39 cm)	73.98	14.26	2.03	0.27	0.05	1.41	0.31	4.53	3.17	100.01	0.9633
9	LD-30	74.08	14.03	2.11	0.30	0.06	1.38	0.32	4.51	3.21	100.00	0.9619
12	LD-30	74.10	14.03	2.11	0.30	0.06	1.38	0.32	4.53	3.17	100.00	0.9593
17	NIXON-1 (minor)	74.60	13.77	2.06	0.31	0.05	1.33	0.32	4.46	3.11	100.01	0.9553
18	NIXON-2 (major)	74.54	13.81	2.10	0.30	0.06	1.34	0.30	4.46	3.10	100.01	0.9534
Tephra layer in southeastern Mono Basin (1). Closest matches are with the tephra layers in Willow Wash section (3, 11; 5.9–5.4 Ma; and 5; <2.57, >2.22 Ma) and various tephra layers (7, 8, 12, 14) of indeterminate age, probably late Miocene and early Pliocene age.												
1	EL-53-ML (high K)	76.86	12.60	0.58	0.04	0.07	0.43	0.09	2.47	6.85	99.99	1.0000
3	FLV-138-WW	76.77	12.96	0.56	0.04	0.09	0.42	0.09	2.65	6.42	100.00	0.9638
5	FLV-29-WW	76.85	12.65	0.55	0.06	0.08	0.41	0.06	2.20	7.13	99.99	0.9582
7	86LP39	76.57	12.90	0.57	0.04	0.08	0.56	0.07	2.47	6.75	100.01	0.9515
8	OT-2	78.22	12.23	0.58	0.05	0.08	0.39	0.08	2.33	6.05	100.01	0.9478
11	FLV-28-WW	77.46	12.55	0.53	0.06	0.08	0.39	0.09	2.17	6.67	100.00	0.9436
12	D3SW-1	77.93	11.76	0.54	0.05	0.07	0.43	0.08	2.80	6.33	99.99	0.9428
14	BE-62	77.36	12.59	0.58	0.05	0.06	0.40	0.11	1.81	7.04	100.00	0.9381
Tephra layer in southeastern Mono Basin (1). Closest matches are with a tephra layer in northeastern Fish Lake Valley (2; <2.57, >2.22 Ma by correlation), a tephra layer at Mud Spring Canyon (3), the tuff near Mount Jackson (5), and the tephra layer in Yellowjacket Canyon, California (7; <2.57, >2.22 Ma, Sarna-Wojcicki et al., In review).												
1	EL-53-ML #1	77.27	12.69	0.57	0.04	0.06	0.45	0.08	3.63	5.22	100.01	1.0000
2	FLV-63-CS	76.87	12.94	0.58	0.04	0.09	0.43	0.06	3.77	5.23	100.01	0.9791
3	EL-36-MS	77.31	12.71	0.59	0.05	0.06	0.48	0.07	3.53	5.20	100.00	0.9784
5	MJ-1B	76.90	13.00	0.59	0.04	0.08	0.49	0.07	3.62	5.20	99.99	0.9749
7	YJC-4-87	77.17	12.92	0.56	0.04	0.10	0.42	0.07	3.45	5.28	100.01	0.9726
Tephra layer in southeastern Mono Basin (1). Closest matches are with the adjacent tephra layer (2; 2.3 Ma, R. Fleck, in litt. to A.S.-W., 1997), with the tephra layer at Teels Lake, Nevada (5), and with the tephra layer south of Rhodes Salt Marsh (7).												
1	EL-54B-ML	77.53	12.64	0.53	0.03	0.07	0.41	0.07	3.82	4.91	100.01	1.0000
2	EL-54A-ML	77.38	12.76	0.55	0.04	0.07	0.40	0.08	3.83	4.91	100.02	0.9875
5	TLN-3	77.20	12.87	0.54	0.04	0.09	0.43	0.09	4.03	4.70	99.99	0.9697
7	EL-2-RM	77.54	12.72	0.55	0.03	0.06	0.44	0.06	3.94	4.65	99.99	0.9676
Tephra layer in southeastern Mono Basin (1), dated 2.3 Ma (R. Fleck, in litt. to A.S.-W., 1997). Closest matches are with the adjacent tephra layer (2) and with the tephra layers south of Rhodes Salt Marsh (6) and at Teels Lake (9).												
1	EL-54A-ML	77.38	12.76	0.55	0.04	0.07	0.40	0.08	3.83	4.91	100.02	1.0000
2	EL-54B-ML	77.53	12.64	0.53	0.03	0.07	0.41	0.07	3.82	4.91	100.01	0.9875
6	EL-2-RM	77.54	12.72	0.55	0.03	0.06	0.44	0.06	3.94	4.65	99.99	0.9705
9	TLN-3	77.20	12.87	0.54	0.04	0.09	0.43	0.09	4.03	4.70	99.99	0.9681
Tephra layer in alluvial deposits at McGee Wash (1). Closest matches are with the ash flows in the Silver Peak Range (5, 8, 20) in the McAfee Creek area (tuff of Cottonwood Springs, 6.1 Ma; R. Fleck, in litt. to A.S.-W., 1997) and in the Volcanic Hills (22), and with a tephra layer in the Cave Springs Wash area (14; 1.2–0.8 Ma, upper tuffs of Glass Mountain), all in the Fish Lake Valley area of California and Nevada.												
1	EL-57-WD	76.73	12.97	0.69	0.05	0.07	0.43	0.09	3.65	5.33	100.01	1.0000
5	FLV-SP-1	76.87	12.99	0.71	0.04	0.08	0.41	0.10	3.67	5.13	100.00	0.9798
8	FLV-SP-2	76.79	13.07	0.71	0.05	0.07	0.44	0.10	3.73	5.02	99.98	0.9768
14	FLV-55-CS	77.07	12.89	0.73	0.03	0.07	0.41	0.07	3.66	5.07	100.00	0.9728
20	FLV-SP-3	77.18	12.76	0.73	0.07	0.07	0.44	0.09	3.71	4.95	100.00	0.9688
22	FLV-VH-5B	77.29	12.69	0.70	0.05	0.07	0.43	0.10	3.85	4.82	100.00	0.9682
Tephra layer at McGee Wash (1). Closest matches are with the younger tephra layers of Glass Mountain (4, 6; 1.2–0.8 Ma) and similar tephra layers in Fish Lake Valley, Nevada (16), and with the Bishop ash bed (10; 0.76 Ma).												
1	EL-58-WD (1)	77.65	12.76	0.78	0.04	0.05	0.45	0.07	3.52	4.68	100.00	1.0000
4	BT-14	77.41	12.77	0.77	0.04	0.04	0.45	0.07	3.53	4.92	100.00	0.9886
6	BT-1C	77.84	12.73	0.77	0.03	0.05	0.42	0.06	3.52	4.57	99.99	0.9820
10	63CJ-26 (2)	77.93	12.45	0.72	0.03	0.05	0.45	0.06	3.53	4.77	99.99	0.9789
16	FLV-162-CS	77.36	12.89	0.77	0.03	0.07	0.46	0.07	3.40	4.95	100.00	0.9772

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer at McGee Wash (1). Closest matches are with the younger tephra layers of Glass Mountain (3; 1.2–0.8 Ma) and with the Bishop ash bed (4, 6, 7, 11, 12; 0.76 Ma).												
1	EL-58-WD (2)	77.99	12.31	0.74	0.03	0.03	0.44	0.07	3.65	4.73	99.99	1.0000
3	BT-2	77.64	12.67	0.74	0.03	0.03	0.43	0.07	3.66	4.73	100.00	0.9903
4	FLV-69-PA	78.04	12.31	0.74	0.02	0.06	0.44	0.05	3.77	4.55	99.98	0.9882
6	FLV-4-WP	77.93	12.49	0.74	0.05	0.04	0.44	0.06	3.73	4.53	100.01	0.9868
7	FLV-S2 (also FLV-148A-CS)	77.81	12.55	0.72	0.03	0.03	0.43	0.07	3.66	4.70	100.00	0.9866
11	FRIANT 5A	77.73	12.41	0.75	0.05	0.04	0.46	0.09	3.66	4.81	100.00	0.9854
12	BT-8 (2) (bulk)	77.75	12.48	0.73	0.03	0.05	0.44	0.05	3.82	4.65	100.00	0.9847
Tephra layer at Drumm Summit in Fairview Valley (1). Closest matches are with the upper Miocene to lower Pliocene tephra layers (2, 4, 6) and with the Lava Creek B ash bed, except for a high-iron mode found in the Burmeister core (5; Williams, 1993; correlated age, 0.65 Ma). Note: 7-element comparison, includes Ti.												
1	EL-59-FV (2)	76.52	11.99	1.88	0.04	0.03	0.58	0.17	2.73	6.06	100.00	1.0000
2	VW-CIMA (2)	76.59	11.91	1.88	0.06	0.04	0.54	0.17	2.70	6.12	100.01	0.9861
4	EL-59-FV	76.47	12.25	1.92	0.04	0.02	0.58	0.19	2.63	5.91	100.01	0.9701
5	BUR-281.9 (high Fe)	76.59	12.10	1.98	0.02	0.05	0.59	0.16	2.79	5.72	100.00	0.9694
6	VW-CIMA-1	76.79	11.87	1.84	0.06	0.04	0.55	0.19	2.69	5.98	100.01	0.9686
Tephra layer at Drumm Summit, Fairview Valley (1). Replicate of EL-59-FV, above; same comments apply. Note: 7-element comparison, includes Ti.												
1	EL-59-FV	76.47	12.25	1.92	0.04	0.02	0.58	0.19	2.63	5.91	100.01	1.0000
2	VW-CIMA-1	76.79	11.87	1.84	0.06	0.04	0.55	0.19	2.69	5.98	100.01	0.9768
5	EL-59-FV (2)	76.52	11.99	1.88	0.04	0.03	0.58	0.17	2.73	6.06	100.00	0.9701
6	EL-66-FV	76.28	12.22	1.86	0.04	0.02	0.60	0.18	2.94	5.87	100.01	0.9665
7	083089-A	76.95	12.15	1.84	0.05	0.03	0.59	0.21	2.60	5.58	100.00	0.9664
8	08309-A (2)	77.05	12.20	1.84	0.05	0.03	0.62	0.19	2.46	5.55	99.99	0.9652
Tephra layers in Truckee River canyon (1, 2). Samples 1 and 2 are indistinguishable at analytical precision levels. Similar to Ishi tuff (4, 10; ~2.5 Ma) and to the tephra layer at I-80 at 320 mile marker (14; J.D. Davis, unpub. data); age unknown. Note: 8-element comparison, excludes Mn.												
1	EL-60-TC	77.35	13.29	0.83	0.15	0.08	0.69	0.13	2.47	5.02	100.01	1.0000
2	EL-61-TC	77.34	13.34	0.81	0.14	0.07	0.69	0.11	2.49	5.01	100.00	0.9677
4	RS-2 (3)	77.97	12.48	0.85	0.14	0.05	0.78	0.13	2.81	4.78	99.99	0.9446
10	RS-2 (2)	77.51	12.82	0.81	0.16	0.02	0.74	0.15	3.39	4.40	100.00	0.9100
14	GS-85	77.68	12.63	0.83	0.15	0.04	0.69	0.16	3.71	4.11	100.00	0.9054
Tephra layer at Drumm Summit (1). Matches samples 2, 4, and 5 (this study); generally similar to upper Miocene and lower Pliocene tephra from Snake River Plain sources, Idaho (8, 9), and with the tephra layer from gravels in Las Vegas Wash in pre-Chemehuevi Formation (14). Note: 7-element comparison, includes Ti.												
1	EL-66-FV	76.28	12.22	1.86	0.04	0.02	0.60	0.18	2.94	5.87	100.01	1.0000
2	EL-59-FV (2)	76.52	11.99	1.88	0.04	0.03	0.58	0.17	2.73	6.06	100.00	0.9680
4	EL-59-FV	76.47	12.25	1.92	0.04	0.02	0.58	0.19	2.63	5.91	100.01	0.9665
5	EL-24-M	75.58	12.56	1.77	0.06	0.03	0.59	0.17	3.17	6.09	100.02	0.9621
8	VW-CIMA-1	76.79	11.87	1.84	0.06	0.04	0.55	0.19	2.69	5.98	100.01	0.9592
9	2-8-16J	76.32	12.28	1.82	0.06	0.03	0.62	0.21	2.71	5.94	99.99	0.9583
14	083089-A (2)	77.05	12.20	1.84	0.05	0.03	0.62	0.19	2.46	5.55	99.99	0.9536
Tephra layer at Lone Mountain, Kobeh Valley (1). Matches with the Rye Patch Dam ash bed at Tulelake, California (3), with other samples of this ash bed at Kobeh Valley (4, 10), and with samples at the type locality of this ash bed at Rye Patch Dam, Nevada (12, 14). Similar to Desert Springs tuff (ash-flow) in the Bend, Oregon, area (15), which is probably a near-source site of the Rye Patch Dam ash bed. Note: 6-element comparison, excludes alkalies and Mn.												
1	EL-69-KV	71.76	14.86	3.32	0.37	0.06	1.41	0.43	4.35	3.44	100.00	1.0000
3	TULELAKE-321	70.85	14.80	3.35	0.37	0.08	1.46	0.43	5.16	3.51	100.01	0.9900
4	EL-70B-KV	71.81	14.79	3.33	0.36	0.07	1.39	0.44	4.34	3.46	99.99	0.9879
10	AA-04-JOD	71.37	14.34	3.35	0.36	0.09	1.44	0.42	5.01	3.60	99.98	0.9799
12	JOD-18-7-78B (1)	71.25	14.82	3.22	0.34	0.06	1.39	0.43	5.00	3.49	100.00	0.9775
14	JOD-18-7-78A (1,2)	71.34	14.37	3.37	0.39	0.09	1.45	0.44	5.08	3.47	100.00	0.9741
15	DST-3	71.31	14.58	3.19	0.39	0.09	1.48	0.44	4.40	4.12	100.00	0.9691

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer at Lone Mountain, Kobeh Valley (1); low-Fe fraction. Similar to the tephra layers at Pringle Falls, Oregon, about ~180–220 Ka (Herrero-Berver et al., 1994) (2, 3, 6, 7, 8), to the Summer Lake bed NN, Oregon (4) (Davis, 1985), and to the Columbia Canal ash-flow tuff near Bend, Oregon (10). Note: 8-element comparison, excludes Mn.												
1	EL-72-KV #1 (low Fe)	69.86	15.46	3.68	0.79	0.10	2.14	0.70	4.71	2.55	99.99	1.0000
2	PF-88-O (mafic)	69.21	15.37	3.81	0.73	0.12	2.14	0.69	5.40	2.53	100.00	0.9656
3	PF-88-O (silicic-ct)	68.64	15.68	3.85	0.80	0.12	2.27	0.71	5.56	2.38	100.01	0.9526
4	DR-70	69.70	15.07	3.79	0.67	0.09	2.16	0.68	5.12	2.71	99.99	0.9518
6	PF-88-P	69.95	15.17	3.87	0.69	0.11	2.12	0.61	5.00	2.47	99.99	0.9471
7	PF-88-Q (silicic)	68.38	15.51	3.85	0.79	0.12	2.23	0.73	5.94	2.37	99.92	0.9465
8	PF-88-O (silicic-b)	69.36	15.27	3.91	0.74	0.14	2.11	0.65	5.44	2.38	100.00	0.9465
10	BPT-CC	69.34	15.31	3.70	0.72	0.13	2.12	0.67	5.70	2.30	99.99	0.9456
Tephra layer at Lone Mountain, Kobeh Valley (1); high-Fe fraction. Similar to the tephra layer from Honey Lake, California, stratigraphically close above Huckleberry Ridge ash bed at Honey Lake, California (2); other similar samples are the upper Miocene tephra from Balcolm Canyon, southern California (3), and the upper Pleistocene tephra layer from the Tulelake area, California (4). Note: 8-element comparison, excludes Mn.												
1	EL-72-KV #2 (high Fe)	61.09	16.78	6.84	2.28	0.14	5.04	1.28	5.02	1.53	100.00	1.0000
2	CDGD-1	60.70	16.14	7.71	2.27	0.15	4.92	1.36	5.08	1.68	100.01	0.9568
3	MOD-13	61.37	16.03	6.81	2.47	0.15	5.29	1.21	4.85	1.82	100.00	0.9468
4	ASW-61085-14 (mafic)	63.69	14.75	7.13	1.84	0.10	4.86	1.26	4.87	1.50	100.00	0.9380
Tephra layer in roadcut section, Lone Tree Mine (1). Most similar to the younger Glass Mountain tephra layers, including Bailey ash bed, Ventura, California (4), and tephra layer beneath Bishop ash bed, northern Fish Lake Valley, Nevada (5). Also similar to the Bishop ash bed at Friant, California (6–8).												
1	EL-76A-LT	77.18	12.97	0.69	0.03	0.05	0.49	0.07	3.59	4.92	99.99	1.0000
4	PICO-5 (2)	77.24	12.73	0.71	0.03	0.03	0.49	0.06	3.56	5.15	100.00	0.9833
5	FLV-160-CS	77.40	12.82	0.73	0.01	0.06	0.50	0.07	3.50	4.91	100.00	0.9806
6	FRIANT 4A	77.23	12.90	0.71	0.03	0.03	0.51	0.05	3.70	4.83	99.99	0.9798
7	FRIANT-1	77.54	12.73	0.73	0.03	0.03	0.48	0.06	3.56	4.83	99.99	0.9792
8	FRIANT-2	77.53	12.86	0.68	0.03	0.03	0.47	0.06	3.40	4.94	100.00	0.9791
Tephra layer in roadcut section, Lone Tree Mine (1). Most similar to the younger Glass Mountain tephra layer at Lake Tecopa, California (3), and to the Bishop ash bed at the southern end of volcanic tableland north of Bishop, California (11).												
1	EL-78-LT	77.29	12.90	0.71	0.03	0.05	0.48	0.05	3.82	4.66	99.99	1.0000
3	TECO-26	77.61	12.73	0.72	0.03	0.03	0.48	0.06	3.70	4.63	99.99	0.9885
11	BT-8 (2)	77.48	12.68	0.71	0.03	0.02	0.45	0.06	3.85	4.72	100.00	0.9829
Tephra layer at Lone Mountain, Kobeh Valley (1). Most similar to the Huckleberry Ridge ash bed near Ventura, California (2, 4), and in Meade County, Kansas (5, 6); somewhat less similar to the Lava Creek B ash bed from Butte Valley, California (7), Lake Tecopa, California (8), and Onion Creek, Utah (9). Note: 7-element comparison, includes Ti.												
1	EL-80-KV	76.73	12.32	1.67	0.02	0.04	0.60	0.10	3.54	4.98	100.00	1.0000
2	PICO 158	76.71	12.25	1.71	0.03	0.03	0.60	0.10	3.62	4.95	100.00	0.9918
4	ASW-3-23-75-1	76.62	12.13	1.83	0.02	0.05	0.60	0.10	3.63	5.02	100.00	0.9804
5	68W98	76.65	12.53	1.69	0.02	0.03	0.58	0.10	3.32	5.08	100.00	0.9793
6	68W98	76.99	12.30	1.66	0.02	0.04	0.58	0.10	3.22	5.09	100.00	0.9777
7	#4078	76.64	12.22	1.65	0.03	0.03	0.55	0.10	3.51	5.27	100.00	0.9760
8	RM880904	76.63	12.19	1.65	0.02	0.05	0.53	0.10	3.55	5.28	100.00	0.9714
9	67W104	77.00	12.23	1.51	0.02	0.03	0.54	0.10	3.58	4.99	100.00	0.9686
Tephra layer on southwest side of Lone Mountain, Kobeh Valley (1). Closest matches are with the tephra layers of Cowan Pumice Mine, Blind Springs Valley, California (4, 8), from northeastern Fish Lake Valley, Nevada (3, 6), and from stratigraphically beneath the Huckleberry Ridge ash bed at Ventura, California (7).												
1	EL-81-KV	77.63	12.59	0.60	0.04	0.08	0.33	0.08	3.95	4.69	99.99	1.0000
3	FLV-13-CS	77.48	12.82	0.60	0.04	0.08	0.33	0.04	3.85	4.75	99.99	0.9904
4	TTC-19 (2)	77.54	12.57	0.59	0.05	0.07	0.33	0.06	3.91	4.89	100.01	0.9883
6	FLV-151-CS	77.34	12.70	0.60	0.04	0.09	0.34	0.05	4.09	4.74	99.99	0.9856
7	P-169Q	77.59	12.55	0.58	0.04	0.10	0.33	0.06	3.87	4.87	99.99	0.9843
8	TTC-9A	77.51	12.83	0.59	0.05	0.10	0.34	0.07	3.87	4.65	100.01	0.9841

TABLE 3.—Continued.

Output no.	Field sample no.	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MgO	MnO	CaO	TiO <sub>2</sub>	Na <sub>2</sub> O	K <sub>2</sub> O	Total (R)	Similarity coefficient
Tephra layer in core at Lone Tree Mine (1). Closest matches are with the Lava Creek B ash bed near Oreana, Nevada (2; J.O. Davis, Desert Research Institute, Nevada), the Huckleberry Ridge ash bed in Meade County, Kansas (3, 5, 7; Izett and Wilcox, 1983), and with the Lava Creek B ash bed, Lake Tecopa, California (4), and Ventura, California (8).												
1	EL-92-LT	76.89	12.31	1.66	0.02	0.03	0.56	0.12	3.30	5.12	100.01	1.0000
2	LM-24	76.70	12.62	1.67	0.03	0.03	0.56	0.08	3.30	5.01	100.00	0.9909
3	68W98	76.99	12.30	1.66	0.02	0.04	0.58	0.10	3.22	5.09	100.00	0.9889
4	T89-5/6/9 #1	76.88	12.16	1.67	0.03	0.04	0.56	0.13	3.49	5.05	100.01	0.9856
5	68W98	76.65	12.53	1.69	0.02	0.03	0.58	0.10	3.32	5.08	100.00	0.9855
7	68W98	76.67	12.28	1.71	0.02	0.05	0.58	0.12	3.35	5.22	100.00	0.9828
8	PICO-133C	75.71	12.37	1.59	0.02	0.00	0.56	0.11	3.40	5.25	99.01	0.9806
Tephra layer near U.S. Highway 50 in Kobeh Valley, Nevada (1). Closest matches are with the Rye Patch Dam ash bed at Rye Patch Dam, Nevada (4, 7), at a nearby site in Kobeh Valley (15), and in a core from Tulelake, California (5); and with Desert Springs tuff, Bend, Oregon (13). Note: 8-element comparison, excludes Mn.												
1	AA-04 JOD	71.37	14.34	3.35	0.36	0.09	1.44	0.42	5.01	3.60	99.98	1.0000
4	LD-61	71.07	14.70	3.32	0.37	0.09	1.45	0.45	4.99	3.56	100.00	0.9808
5	TULELAKE-321	70.85	14.80	3.35	0.37	0.08	1.46	0.43	5.16	3.51	100.01	0.9804
7	JOD-18-7-78A (1,2)	71.34	14.37	3.37	0.39	0.09	1.45	0.44	5.08	3.47	100.00	0.9765
13	DST-1	72.69	13.39	3.21	0.38	0.07	1.47	0.43	4.75	3.61	100.00	0.9654
15	EL-69-KV	71.76	14.86	3.32	0.37	0.06	1.41	0.43	4.35	3.44	100.00	0.9629
Tephra layer at depth of ~175 m in a core from Clayton Valley, Nevada (1). Best matches are with the reworked Bishop ash at Friant, California (3), the airfall Bishop ash bed at Yellowjacket Canyon near Benton, California (7), the Bishop ash bed in the Ventura basin, California (12), and the airfall Bishop ash bed at Insulating Aggregates Quarry north of Bishop, California (16).												
1	D77-2D	77.39	12.66	0.73	0.03	0.05	0.45	0.07	3.72	4.89	99.99	1.0000
3	63CJ-26 (1)	77.37	12.69	0.73	0.04	0.05	0.45	0.08	3.60	4.99	100.00	0.9908
7	YJC-1-87	77.28	12.91	0.73	0.04	0.05	0.44	0.07	3.74	4.75	100.01	0.9872
12	PICO-141	77.29	12.84	0.73	0.03	0.02	0.42	0.07	3.68	4.91	99.99	0.9839
16	BT-8 (2)	77.48	12.68	0.71	0.03	0.02	0.45	0.06	3.85	4.72	100.00	0.9836
Tephra layer in large pit 9.5 m below surface at Columbus Marsh, Nevada (1). Best matches are with the airfall Bishop ash bed near Westgard Pass, California (7), the Glass Mountain D tephra at Chalk Bluffs north of Bishop, California, ~0.9 Ma (9), the airfall Bishop ash bed at Friant, California (11), and the airfall Bishop ash bed at Insulating Aggregates Quarry north of Bishop, California (15).												
1	29068501	78.06	12.27	0.76	0.04	0.04	0.44	0.07	3.64	4.67	99.99	1.0000
7	FLV-4-WP	77.93	12.49	0.74	0.05	0.04	0.44	0.06	3.73	4.53	100.01	0.9834
9	BT-2	77.64	12.67	0.74	0.03	0.03	0.43	0.07	3.66	4.73	100.00	0.9826
11	FRIANT 5A	77.73	12.41	0.75	0.05	0.04	0.46	0.09	3.66	4.81	100.00	0.9822
15	BT-8 (2) bulk	77.75	12.48	0.73	0.03	0.05	0.44	0.05	3.82	4.65	100.00	0.9814

about 1330 m; two higher, older barriers, units Q16<sub>T</sub> and Q15<sub>T</sub>, representing different lake cycles that reached altitudes between about 1330–1350 m and 1350–1370 m, respectively; and at least one old bar, unit Q14<sub>T</sub>, that reached a minimum altitude of about 1402 m.

An excellent small outcrop about 4 km north of Thorne Bar (Figures 2, 3) exposes four sequences of lacustrine gravel and sand that overlie bedrock (Figures 3, 4B), all lying well above the Seho shoreline. The four sequences are separated by paleosols and alluvium. The second youngest lacustrine unit here, Q13<sub>T</sub>, contains a tephra (EL-21-WL, Table 2) that is chemically correlative with the Bishop–Glass Mountain family of tephra erupted from Long Valley, California. Paleomagnetic measurements on the silty sand layers containing the tephra are not definitive in their polarity; thus, the tephra may be either the

Bishop ash bed dated from 0.76 Ma (normal polarity) or one of the tuffs of Glass Mountain dated from 1.2 to 0.8 Ma (reversed polarity; Sarna-Wojcicki et al., 1991). Small fragments of fish bones were found in the ashy layers (G.R. Smith, University of Michigan, in litt. to M.C.R., 1998). The youngest unit at this site, Q14<sub>T</sub>, consists of about 38 m of tufa-cemented, well-bedded pebble and cobble shore gravel that is commonly steeply bedded (backset beds) and that rises to an altitude of about 1393 m. Beach pebbles continue upward as lag on bedrock to an altitude of about 1398 m. Because these outcrops and the outcrops of the oldest morphologic unit at the Thorne Bar site are similar in cementation and preservation and because they rise to about the same altitude, we infer that they are equivalent.

The Bishop ash bed, identified by chemical analyses conducted by Davis (1978) and by paleomagnetic data from the

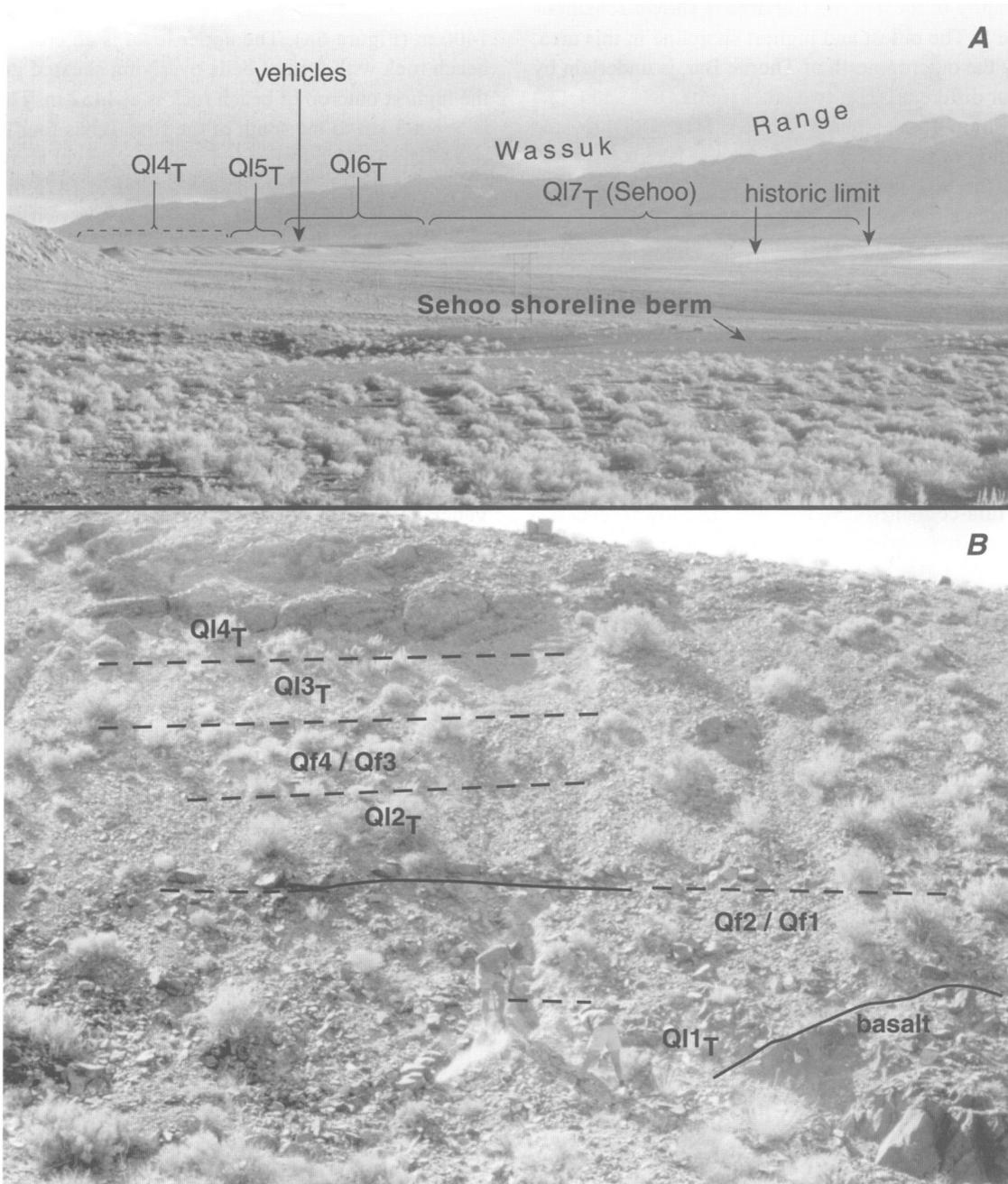


FIGURE 4.—Photographs of Thorne Bar area. A, View south toward Thorne Bar (Figure 3); bedrock of the Gillis Range is on left. Small white dots are vehicles parked on pre-late Pleistocene berm at about 1353 m, 20 m above the Sehoo shoreline. B, View of outcrop 4 km north of Thorne Bar (Figure 3); people are for scale. East-dipping gravels in upper part are tufa-cemented backset beds of unit Q14<sub>T</sub>. Line of coarse boulders at top of trench are shoreface clasts at base of unit Q12<sub>T</sub>. Trench exposes paleosols, fan deposits, and lake unit Q11<sub>T</sub> just above basalt outcrop.

present study (data not shown), is present in beach gravel beneath Sehoo-aged deposits about 4 km south of Schurz, Nevada (Figure 2). This outcrop indicates that a lake of uncertain size existed in the Walker Lake subbasin at about 0.76 Ma. We tentatively assign the tephra-bearing lake deposits of unit Q13<sub>T</sub> north of Thorne Bar to this period, but we recognize that they may be as old as 1 My. Four of the six paleosols formed

in units Q11<sub>T</sub> and Q12<sub>T</sub> and the intervening fan deposits (Figures 3, 4B) have moderately developed to well-developed argillic horizons that are 20–90 cm thick. This degree of development indicates lengthy (≥50 thousand years (Ky)) periods of nondeposition (Reheis et al., 1995) and thus a relatively long stratigraphic record prior to deposition of unit Q13<sub>T</sub>.

The stratigraphy in the Thorne Bar area is shown schematically in Figure 5. The oldest and highest shoreline in this area, as revealed by the outcrop north of Thorne Bar, is underlain by deposits of four different lakes: two lakes (units Q11<sub>T</sub> and Q12<sub>T</sub>) predated deposition of the tephra layer; one lake (Q13<sub>T</sub>) existed during deposition of the tephra layer; and one lake (Q14<sub>T</sub>) was younger than the tephra layer. Units Q11<sub>T</sub>, Q12<sub>T</sub>, and Q13<sub>T</sub> reached minimum altitudes of about 1355 m, whereas Q14<sub>T</sub> rose to a minimum altitude of about 1400 m. In addition, barriers with preserved morphology at the Thorne Bar site indicate that three younger lakes (units Q15<sub>T</sub>, Q16<sub>T</sub>, and Q17<sub>T</sub>) successively reached altitudes of about 1365 m, 1350 m, and 1330 m (the Sehoos highstand).

**20-Mile Beach:** At least two localities preserve beach gravels along the Wassuk Range front (Figure 2). These localities are at much higher altitudes than most other sites in the Walker Lake subs basin. The first site is north of 20-Mile Beach and has two levels of tufa-cemented beach gravel. The lower level is a moderately preserved wave-cut bench overlain by 1–2 m of

tufa-cemented beach rock; it extends up to an altitude of about 1400 m (Figure 6A). The upper level is an eroded remnant of beach rock with foreset beds overlying sheared granitic rocks; the highest outcrop of beach rock is at 1452 m. The second site is about 3 km to the south of the first. It has four exposed beds of beach gravel interbedded with fan gravel above the Sehoos shoreline; the highest bed caps a ridge at 1475 m (Figure 6B). The super-elevated beach gravels at these two sites are interpreted to reflect absolute uplift of the footwall block of the Wassuk fault. Demsey (1987) showed that this active normal fault had about 7 m of displacement during the Holocene, of which about 20%–25% was the result of uplift of the Wassuk Range.

**McGee Wash:** The study site at McGee Wash (Figure 2) extends from the Walker River just below Weber Reservoir eastward to U.S. Highway 95 (Figure 7). Exposures indicate that sediments there are faulted and tilted (Morrison and Davis, 1984); only the larger faults are shown in Figure 7. Dips are generally greatest on the eastern side near the highway and decrease toward the west. Younger units are progressively less de-

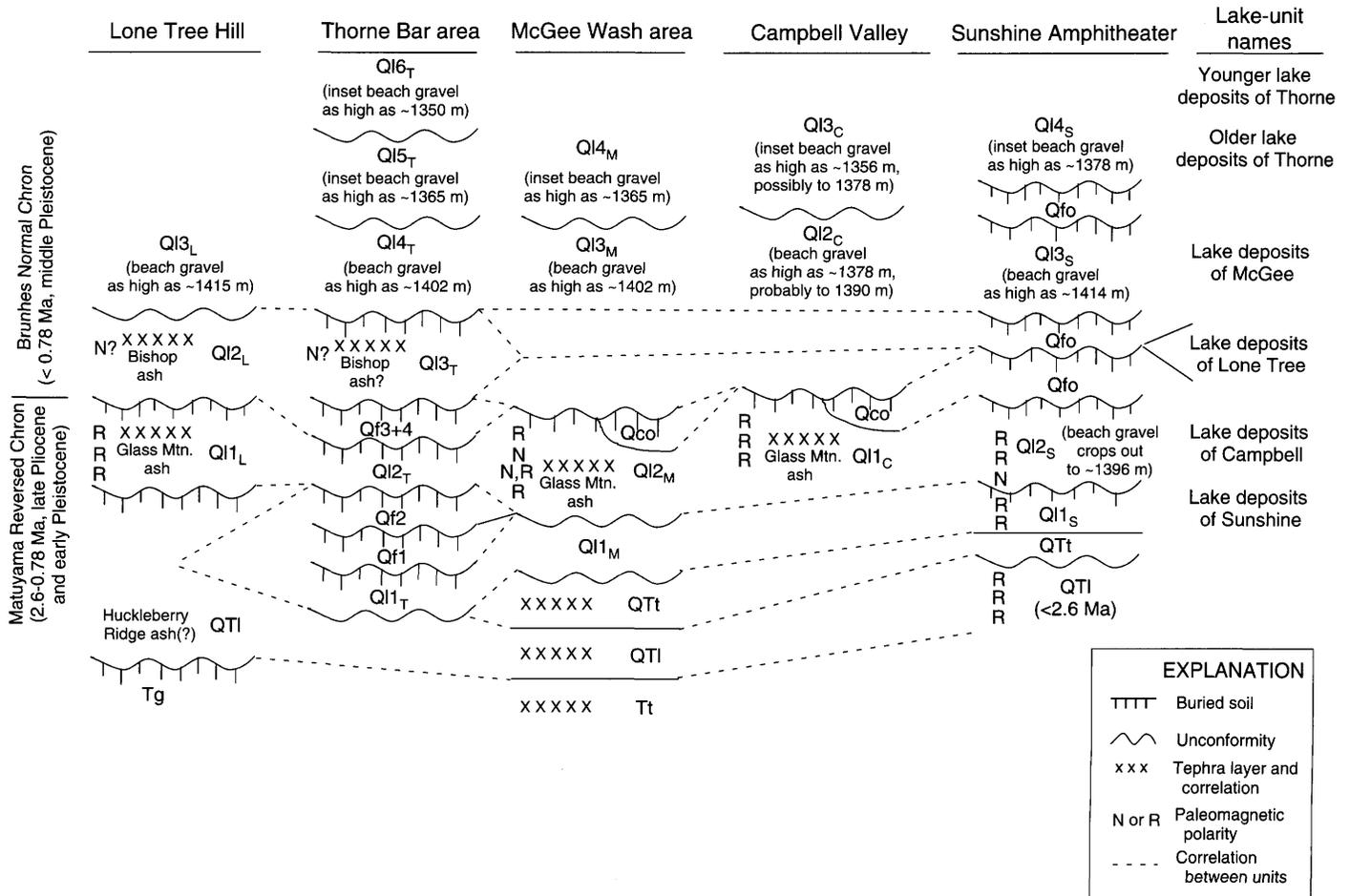


FIGURE 5.—Schematic stratigraphic correlations in the Walker Lake subs basin. Units and symbols are the same as in Figures 3, 6, 8, and 11. Deposits of Sehoos-aged lake not shown (Q17<sub>T</sub> in Thorne Bar area, grouped with fan deposits as unit Q1f<sub>y</sub> in other site maps). Wavy lines represent unconformities; attached vertical lines are paleosols. N and R indicate normal and reversed polarities, respectively, of sampled horizons, not shown to scale.

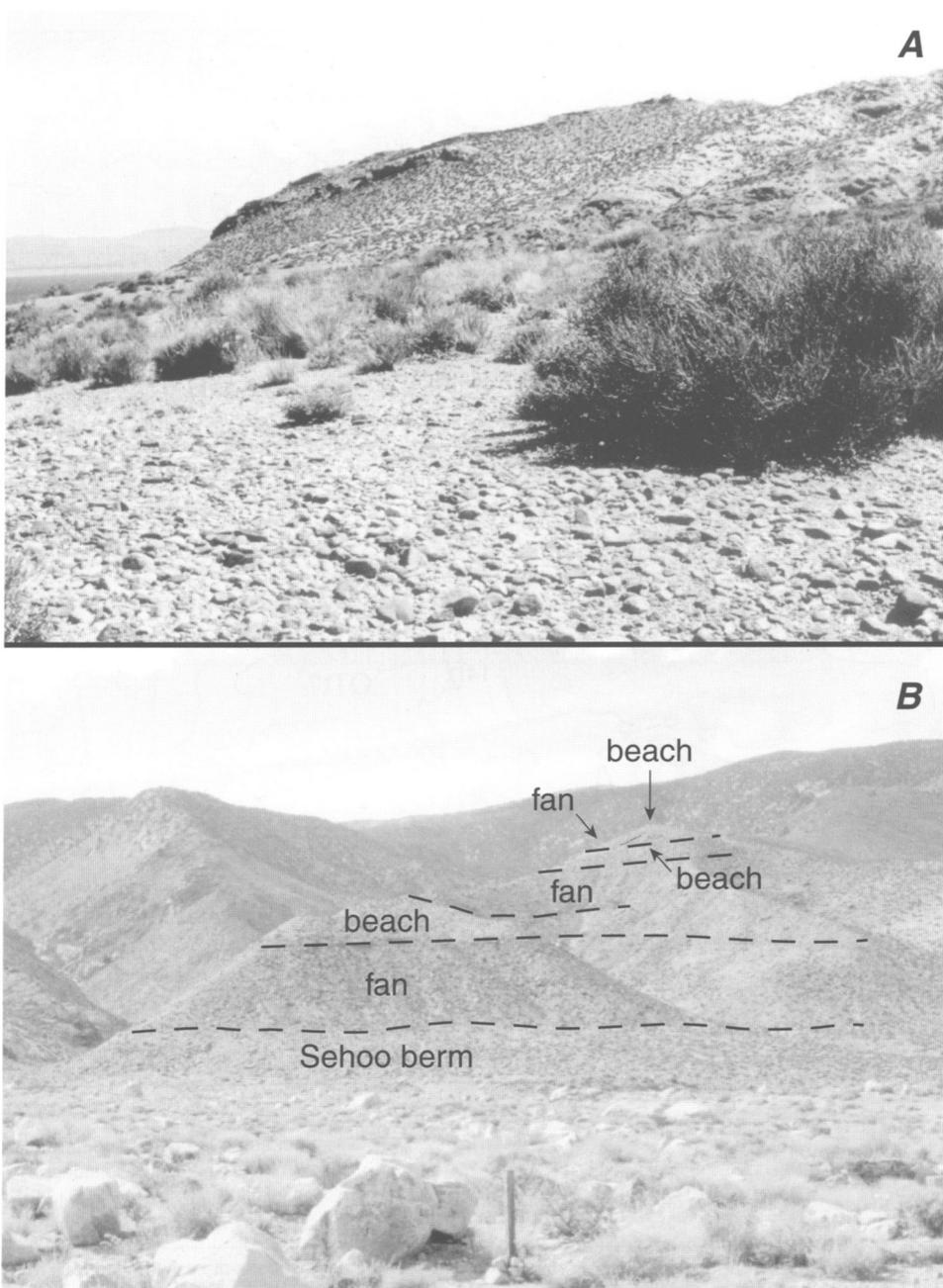
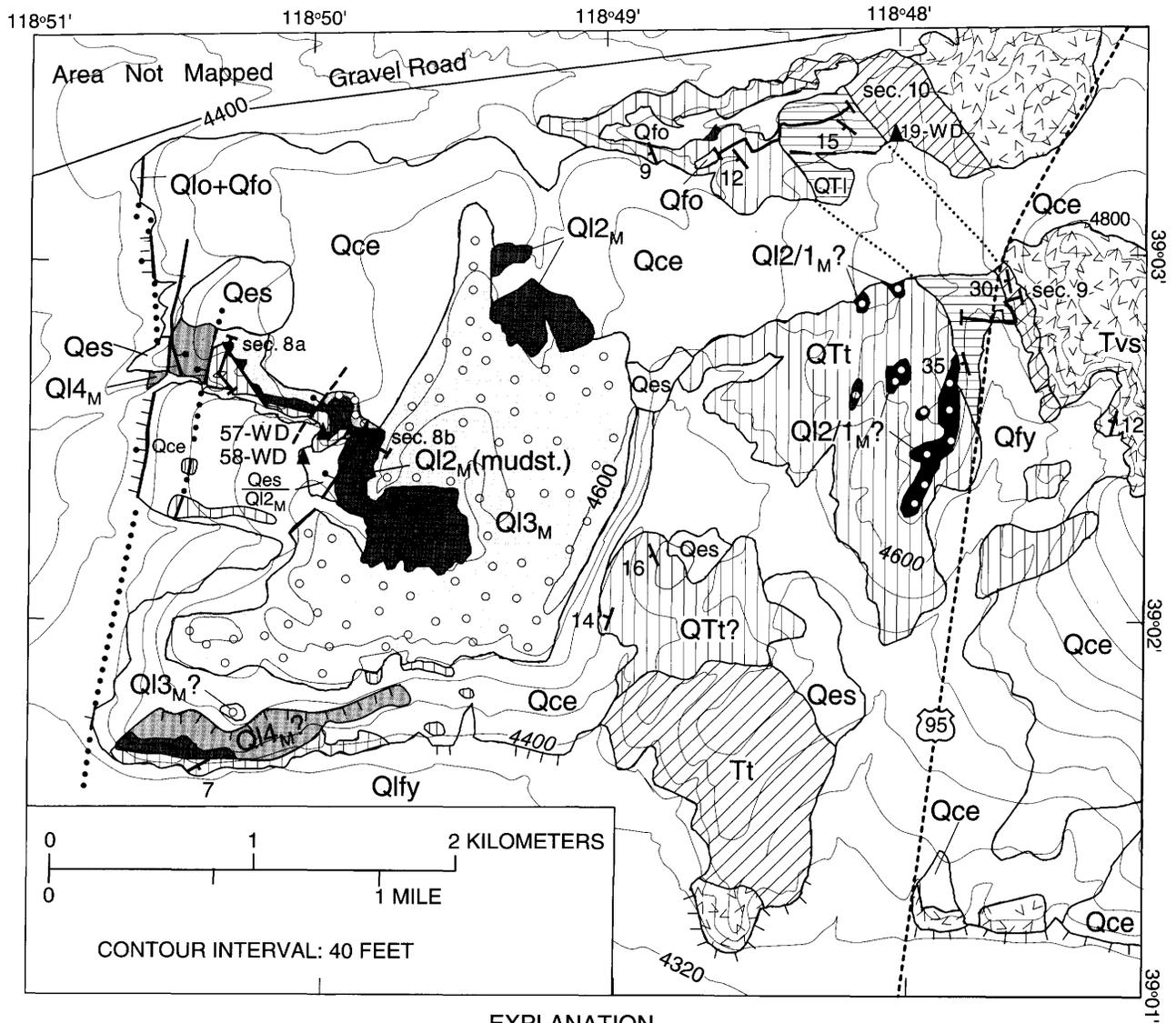


FIGURE 6.—Photographs of very high beach gravels on the footwall block of the Wassuk fault (see Figure 2 and Table 1). A, View south from gravel- and tufa-covered bench at 1399 m to sloping, eroded remnants of tufa-cemented beach rock on skyline as high as 1452 m. Bush on right is about 1 m high. B, View west of beach gravel interbedded with fan gravel above Sehooh shoreline at about 1330 m. Beach gravels crop out as high as 1475 m at top of hill.

formed. The overall structure appears to be that of a block or horst tilted progressively westward with time. This block was periodically partly or entirely covered by lakes that prograded eastward and by alluvial and eolian deposits that prograded westward. The stratigraphic units at this site are shown schematically in Figure 5.

The oldest units are exposed near the highway and consist of a conformable sequence (Figures 7, 8) of alluvial deposits (unit

Tt) overlain by about 50 m of well-bedded lacustrine mudstone, siltstone, and sandstone capped by beach gravel (unit QT1), which in turn is overlain by a very thick (unmeasured, but more than 50 m) sequence of alluvium and eolian deposits (unit QTt) containing numerous carbonate-enriched paleosols. All three of these units contain tephra layers, but only one, EL-19-WD in alluvial unit Tt, has been identified; it is tentatively correlated with an upper Miocene to lower Pliocene tephra erupted from



EXPLANATION

- |                    |  |     |   |
|--------------------|--|-----|---|
| Qes                | Eolian sand (Holocene)   | Qlo | Lacustrine deposits, undifferentiated (middle and early Pleistocene)                  |
| Qfy                | Fan deposits (Holocene and late Pleistocene)   | QTt | Alluvial, eolian, and colluvial deposits (early Pleistocene and Pliocene)             |
| Qlfy               | Lacustrine and fan deposits, undifferentiated (Holocene and late Pleistocene)                    | QTI | Deposits of early Pleistocene? or Pliocene lake                                       |
| Qce                | Colluvial and eolian deposits (Holocene and late Pleistocene)                                    | Tt  | Alluvial deposits (Pliocene and Miocene)  |
| Ql4 <sub>M</sub>   | Deposits of early late(?) Pleistocene lake   | Tvs | Volcanic and sedimentary rocks (Pliocene and Miocene)                                 |
| Qfo                | Fan deposits (middle Pleistocene)  |     | Fault; bar and ball on downthrown side; dashed where inferred, dotted where concealed |
| Ql3 <sub>M</sub>   | Deposits of middle Pleistocene lake; pattern shows beach gravel                                  |     | Shoreline scarp   |
| Qco                | Colluvial deposits (middle Pleistocene)  |     | Tephra locality and sample number of sites not within measured sections (Fig. 8)      |
| Ql2/1 <sub>M</sub> | Deposits of middle? and early Pleistocene lakes; pattern shows possibly correlative beach gravel |     | Line of measured section (see Fig. 8)   |
|                    |  |     | Strike and dip of beds  |

FIGURE 7.—Geologic map of area around McGee Wash (see Figure 2, Table 1), east of Weber Reservoir.

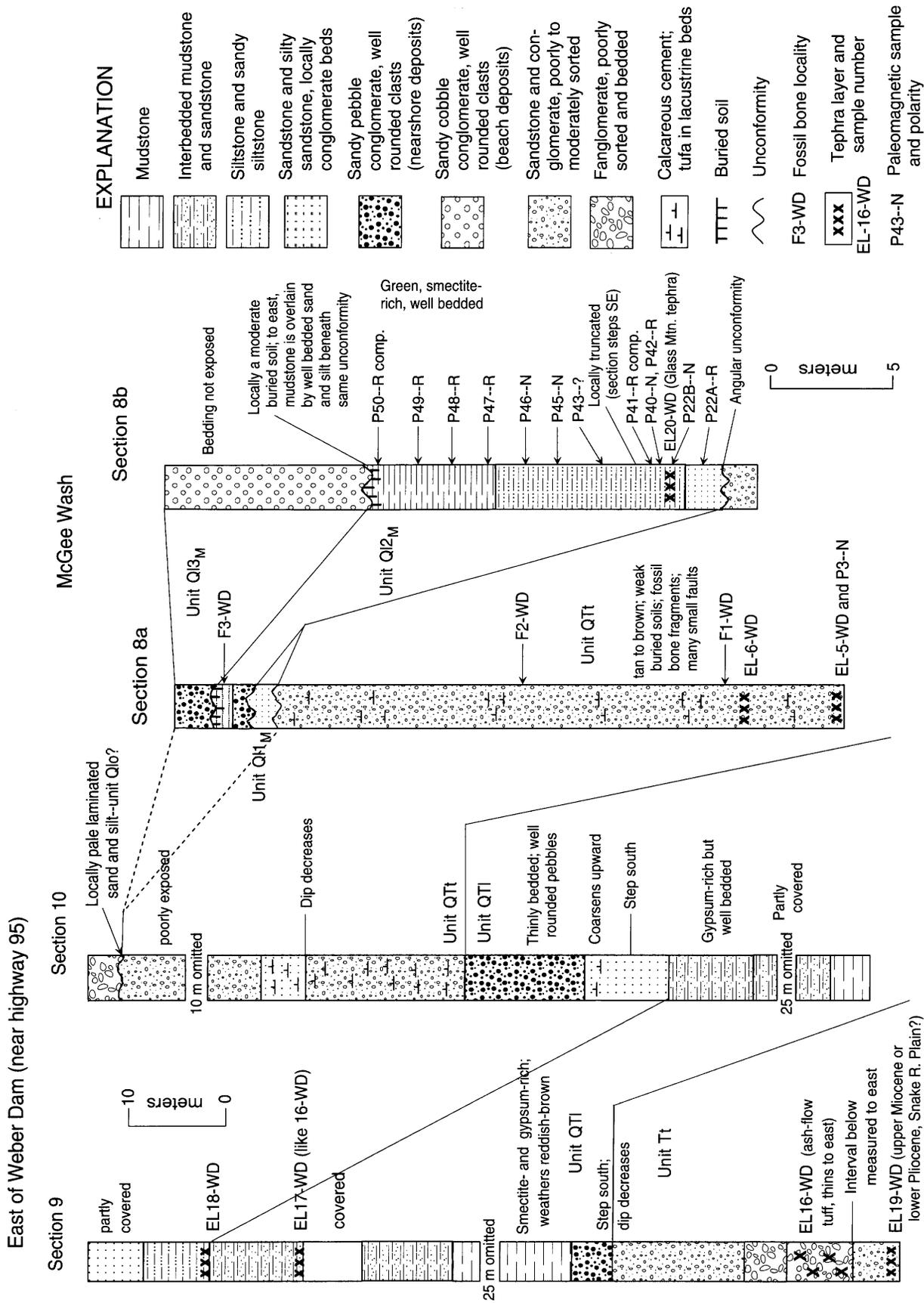


FIGURE 8.—Measured sections of lacustrine and other deposits in the area around McGee Wash. See Figure 7 for locations. Note scale difference between sections 9 and 10 near U.S. Highway 95 and sections 8a and 8b in McGee Wash. Question mark (?) in place of N or R indicates polarity uncertain; comp. is component of magnetization present.

the Snake River Plain (Table 3). In the south-central part of the map area (Figure 7), erosion between the time of deposition of alluvial units Tt and QTt has removed lacustrine unit QTl. Unit QTt apparently extends westward to underlie younger lacustrine units around McGee Wash. Three tephra layers crop out in unit QTt in McGee Wash. Sample EL-57-WD may be of Pliocene age (Table 3); two paleomagnetic samples (P3, Figure 8) indicate that EL-5-WD has normal polarity. Sample EL-6-WD has not been correlated with tephra of known age.

Four pre-Sehoo lacustrine units separated by unconformities overlie unit QTt in McGee Wash. The oldest, Q11<sub>M</sub>, is a thin (1–2 m) bed of pebble gravel overlain by silty sand (Figure 8); this unit is preserved in only a few small outcrops. Unit Q12<sub>M</sub> is locally much thicker and crops out around the head of McGee Wash (Figure 7) to a maximum altitude of about 1390 m (4560 ft). This unit consists of a basal bed of sand and pebble gravel that grades up into well-bedded silt and sand containing at least one tephra layer. Two samples (EL-20-WD, EL-58-WD; Tables 2, 3) have been identified as Bishop- or Glass Mountain-like tephra layers. Paleomagnetic data show a sequence of stable reversed magnetization in sediments below the tephra bed, stable normal magnetization in silt overlying the tephra bed, and stable reversed magnetization in overlying mudstone (Figures 8, 9). A couple of normal-magnetization samples near the tephra bed lie in between samples of reversed magnetization. We have not assessed magnetic mineralogy to determine whether these normal directions represent some type of remagnetization during a later normal-polarity interval. Nevertheless, the pattern of reversed-normal-reversed magnetizations and ash chemistry indicate that the ash is a Glass Mountain tephra that erupted at about 1 Ma, just before the Jaramillo Normal Subchron (Sarna-Wojcicki et al., 1991). If a beach-pebble facies of unit Q12<sub>M</sub> had been deposited, it has mostly been removed by erosion, but remnants of beach gravel that are probably older than that of unit Q13<sub>M</sub> are locally preserved capping units QTl and QTt near the highway at an altitude of about 1430 m (4700 ft; Figure 7).

Unit Q13<sub>M</sub> unconformably overlies silt and sand of unit Q12<sub>M</sub> around the head of McGee Wash, and it consists mainly of loose sand and gravel (Figures 7, 8). A buried soil and colluvium is locally preserved at the unconformity. Unit Q13<sub>M</sub> is poorly exposed, but in aerial photographs it has arcuate morphology resembling that of a shoreline berm. The berm rises to an altitude of 1402 m (4600 ft), the same altitude as the highest beach gravel at Thorne Bar (Figure 3).

The youngest of the four pre-Sehoo lacustrine sequences, unit Q14<sub>M</sub>, is inset into all older units (Figure 7). It consists mostly of pebbly sand; in McGee Wash the pebbly sand overlies a gray clay layer that Morrison and Davis (1984) assigned to the Eetza Alloformation. The isolated remnants of this unit lie at altitudes of 1350–1365 m and may represent faulted deposits of one lake cycle or deposits of more than one lake cycle.

*Sunshine Amphitheater:* Sunshine Amphitheater is a very large exposure of lacustrine deposits of five different ages (Figures 2, 10; stratigraphic summary in Figure 5). It is remarkable for the abundance of vertebrate fossils and the quality

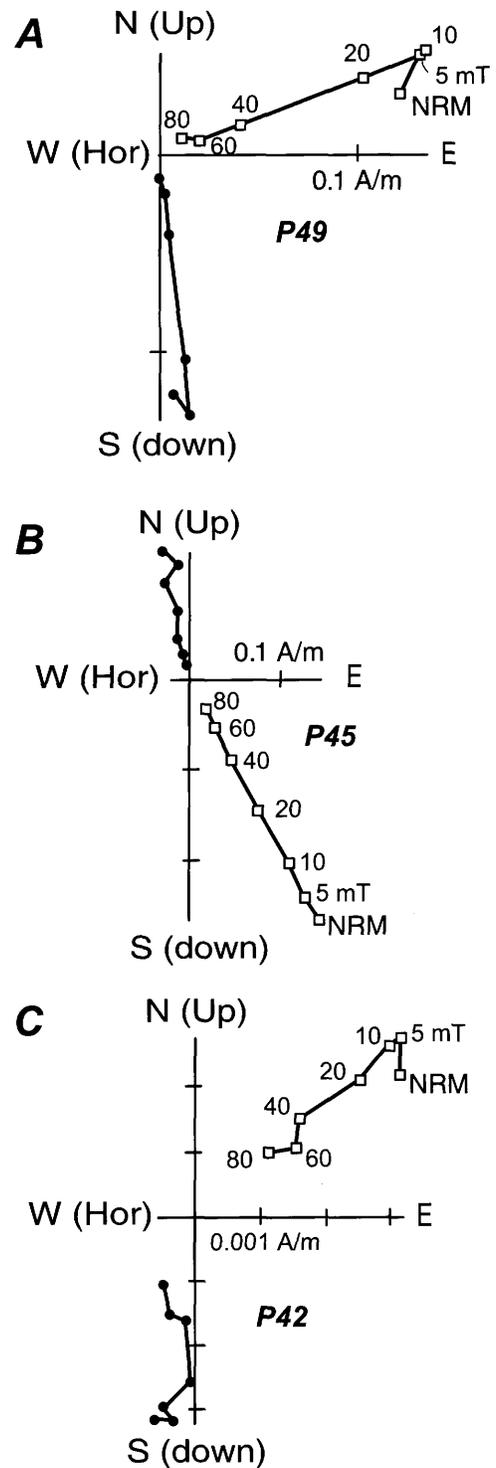


FIGURE 9.—Orthogonal demagnetization diagrams (method of Zijderveld, 1967) shown in stratigraphic order for specimens from unit Q12<sub>M</sub>, section 8b, McGee Wash. The closed symbols represent projections of the magnetic vector onto the vertical plane, whereas the open symbols represent projections of the magnetic vector onto the horizontal plane. Remanent magnetizations are given in amperes/meter (A/m). Demagnetization steps are in milliTesla (mT). A, Reversed magnetization in sample P49; B, normal magnetization in sample P45; C, reversed magnetization in sample P42, from 26 cm above tephra bed EL-20-WD.

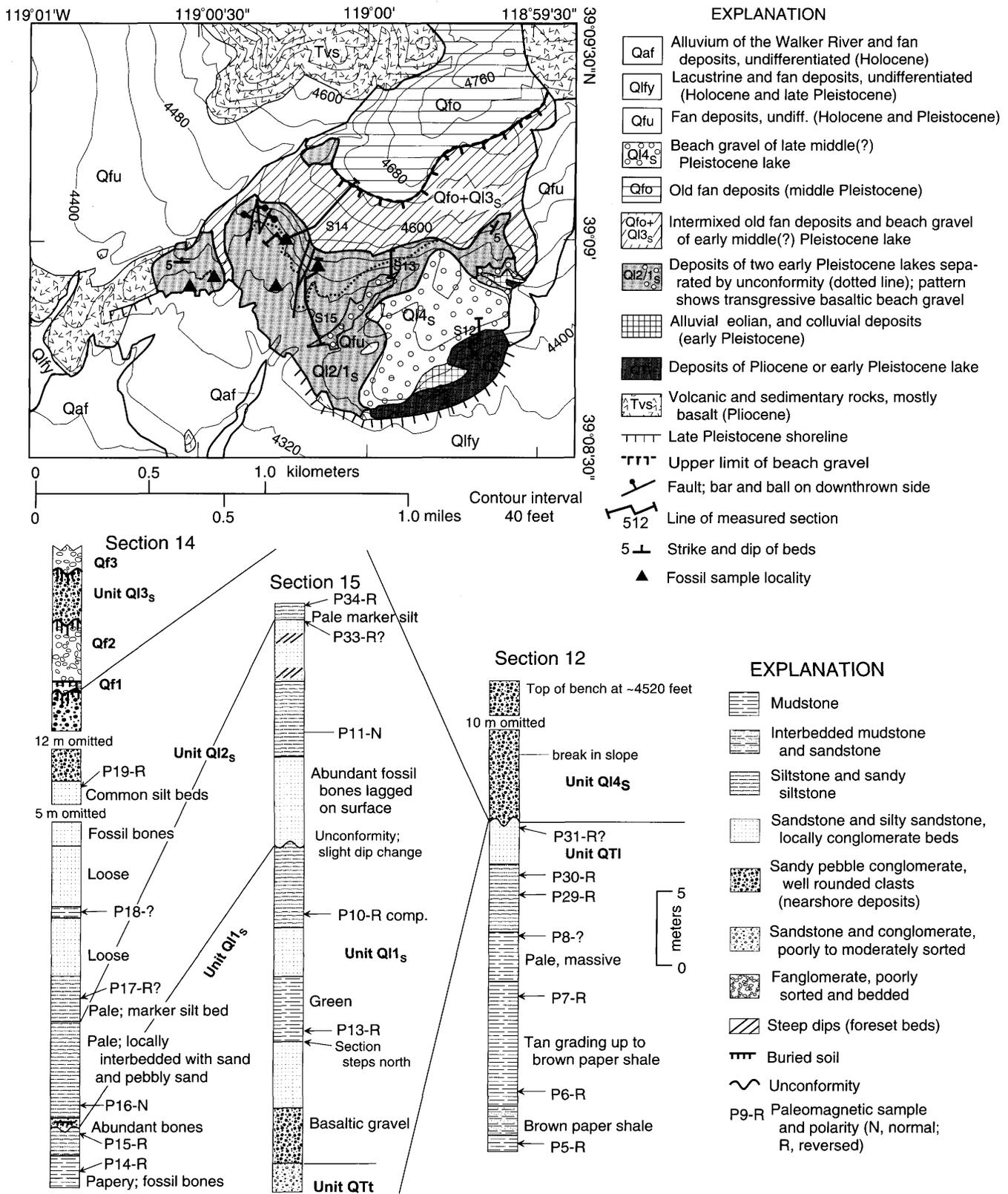


FIGURE 10.—Geologic map of Sunshine Amphitheater (Figure 2, Table 1) and selected measured sections. The portion of section 14 above the closely spaced contours (top of unit Ql2<sub>s</sub>) was not measured and is schematic. Question mark (?) in place of N or R indicates polarity uncertain.

of their preservation; thus far, identified remains include those of giant sloth, bird, horse, camel, mammoth, and fish. The abundance of fossil remains at Sunshine Amphitheater may be the result of its location adjacent to the Walker River near the point where the river bends in a U-turn (Figure 2). Floods coming down the north-flowing reach of the river would have been forced to slow and drop part of their loads; the natural deposition site would have been on the outside of the bend. Small faults are exposed, but the units do not appear to be greatly offset, in contrast to the McGee Wash and Campbell Valley sites.

The oldest non-bedrock unit, QT1, consists mainly of brown, finely laminated mudstone capped by pebbly sandstone; the mudstone has reversed magnetization (Figures 10, 11D). It is overlain by unit QTt, which has alluvial and eolian deposits containing carbonate-enriched paleosols. Unit QTt is conformably overlain by well-bedded pebbly sandstone, siltstone, and mudstone of unit Q11<sub>s</sub>, which also has reversed magnetization (Figure 11C). A distinctive horse bone (*Equus excelsus*(?) Leidy, 1858) from unit Q11<sub>s</sub> appears to constrain the age to less than 1.4 Ma. The jaw of a Lahontan cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)) and a vertebra of a sucker

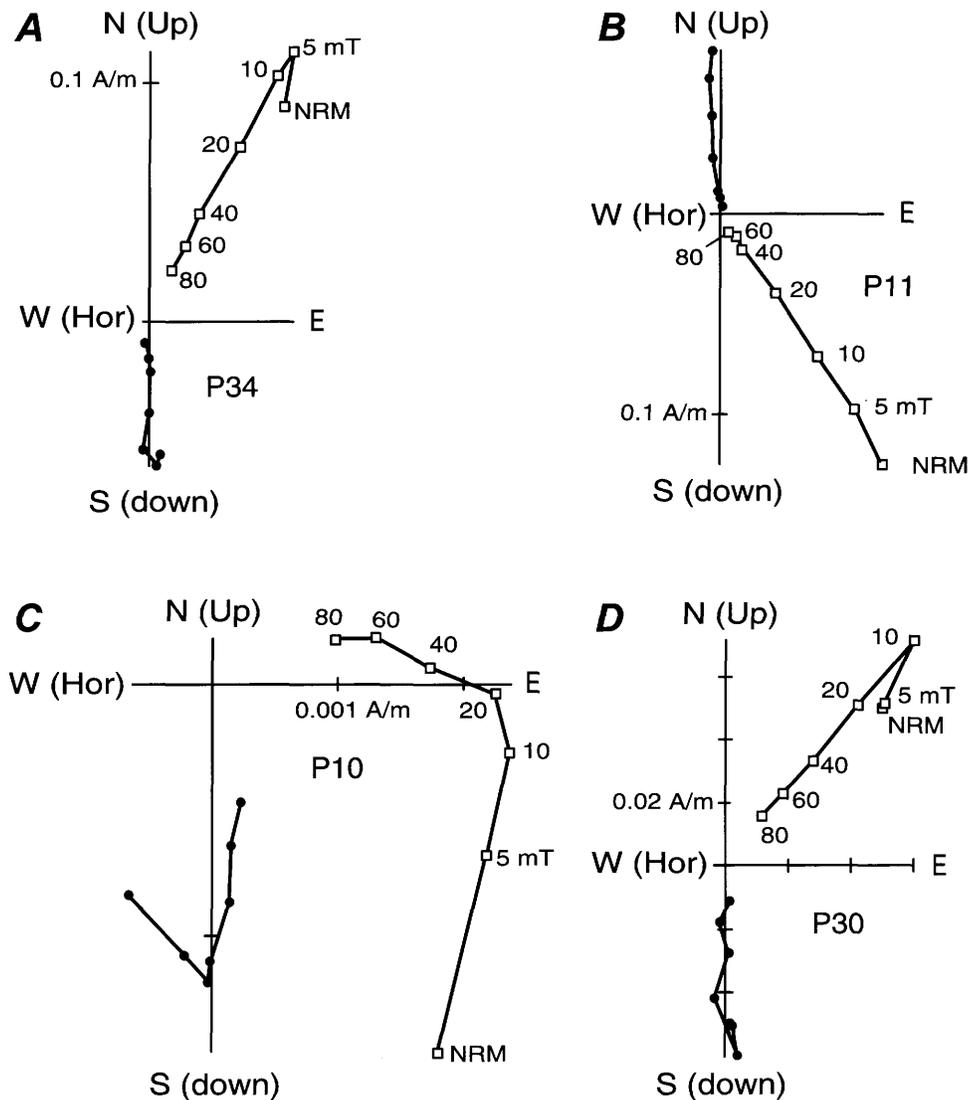


FIGURE 11.—Orthogonal demagnetization diagrams (method of Zijdeveld, 1967) shown in stratigraphic order for specimens from Sunshine Amphitheater sections. Symbols are the same as in Figure 9. A, Reversed magnetization in sample P34 in unit Q12<sub>s</sub>, section 15; B, normal magnetization in sample P11, lower part of unit Q12<sub>s</sub>, section 15; C, reversed magnetization component in sample P10 in unit Q11<sub>s</sub>, section 15 is indicated by the isolation of southward, negative-inclination (up) vector after the removal of a northward, positive-inclination (down) vector following demagnetization at and above 40 mT; D, reversed magnetization in sample P30 in unit QT1, section 12.

(*Catostomidae* sp.; G.R. Smith, University of Michigan, in litt. to M.C.R., 1996) also were collected from this unit. This age range is consistent with the assignment of the reversely magnetized sediments to the Matuyama Reversed Chron (2.6–0.8 Ma; magnetic-polarity ages of Cande and Kent, 1995). An unconformity, locally marked by thin colluvium and a paleosol, separates units Q11<sub>s</sub> and Q12<sub>s</sub> (Figures 10, 12A). Many of the fossils are associated with this stratigraphic interval, including mammoth bones (*Mammuthus* sp., also less than 1.4 Ma) and the astragalus of a sloth identified as post-Blancan in age (<2.6 Ma; J. Honey, University of Colorado, pers. comm. to M.C.R., 1995). Unit Q12<sub>s</sub> extends to an altitude of 1396 m and consists of poorly indurated siltstone and sandstone that coarsen upward into beach gravel. These deposits also contain fossilized horse and bird bones. Paleomagnetic measurements indicate that this unit has reversed magnetization except for an interval near the base, which has normal magnetization (Figures 10, 11A,B). These data and the presence of a horse bone beneath the unconformity indicate that the normal polarity interval probably correlates with the Jaramillo Normal Subchron from about 1 Ma. Thus, the three oldest lacustrine units at Sunshine Amphitheater lie within the Matuyama Reversed Chron; unit Q11<sub>s</sub> was deposited between 1.4 and 1.0 Ma, and unit Q12<sub>s</sub> was deposited beginning at about 1 Ma (Figure 5).

Unit Q12<sub>s</sub> at the top of the bluff (section 14, Figures 10, 12A) bears a well-developed argillic paleosol (Figure 12B) overlain by fan gravel that forms a sloping bench. Exploratory soil pits on this bench indicate that the fan gravel is capped by a paleosol and is buried in turn by beach sand and gravel of unit Q13<sub>s</sub>, another paleosol, and a younger fan gravel; unit Q13<sub>s</sub> rises to an altitude of about 1414 m. Unit Q14<sub>s</sub> consists of sandy beach gravel inset into all of the older units; it rises to an altitude of about 1378 m.

*Campbell Valley and Vicinity:* The interpretation of outcrops in Campbell Valley (Figures 2, 13) is complicated by a network of northwest-striking strike-slip faults of the Walker Lane. Displacement along these faults has juxtaposed lake sediments of different ages, making it difficult to correlate deposits of beach gravel that mark shorelines with the finer-grained sediment that contains age-related information. Three lacustrine units are locally exposed (Figures 13, 14). The oldest, Q11<sub>c</sub>, consists mainly of mudstone that grades up into beach sand and gravel; four samples from the mudstone have reversed magnetization. Deposits in another outcrop, herein assigned to the same unit as the mudstone but possibly belonging to a younger lake cycle, consist of shoreface gravel that rapidly grades laterally into fine-grained beds lapping onto subjacent basalt. A tephra layer, sample EL-15-CA, drapes this facies change from shoreface into deep-water deposits (Table 2; Figure 14A). The tephra, a sample from which has normal magnetization, is correlated with the Bishop–Glass Mountain family of tephra (Table 3). The reversed magnetization of sediment just above and below the tephra layer, however, indicates that the tephra cannot be Bishop ash on the basis of enveloping re-

versed magnetizations; thus, the tephra is probably a Glass Mountain tephra from about 1 Ma. Unit Q11<sub>c</sub> is unconformably overlain by beach gravel of unit Q12<sub>c</sub>; a paleosol and colluvium are locally preserved at the contact. Unit Q12<sub>c</sub> rises to at least 1378 m, and beach pebbles that probably represent this unit are present as lag on basalt up to an altitude of 1390 m. The pebbles are found up to an abrupt change in slope that resembles a preserved shoreline angle cut on a small island, or stack (Figure 14B). Beach gravel of unit Q13<sub>c</sub> is apparently inset into the older units and forms a berm at an altitude of 1356 m.

Another site in Campbell Valley, between Sunshine Amphitheater and Weber Reservoir on the east side of the Walker River (Figure 2), records shorelines cut into two basalt hills. Subdued breaks in slope occur on the west sides of these hills, with the most prominent slope break occurring at an altitude of 1365 m. From a distance these slope breaks resemble flow contacts, but they are actually degraded shoreline angles. Rounded beach pebbles locally lie below the most prominent slope break, and they are identical to pebbles that abundantly mark the Seho shoreline-cut on the same hills at 1330 m. Additional small remnants of slope breaks may also record shoreline angles at altitudes of 1353 m and 1396 m. A high shoreline is further supported by an outcrop on the east side of one of the hills. There, rounded clasts of rhyolite and basalt overlie a rhyolite flow weathering into angular clasts; the rounded clasts, interpreted as beach gravel, crop out as high as 1390 m.

EVIDENCE FROM THE NORTHEASTERN LAHONTAN BASIN (HUMBOLDT RIVER).—During the Seho highstand, the northern subbasins of Lake Lahontan were filled to an altitude of ~1330 m. According to Davis (1982), Lake Lahontan could have been connected to the Walker Lake subbasin only by the narrow Adrian Valley (Figures 1, 2). King (1993), however, thought that Adrian Valley did not exist during the early-middle(?) Pleistocene. If his theory is correct, high lakes in the Walker Lake subbasin would have been isolated from Lake Lahontan during this time. Yet in the foregoing discussion, we have documented a lake in the Walker Lake subbasin that rose to an altitude of about 1400 m. This lake could have spilled over a pair of sills at 1370 m into the northern subbasins of Lake Lahontan through Rawhide Flats (Figure 2), if the sills leading into Rawhide Flats were not much higher than they are now. If such a connection existed, evidence of high shorelines north of the Desert Mountains would be required to establish that the very high shorelines found in the Walker Lake subbasin were coextensive with Lake Lahontan as a whole. No such evidence had been previously reported. Roberts (1965), however, suggested that the region around Lone Tree Hill contained evidence of a lake, but because the sites he described were above the Seho highstand, he inferred that this lake was separate from Lake Lahontan and must have been impounded by a dam in the Humboldt River canyon east of Winnemucca. Most of Roberts' sites, except that at Treaty Hill, consist of fluvial terrace deposits of the Humboldt River.

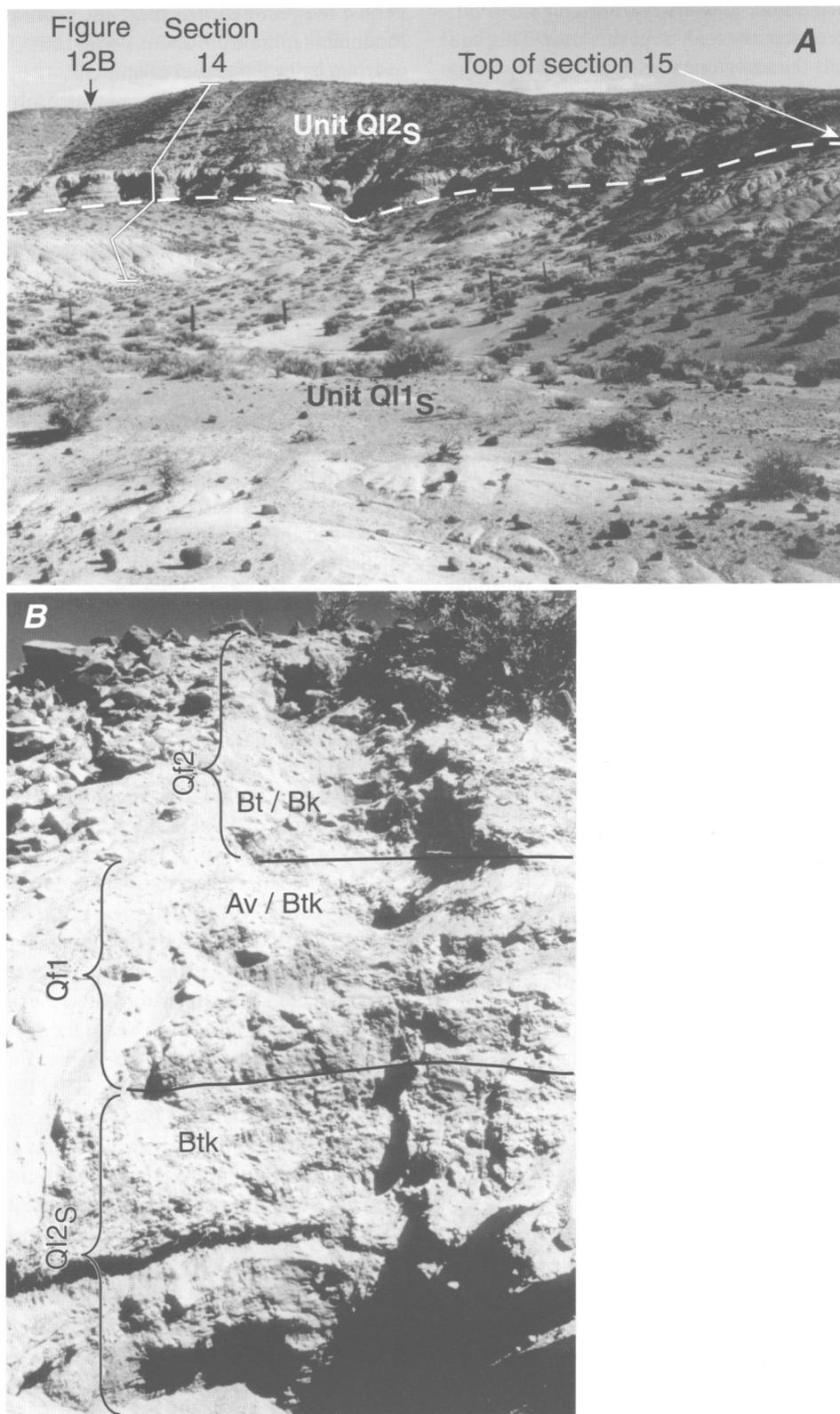


FIGURE 12.—Photographs of central part of Sunshine Amphitheater. A, View north showing area of sections 14 and 15 (see Figure 10); fence posts show scale. B, Paleosols and fan deposits separating units Q12<sub>s</sub> and Q11<sub>s</sub> at the top of section 14, exposed at top of bluff in A. Trowel indicates top of unit Q12<sub>s</sub>.



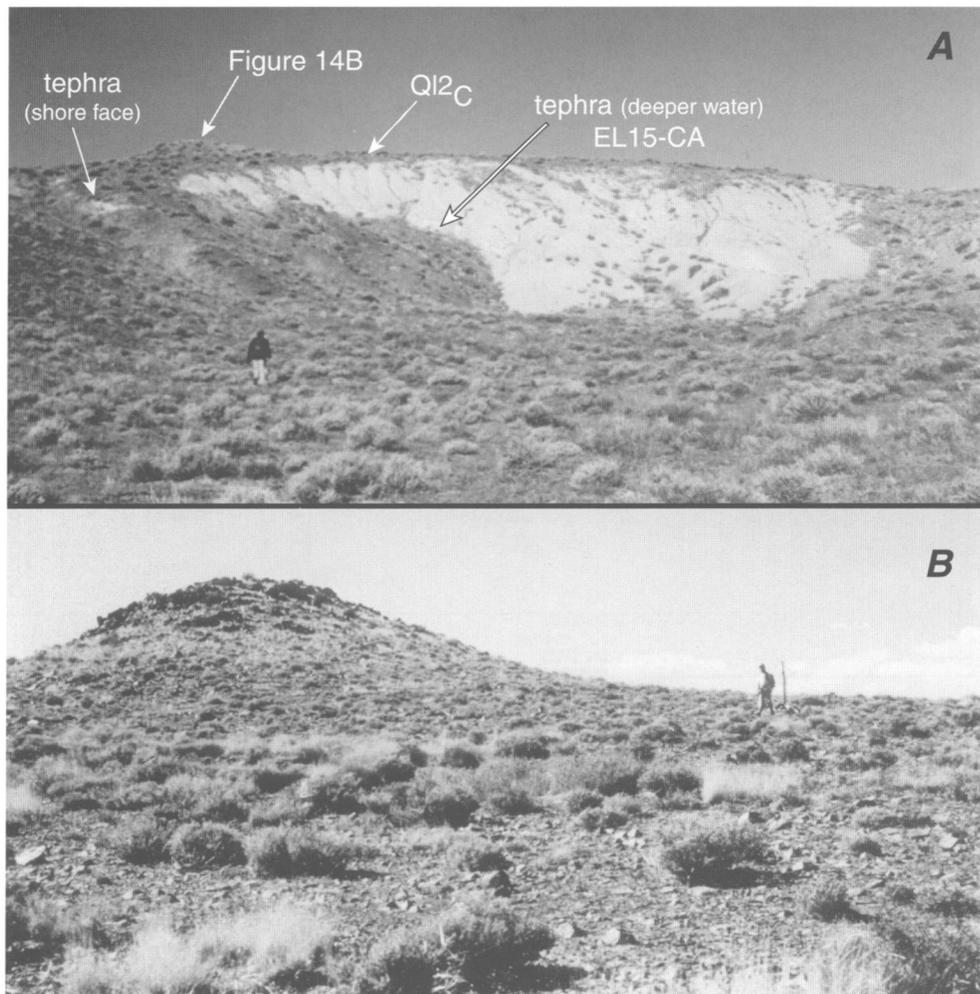


FIGURE 14.—Photographs of Campbell Valley area; person is for scale. A, View west of outcrop of tephra EL-15-CA, showing drape of tephra from shoreface position atop basalt into deeper-water sediments. See Figure 13 for location. B, View north of shoreline angle cut on outcrop marking shoreline (~1390 m) reached by lake during deposition of unit Q12C. Hill is just behind highest point visible in A.

Work began in 1997 at a new site on the Humboldt River between Winnemucca and Battle Mountain (Figure 1), within the area studied by Roberts (1965). This site has both spectacular exposures and geomorphic evidence of pre-late Pleistocene lakes. The outcrops are within large open pits of the Lone Tree gold mine, currently operated by Newmont Gold Corporation; as a result of mining operations, the exposures are excellent but change constantly. Our work has focused on a less frequently remodeled roadcut within the mine on the south flank of Lone Tree Hill (Table 1) and on samples from a core drilled southeast of the hill (Figure 15). The data from these sites are supported by observations and tephra samples from other, now-destroyed pit walls.

Premining topographic maps show a prominent berm as high as 1410 m extending south from Lone Tree Hill. The roadcut sequence (Figures 15, 16) is within this berm. Well-rounded cobbles are lagged on slopes above the berm as high as about 1415 m. Outcrops of lacustrine deposits form the upper 5–50 m

of the walls of all of the open pits south and west of the hill, providing a three-dimensional view of kilometers of outcrop. The lacustrine deposits and older units are cut by three normal faults that bound the hill on the east, south, and west; thus, Lone Tree Hill is a horst. From outcrops and core data, the base of the lake deposits appears to be offset at least 40 m by the eastern fault, 8 m by the southern fault, and 50 m by the western fault. The amount of absolute uplift of the horst is unknown, but it could be considerable in such an active tectonic setting. A younger, lower berm at about 1370 m in altitude was present on the northwest side of the hill, but the berm is now obscured by construction.

Outcrops in Lone Tree Mine and core samples are tentatively interpreted to represent four lake units separated by unconformities and paleosols. In the roadcut exposure, unit Q11<sub>L</sub> is reversely magnetized where the sediments are fine-grained; these sediments interfinger with coarser sand and gravel with steep foreset beds (Figures 15, 16) containing a tephra layer (sample

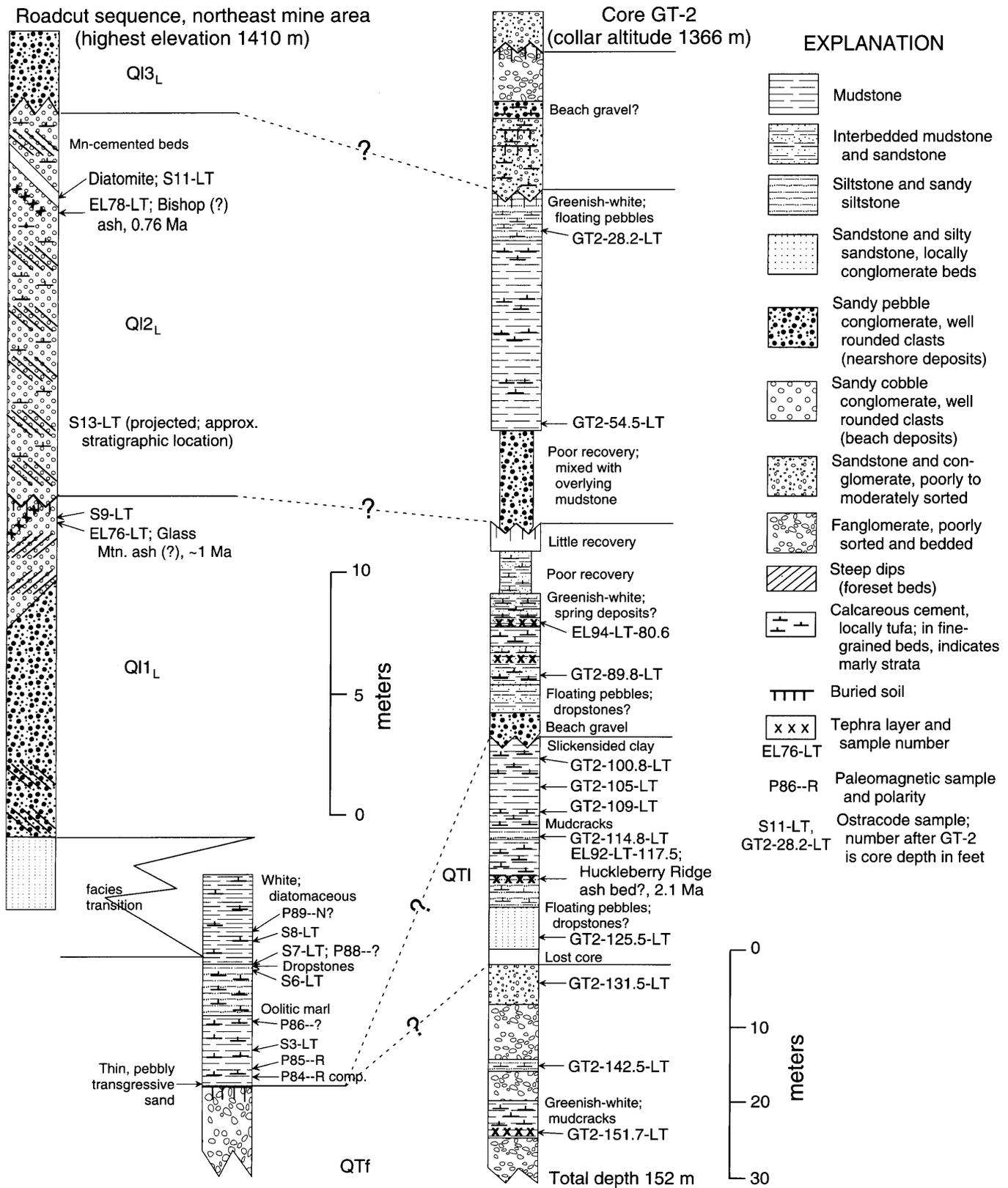


FIGURE 15.—Measured section and core description of lacustrine deposits in Lone Tree mine on the flanks of Lone Tree Hill (see Figure 1, Table 1 for location). Question mark (?) in place of N or R indicates polarity uncertain. Correlation lines between measured section and core are only tentative. Note scale difference between roadcut sequence and core GT-2.

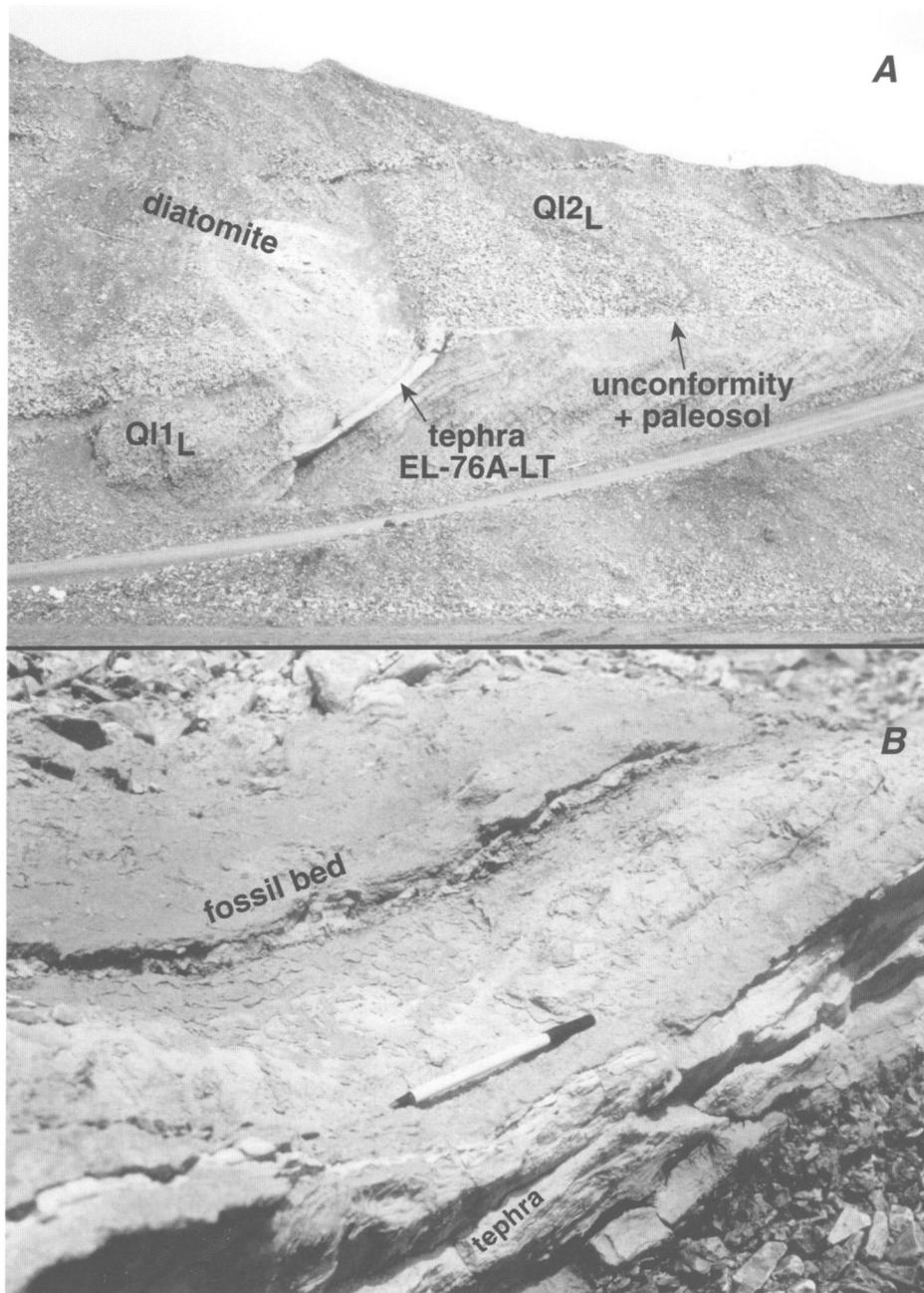


FIGURE 16.—Photographs of central portion of roadcut sequence in Lone Tree Mine. A, East-dipping foreset gravel beds and diatomite in unit QI<sub>2L</sub> overlie a horizontal unconformity and paleosol that formed on west-dipping foreset beds and tephra EL-76A-LT (Table 3) in unit QI<sub>1L</sub>. B, Close-up of fossiliferous sand layer above tephra (pencil for scale); sand contains abundant fish bones (*Catostomus* sp.; G.R. Smith, University of Michigan, in litt. to M.C.R., 1998) and ostracode shells.

EL-76A-LT, Tables 2, 3) with Bishop–Glass Mountain-type chemistry. A sandy layer above the tephra layer (sample S9-LT, Figures 15, 16B) contains abundant ostracodes and small bones of *Catostomus* sp. (sucker; G.R. Smith, University of Michigan, in litt. to M.C.R., 1998). Unit QI<sub>2L</sub> in the roadcut consists entirely of sandy gravel, which is commonly steeply bedded,

and a 1 m thick diatomite bed (Figure 16A); the unit overlies an unconformity and a paleosol. In two places, gravel clasts of unit QI<sub>2L</sub> are embedded in a matrix of tephra (sample EL-78-LT), which also has Bishop–Glass Mountain-type chemistry. These characteristics indicate that units QI<sub>1L</sub> and QI<sub>2L</sub> are from about 1 Ma and 0.76 Ma, respectively. It is possible that the

lower tephra could be the Bishop ash because the sediment enclosing the tephra was too coarse-grained for paleomagnetic determination, but this is unlikely because this coarse sediment interfingers laterally with fine sediment that is reversely magnetized, as noted above. Also, the presence of a paleosol separating the units indicates that the upper tephra was probably not reworked from the lower tephra. The youngest and highest lake unit in the roadcut is undated.

Correlation of the roadcut exposures to the core samples is problematic because of differences in grain size, fault displacement between the core and the roadcut, and alteration in the core sediments that prevented analysis of most of the tephra samples. However, the core should contain a more complete record of lacustrine deposition because of its location on a subsiding fault-block. A tephra layer (sample EL-92-LT) from the lowest lake unit in the core contains shards that are chemically similar to the Lava Creek B ash bed and to the Huckleberry Ridge ash bed, both of which erupted from the Yellowstone area (Izett, 1981) 0.66 Ma and 2.1 Ma, respectively (Pluhar et al., 1992; Sarna-Wojcicki et al., In review). Ostracodes that became extinct by about 0.6 Ma (*Elkocythereis bramletti* (Dickinson and Swain, 1967); R. Forester, USGS, in litt. to M.C.R., 1998) are present throughout the core, indicating the older age is likely correct. The older lake unit (from 2.1 Ma) in the core is not present in the roadcut (Figure 15).

Environmental conditions interpreted from ostracodes throughout most of the core and from unit Q11<sub>L</sub> in the roadcut indicate this area had shallow to moderate water levels, relatively saline alkaline water, and cool-season runoff as well as warm summers (R. Forester, USGS, in litt. to M.C.R., 1998). An unusual suite of ostracodes in sample S-13-LT from unit Q12<sub>L</sub> (Figure 15) includes several highly ornate, endemic species that are thought to have evolved in a long-lived, stable lake (discussed in Forester, 1991) and a species that can live in a relatively deep-water lake (*Candona* aff. *C. caudata* Kaufmann, 1900). We speculate that the endemic species, which clearly did not evolve locally because they are not present in any other samples, could have arrived during a sudden influx of water from a previously undrained lake basin upstream. The *Candona* shells suggest deeper water prevailed during the time of deposition of unit Q12<sub>L</sub> than during that of Q11<sub>L</sub>. A few samples from the core and the roadcut exposures contained ostracodes and diatoms (J. Bradbury, USGS, in litt. to M.C.R., 1998) that live in springs. This is consistent with sediments in the core and outcrops that are interpreted as spring deposits and with the presence of modern springs at Lone Tree Hill.

Other localities near Lone Tree Hill provide additional evidence of pre-late Pleistocene highstands. On the north side of the Humboldt River, a saddle between the two summits of Treaty Hill (Figure 1, Table 1) has the form of a beach berm and consists of very well-rounded pebble to cobble gravel of diverse lithologies. The saddle is at an altitude of 1402 m; pebble lag extends up the south hillslope to as high as 1414 m. This gravel is unlikely to be a terrace deposit of the Humboldt

River because the shape and orientation of the berm seem to preclude deposition by the river, and because the river does not flow in an antecedent course across a rising block at this location. However, some tectonic uplift of Treaty Hill, like that inferred at Lone Tree Hill, is certainly possible. A lower erosional bench on the east side of Treaty Hill also may represent a shoreline at about 1360 m, as noted by Roberts (1965). West of Lone Tree Hill, at Iron Point on the Humboldt River, scattered, very well-rounded pebbles lie on gently sloping basalt surfaces at altitudes from 1350 m to 1370 m (Table 1).

Northeast of Treaty Hill is a broad, very flat surface that slopes gently westward for several kilometers from an altitude of 1362 m to 1344 m (Table 1) and is underlain by well-rounded gravel and sand. This surface is interrupted by a subdued break in slope at 1356 m. A drainage ditch exposes a well-developed argillic soil that formed on these gravel deposits and that is buried beneath nearly 2 m of loess. Although exposures are few and poor, the evidence suggests that this surface and the underlying deposits may represent pre-late Pleistocene deltaic deposits of the Humboldt River graded to a lake level that reached as high as about 1356 m.

EVIDENCE FROM OTHER SUBBASINS OF LAKE LAHONTAN.—Soda Springs Valley (Figures 1, 2) extends southeast of Walker Lake. Modern elevations of the valley floor are below 1400 m; small basins in the valley are as low as 1330–1352 m, and sills are between 1377 m and 1396 m. It is likely that valley-floor altitudes are higher at present than in the past because of alluvial-fan sedimentation. These sediments accumulate because rates of vertical displacement along the active strike-slip faults in this part of the Walker Lane belt are low (Yount et al., 1993). Thus, the 1400 m high lake-level recorded at several sites in the Walker Lake subbasin indicates that the pre-late Pleistocene lake should have flooded Soda Springs Valley. Lacustrine deposits of Miocene to late Pliocene age are preserved along the range fronts on both sides of Soda Springs Valley and south of Rhodes Salt Marsh (discussed below); however, younger lacustrine deposits have not been found.

Several sites along the Truckee and Carson Rivers in canyons below Reno and Carson City, respectively (Figure 1, Table 1), consist mainly of rounded, exotic clasts overlying bedrock. The clasts may represent times when rivers were graded to lake levels far above the Seho shoreline, or they may represent terraces stranded by uplift of the mountain blocks through which the rivers flow. Arcuate geomorphic features with rounded cobbles occur in the Truckee River canyon at an altitude of about 1400 m, and one roadcut exposes sediment that may be lacustrine or deltaic at about 1355 m. At one locality on the Carson River, the rounded clasts are found on slopes protected from river erosion and above a bedrock sill where the Seho-aged lake spilled northward out of the canyon. The clasts at this site are more likely to reflect high lake-stands rather than fluvial gravels.

Good evidence of high, old shorelines exists at three sites in the Smoke Creek Desert (Figure 1, Table 1). These old shore-

lines were first observed by Mifflin while conducting field work during the 1970s. The southern site is near Burro Mountain in the Smoke Creek Desert and lies 1–2 km west of an active Quaternary fault that bounds the western edge of the basin (Weick, 1990). Two subtle benches and risers are underlain by basalt and rhyolite flows (Figure 17A). The upper bench terminates upward at a slope break at an altitude of about 1400 m, and well-rounded small pebbles, many flattened and discoidal in shape, are scattered over the bench at altitudes between 1395 and 1400 m. The lower bench, further east and closer to the fault, is at about 1375 m and is blanketed with abundant well-

rounded pebbles and a few fragments of lacustrine tufa (Figure 17B). A few kilometers to the north, another site also has abundant well-rounded pebbles of similar shape at about 1390 m. Alluvial interbeds that could have weathered to provide rounded gravel were not observed within the volcanic flows at these sites. It is possible that the well-rounded pebbles at these sites could represent deposition by an ancient stream prior to uplift along the Bonham Ranch fault zone (Weick, 1990); three other nearby sites that were field-checked by M.C.R. were so interpreted on the basis of their lithologic composition and broad range of clast sizes, which were similar to those of the

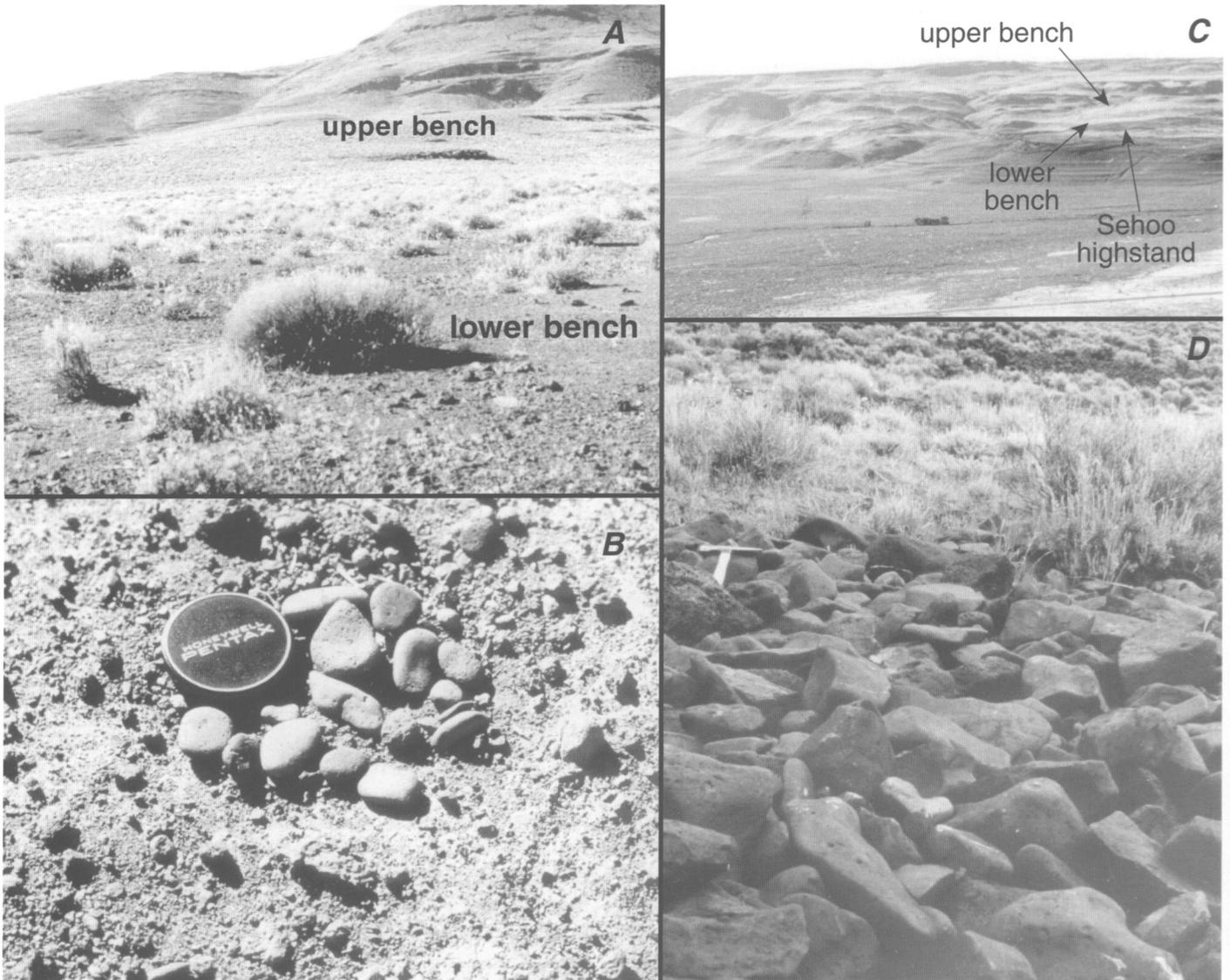


FIGURE 17.—Beach-gravel sites in the Smoke Creek Desert (see Figure 1, Table 1). A, East flank of Burro Mountain. View is to the west from the lower shoreline bench at 1375 m to the upper bench at 1400 m. B Typical scatter of beach pebbles at Burro Mountain site; remnants of lacustrine tufa also present on lower bench. Lens cap is for scale. C, View northwest to Freds Field site. Subtle benches are cut on basalt flows above the Seho shoreline on photo right. D, Well-rounded and polished basalt clasts make up the majority of block streams on the shoreline benches of the Freds Field site. Rock hammer is for scale.

local modern streams, namely, Smoke Creek and Buffalo Creek.

The eastern site in the Smoke Creek Desert (Figure 1; Table 1, Freds Field) consists of two benches and risers underlain by basalt flows (Figure 17C), forming subdued topography above a steep cliff on which the Seho shoreline are cut. The benches are laterally continuous and are covered with basalt clasts closely fitted together in pavements interspersed with rougher surfaces. The risers are also covered with basalt clasts that form matrix-poor stone stripes. More than 50 percent of the clasts on the benches and risers are polished and rounded (Figure 17D) rather than angular or subangular, as is typical of clasts in colluvial block fields. This polishing and rounding requires vigorous transport in water. The upper bench at this site rises gradually from an altitude of about 1370 m to a subtle slope break at about 1400 m; the lower bench rises from a flat surface at 1360 m to a distinct slope break at about 1365 m. The Freds Field site appears to be unaffected by faulting, and it is located well away from possible locations of ancestral streams that might have carried rounded gravel. The Seho shoreline at Freds Field bears clasts of more varied lithologies than do the upper benches. This difference possibly results from the topographic setting; east-flowing longshore currents in the inferred higher lakes might have been channeled along the cliff bearing the Seho shoreline but below the higher benches (Figure 17C).

*Summary: Very High Shorelines of Lake Lahontan*

Several outcrops in the Walker Lake subbasin, one locality in the northeastern Lahontan Basin, and two localities in the Smoke Creek Desert subbasin document highstands of a lake during the early and middle Pleistocene that rose far above the Seho and Eetza(?) shorelines. A conservative correlation among all the sites in the Walker Lake subbasin yields a total of six or seven lacustrine units whose shorelines exceeded that of the Seho lake. Three of the units date from about 1 Ma to less than 2.6 Ma; one tentatively contains the Bishop ash bed; and three are probably younger than the Bishop ash bed, but they definitely date from less than 1 Ma. At Lone Tree Hill, the oldest lake unit is from about 2 Ma, two middle units are probably from about 1 Ma and 0.76 Ma, and the highest unit was deposited less than 0.76 Ma. Other lake units may be present in the core. In the area north of Lone Tree Hill, erosional features and possible deltaic deposits are interpreted to indicate an even younger and lower highstand.

Based upon these correlations, we assign informal names to the deposits that comprise a lake unit—that is, the fine- and coarse-grained lacustrine sediments deposited during the rise and fall of lakes during a pluvial climatic phase. Naming the lake units permits easy revision should a new pluvial phase be identified, and it allows changes in the correlation of lake units at a site if new age information is obtained. This is particularly likely where correlations are made chiefly on the basis of alti-

tude. Variations in altitudes of such old landforms and deposits, especially as they represent minimum altitudes of lacustrine highstands, are expectable in the tectonically dynamic landscape of the Basin and Range. Without independent dating of beach gravels at different sites, we cannot be confident that they represent the same highstand.

Stratigraphic relations among four sites (Figure 5) permit a conservative correlation of the two youngest pre-Seho units; these units always crop out as beach gravel inset into all older units. The maximum altitude of the youngest pre-Seho unit (Q16<sub>T</sub>) at Thorne Bar is about 1350 m; it is characterized by a relatively well-preserved barrier and is henceforth referred to as “younger lake deposits of Thorne.” The delta plain between 1360 m and 1345 m in altitude, north of the Humboldt River near Treaty Hill, is provisionally correlated with this lake unit. Maximum altitudes of the next older lake units range from 1356 m to 1378 m at the three tectonically deformed sites (units Q14<sub>M</sub>, Q13<sub>C</sub>, and Q14<sub>S</sub>). Unit Q15<sub>T</sub> at the Thorne Bar site has not been deformed, and its maximum altitude is about 1370 m, which corresponds with the shoreline angle cut on basalt hills north of Weber Reservoir (Figure 2). We infer that these units represent a highstand at about 1370 m and are herein termed “older lake deposits of Thorne.” The lower of the two shoreline benches at two sites in the Smoke Creek Desert subbasin is correlated with these deposits.

The beach-gravel units overlying older units containing tephra at the sections north of Thorne Bar and at McGee Wash, Campbell Valley, and Lone Tree Hill are also those that rise to the highest altitudes at each site: about 1400 m at Thorne Bar and McGee Wash (units Q14<sub>T</sub> and Q13<sub>M</sub>); 1390 m at Campbell Valley (unit Q12<sub>C</sub>); and 1414 m at Lone Tree Hill. These data suggest, but do not prove, that these units represent the same highstand at about 1400 m altitude. We also tentatively assign unit Q13<sub>S</sub> (altitude 1414 m) at Sunshine Amphitheater to this period, as well as the higher of the two shoreline benches at sites in the Smoke Creek Desert subbasin. This unit is named “lake deposits of McGee” for the arcuate berm composed of beach deposits at that locality.

The tephra layer within unit Q13<sub>T</sub> north of Thorne Bar is tentatively correlated with the Bishop ash bed. The correlation is based upon the chemical composition (Table 3) and stratigraphic position of the tephra layer (Figure 3). The tephra-matrix bed in unit Q12<sub>L</sub> at Lone Tree Hill (Figures 15, 16) has the chemical composition of the Bishop ash and overlies unit Q11<sub>L</sub> containing probable Glass Mountain tephra from 1 Ma. This stratigraphic relation strengthens the interpretations that (1) the tephra layers near Thorne Bar and Schurz (discussed above) are the Bishop ash, and (2) this unit represents a separate lake cycle, herein termed “lake deposits of Lone Tree” (Figure 5).

Unit Q11<sub>C</sub> at Campbell Valley, unit Q12<sub>M</sub> at McGee Wash, and unit Q11<sub>L</sub> at Lone Tree Hill contain a Glass Mountain tephra that erupted at about the time of the Jaramillo Subchron, which occurred about 1 Ma. That would correlate this unit with

Morrison's (1991) younger pre-Eetza unit west of Weber Reservoir (Figure 2). Unit Q12<sub>s</sub> at Sunshine Amphitheater also was deposited during and after the Jaramillo Subchron. We name this unit "lake deposits of Campbell" for the tephra in lacustrine sediments at this locality.

Paleomagnetic data from Sunshine Amphitheater show that the two oldest lacustrine units there lie within the Matuyama Reversed Chron. These units may be correlative to older units at Thorne Bar, McGee Wash, and Lone Tree Hill, and to Morrison's (1991) older pre-Eetza unit west of Weber Reservoir. Unit Q11<sub>s</sub> is from between 1 and 1.4 Ma, based on paleomagnetic data and fossil ages, and is herein named "lake deposits of Sunshine." Unit QTI is from more than 1.4 Ma but less than 2.6 Ma (timescale of Cande and Kent, 1995). The lowest lake unit in the core from Lone Tree Mine (Figure 15) may be equivalent to unit QTI in the Walker Lake subbasin. Because unit QTI seems to represent different environmental conditions than the younger lakes (paper shale at Sunshine Amphitheater, gypsiferous mudstone at McGee Wash) and may include deposits of different ages, we do not assign it a pluvial-lake name.

The combined shoreline sites can be used to infer a partial history of connections among the Lahontan subbasins (Figure 1). Shoreline evidence from Freds Field in the Smoke Creek subbasin and from Thorne Bar in the Walker Lake subbasin, as well as deltaic deposits of the Humboldt River northeast of Treaty Hill, indicate the presence of highstands at altitudes of about 1400 m, 1370 m, and 1350 m (Figure 18), implying that the northern and southern subbasins have periodically merged into a single lake since the early-middle Pleistocene. In the Lone Tree area, faulted deposits of the highest shoreline, assigned to the lake deposits of McGee, are as high as 1414 m in altitude on the footwall block. The lake deposits of Lone Tree and Campbell represent minimum highstands at about 1355 m in the Walker Lake subbasin and at 1405 m and 1390 m, respectively, on the footwall block of Lone Tree Hill. Total displacement in the last one million years is at least 40 m on two of the faults at Lone Tree Hill, and the orientation of the faults suggests that uplift of Lone Tree Hill could account for a significant portion of the displacement. Thus, the discordance in altitudes still permits the possibility of a contiguous Lake Lahontan from the middle Humboldt River to Walker Lake as early as 1 Ma.

The presence of bones of the Lahontan cutthroat trout (R.R. Miller, University of Michigan, in litt. to M.C.R., 1996) in unit Q11<sub>s</sub> at Sunshine Amphitheater (Figure 10) requires a drainage connection (but not necessarily a continuous lake) between the Walker Lake subbasin and the northern subbasins at some time prior to 1 Ma. A continuous lake at 0.76 Ma is supported by the appearance of *Candona caudata*, which can live in colder and thus deeper water than the ostracodes that were preserved in older deposits at Lone Tree Mine (R. Forester, USGS, in litt. to M.C.R., 1998). Possibly these older deposits (>0.76 Ma) reflect damming of the Humboldt River above its canyon east of Winnemucca, as suggested by Roberts (1965). These data do not

refute King's (1993) interpretation that the Walker River flowed into an isolated Walker Lake subbasin in the early Pleistocene, but they may push back the timing of integration to before 1 Ma.

The general correspondence of shoreline altitudes of the lake deposits of McGee and the older and younger lake deposits of Thorne in the Walker Lake subbasin and in the northern subbasins argues for little or no regional northward tilting during the middle Pleistocene, although a few meters of tilt during the late Pleistocene (Mifflin, 1984) are possible. The shorelines, however, have been significantly affected by local faulting, tilting, and isostatic rebound. For example, the proposed correlations among Lahontan sites (Figure 5) imply that the ~1400 m shoreline altitude recorded near Thorne Bar has been raised about 14 m at Sunshine Amphitheater, Lone Tree Hill, and Treaty Hill and lowered about 10 m in Campbell Valley; the sense of these displacements corresponds with those of mapped faults at the four localities (Reheis and Morrison, 1997). Very high beach gravels are preserved at two sites on the west side of Walker Lake (Table 1, Figures 2, 6) on the footwall block of the Wassuk normal fault. If the highest remnant of these gravels corresponds to the 1400 m shoreline, it records 50–75 m of absolute uplift of the Wassuk Range since the early-middle Pleistocene.

#### OTHER BASINS IN WESTERN AND CENTRAL NEVADA

Previous workers inferred the existence of ancient drainage connections or contiguous lakes extending southeastward from the Walker Lake subbasin to Fish Lake Valley (Figure 1). Such "early pluvial" connections were first suggested by Hubbs and Miller (1948) on the basis of remnant populations of Lahontan fish, including *Siphateles bicolor obesus* (Girard, 1856) (tuitchub) in Fish Lake Valley and *S. b. obesus* and *Rhinichthys osculus* (Girard, 1856) (speckled dace) in the basin of Lake Toiyabe in northern Big Smoky Valley. The lowest outlet to Lake Toiyabe at present is south toward Lake Tonopah through an alluvium-filled valley about 60 m above the late Pleistocene shoreline of Lake Toiyabe. Mifflin and Wheat (1979) speculated that Rhodes and Columbus Salt Marshes and Clayton Valley once acted as overflow basins for drainage spilling south from the Lahontan Basin because they contain anomalous concentrations of various salts relative to their drainage basins.

#### *Pre-Pleistocene Lakes*

LAKES SOUTH OF WALKER LAKE SUBBASIN.—We infer that the 1400 m level of Lake Lahontan extended 60 km southeast from Walker Lake through Soda Springs Valley to the south end of Rhodes Salt Marsh (Figure 1). No definite deposits of middle Pleistocene age have been identified in these valleys. Older lacustrine deposits crop out along the range fronts both east and west of Mina, Nevada, and at one site these deposits contain a probable late Miocene tephra layer (EL-24-M, Table

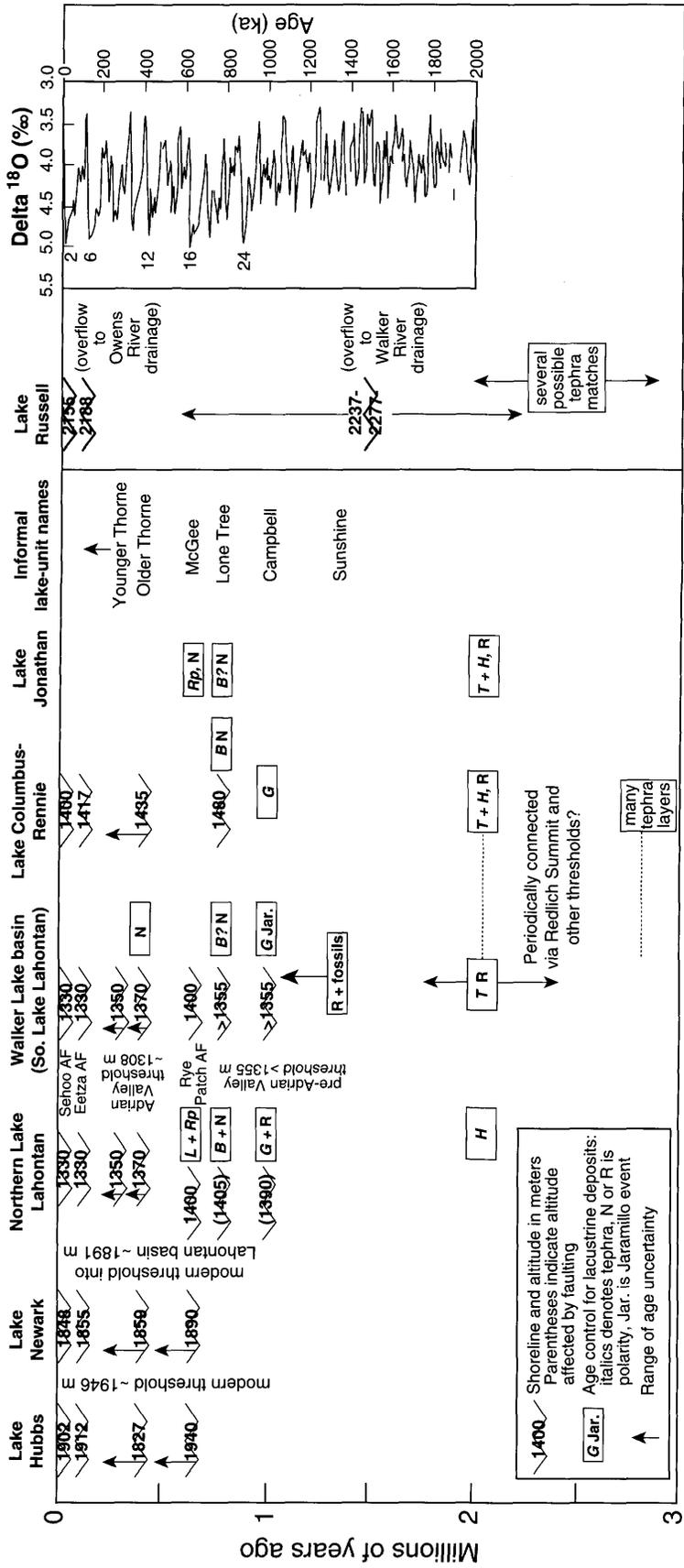


FIGURE 18.—Proposed correlation of late Pliocene and Pleistocene lacustrine deposits and shorelines in western and central Nevada, compared with the marine oxygen-isotope record (data from Imbrie et al., 1993; timescale follows Shackleton et al., 1990; Bassinot et al., 1994). Data in the interval from 0 to 400 Ka is from the Mapping Spectral Variability in Global Climate Project (SPECMAP) stack; data below 400 Ka is from Ocean Drilling Program (ODP) site 677. *Italic letters* are identified tephra layers: B = Bishop, G = Glass Mountain, H = Huckleberry Ridge, L = Lava Creek, Rp = Rye Patch, T = tuff of Taylor Canyon. Arrows indicate range of age uncertainties. AF = Alloformation.

3) and late Tertiary diatoms (J. Bradbury, in litt. to M.C.R., 1996). Younger deposits, probably dated at about 2.5–2.2 Ma based upon tephra correlations (layers EL-2-RM and EL-26-RM, Table 3) and diatoms, crop out along the highway south of Rhodes Salt Marsh up to an altitude of about 1423 m (Figures 1, 19A). These deformed, latest Pliocene lake deposits may either lap onto or underlie old fan gravel that blankets the hills to the south (Figures 19B, 20) that, in turn, lie above a thick sequence of lacustrine sediment beneath Redlich Summit, the present-day divide between Rhodes and Columbus Salt Marshes (Reheis and Morrison, 1997). Lacustrine deposits investigated by J. Liddicoat (Columbia University) at the south end of Teels Marsh, west of Rhodes Salt Marsh, contain a tephra layer identical to tephra EL-2-RM in the roadcut at the south end of Rhodes Salt Marsh (Table 3).

Lacustrine deposits occupy a wide area north of Redlich Summit (Figures 19B, 20). They had been previously mapped (Stewart et al., 1994) but had not been studied in detail. Reconnaissance mapping and several measured sections for this study indicate the presence of two or more lacustrine units separated by unconformities or periods of desiccation. Outcrops northeast of the highway expose an upward sequence of deltaic sandstone, diatomaceous siltstone, green massive mudstone, and nearshore sandstone with oscillatory ripple marks. Chemical analyses of many tephra layers indicate correlations with tephra ranging in age from late Miocene to late Pliocene (e.g., EL-29-RM, EL-34-RM, and EL-50-RM, Table 2). Tephra layers near the top of one section where lacustrine deposits are interbedded with fan deposits exhibit inverse grading of pumice clasts, reflecting a beaching line (shoreline; Sarna-Wojcicki

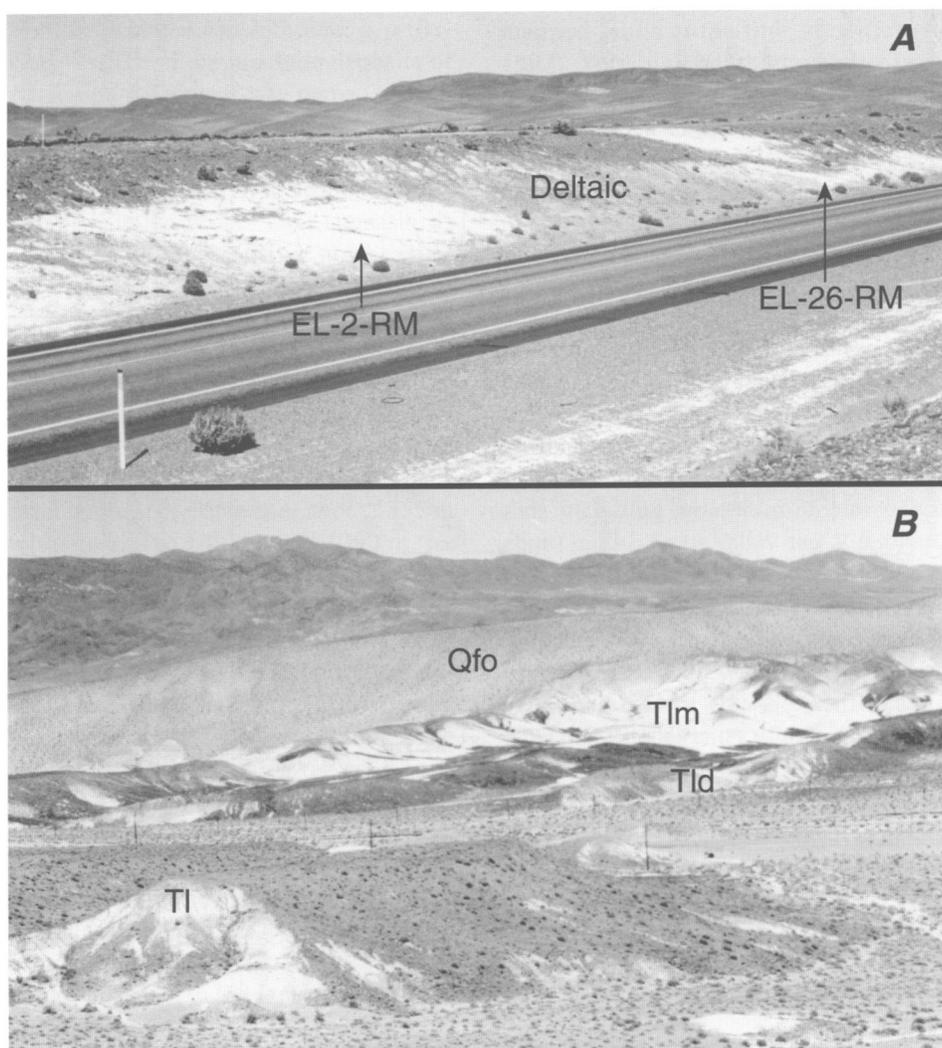


FIGURE 19.—Photographs of lacustrine deposits south of Rhodes Salt Marsh (see Figure 1, Table 1). A, Roadcut exposes two sets of late Pliocene lacustrine sediments containing tephra layers (Tables 2, 3) separated by fluvial or deltaic deposits. B, View northeast near Redlich Summit of late Miocene to late Pliocene lacustrine deposits filling divide between Rhodes and Columbus Salt Marshes (power poles included for scale).

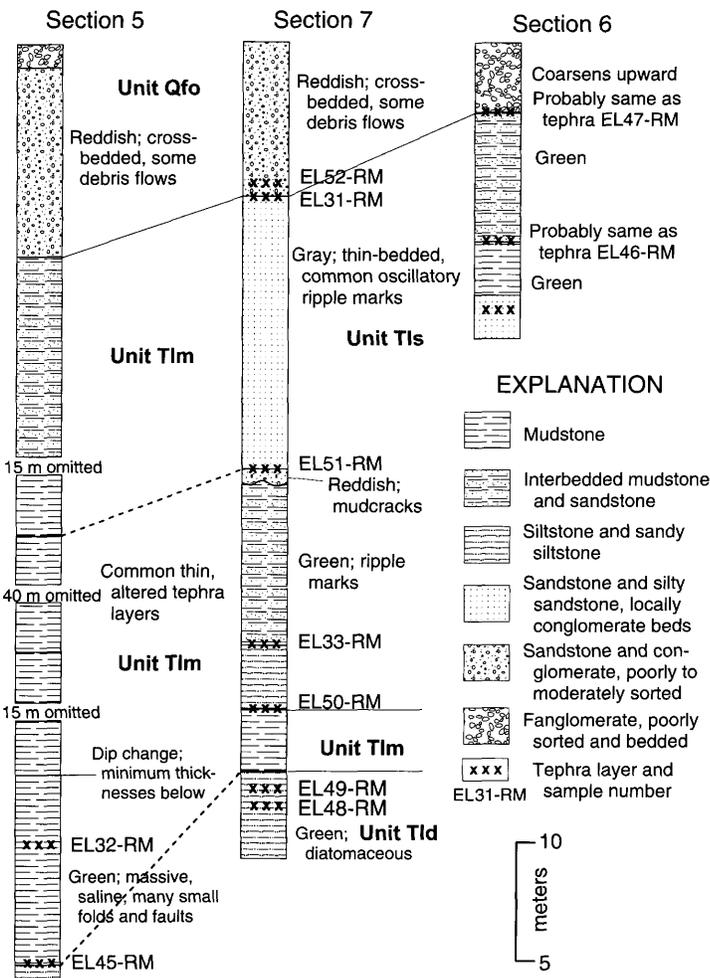
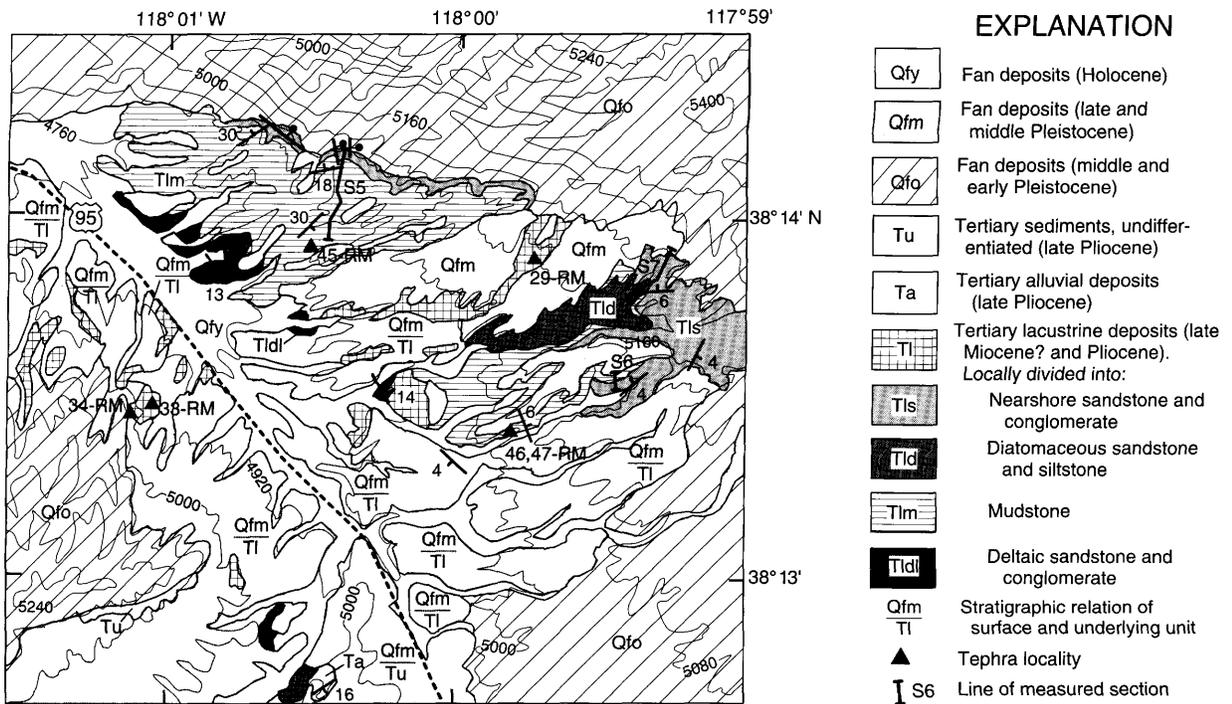


FIGURE 20.—Preliminary geologic map and measured sections of area northwest of Redlich Summit between Rhodes and Columbus Salt Marshes (see Figure 1, Table 1).

and Davis, 1991; Reheis et al., 1993). These deposits indicate that a lake intermittently occupied the present divide between Rhodes and Columbus Salt Marshes up until about 2 Ma.

Fish Lake Valley is located south of Columbus Salt Marsh and presently is part of its drainage area (Figure 1). Pluvial Lake Rennie existed in Fish Lake Valley during at least four intervals from the late Pliocene to the middle Pleistocene (Reheis et al., 1993). Lacustrine deposits in the valley include mudstone, siltstone, sandstone, and conglomerate. Numerous tephra layers (e.g., EL-3-FL, EL-4-FL, and EL-44-FL, Table 3) within the lacustrine deposits document lake episodes from about 3.4 to 2.8 Ma and from about 2.2 to 2.0 Ma. Deposits of similar age do not crop out in Columbus Salt Marsh.

Davis (1981) and Kunasz (1970) used data obtained during field work and data from well records from a lithium-extraction operation to show that Clayton Valley (east of Fish Lake Valley, Figure 1) was periodically filled with fresh to brackish lakes. Exposures on the east side of the valley indicate at least two such intervals occurred (Davis, 1981). A recent analysis of tephra layers (samples EL-42-CV and EL-43-CV, Table 3) from the lower interval suggests the interval occurred between 3 and 2 Ma. Thus, the record of Pliocene lakes in Clayton Valley is in accord with those in Rhodes Salt Marsh and Fish Lake Valley (Figure 18).

The parallel histories of Pliocene lakes south of Rhodes Salt Marsh and in Clayton Valley and Fish Lake Valley, combined with the lack of sills or the presence of very low sills between Columbus Salt Marsh and Fish Lake, Clayton, and Big Smoky Valleys (Figure 18), permits the interpretation that the lakes in these basins were interconnected during the Pliocene. In addition, we infer that a Miocene to Pliocene lake basin that at least included Rhodes and Columbus Salt Marshes was disrupted by faulting and (or) compression along the northeast-striking Huntoon Valley fault system (Stewart, 1988; dePolo et al., 1993) that lifted the area of Redlich Summit, which is presently about 35 m above the highest known shoreline altitude in Columbus Salt Marsh (discussed below) and about 95 m above the 1400 m high shoreline of Lake Lahontan.

#### *Early to Middle Pleistocene Lakes*

**PLUVIAL LAKE COLUMBUS-RENNIE.**—Reheis et al. (1993) showed that a large lake, informally named Lake Rennie, periodically existed in Fish Lake Valley during the Pliocene (discussed above) to middle Pleistocene. They noted that thick, shallow-water deposits of Bishop ash indicate the existence of a large lake at about 760 Ka with a highstand of about 1460 m in elevation; a lake of uncertain size probably also existed at about 1 Ma. These outcrops of lacustrine sediment are supported by data recorded in drilling logs for privately owned water wells. The logs, copies of which are stored at Carson City, Nevada, by the Water Resources Division of the U.S. Geological Survey, record the occurrence of numerous thick beds of clay and sandy clay that are inferred to be deep-water lacustrine deposits. Reheis et al. (1993) speculated that Lake Rennie

and Lake Columbus at times were contiguous through The Gap, the present-day drainage connection between Fish Lake Valley and Columbus Salt Marsh.

New discoveries in Columbus Salt Marsh (Figure 1) indicate the presence of at least four lacustrine units that are higher and older than the late Pleistocene shoreline (altitude 1400 m; Mifflin and Wheat, 1979; Reheis et al., 1993) of Lake Columbus. No Quaternary faults have been mapped in this subbasin (Dohrenwend, 1982a; Stewart et al., 1994). Outcrops in a small hill on the south side of the subbasin expose three units composed of beach gravel, lacustrine sand, and silt; each unit is separated by paleosols that formed in alluvial or eolian deposits (Figures 21, 22). Paleomagnetic measurements yielded mainly indeterminate polarity as a result of diagenetic and pedogenic alteration, but one sample from unit Q12<sub>CM</sub> has reversed magnetization. The uppermost unit in this section, Q13<sub>CM</sub>, consists of tufa-cemented gravelly foreset beds that underlie a prominent berm, which protrudes from the south side of the hill at an altitude of about 1435 m (Table 1). This altitude and the well-preserved morphology are similar to those of beach berms initially identified by J.O. Davis (Desert Research Institute, in litt. to M.C.R., 1989) on the southeast side of the subbasin at Coaldale Junction (Reheis and Morrison, 1997). Very well-rounded gravel clasts (in part reworked from a nearby Tertiary conglomerate) and tufa are present as lag on the slope above the berm to the top of the hill at an altitude of 1452 m. The clasts and tufa suggest a yet higher lake stand that could be equivalent to unit Q13<sub>CM</sub> or to one of the buried lacustrine units. A similar gravel-covered bench on the west side of Columbus Salt Marsh extends to an altitude of 1457 m. These altitudes are very similar to the shoreline altitude of pluvial Lake Rennie (1460 m), and we infer that they record the highest shoreline of the combined lakes at about 760 Ka. Evidence of the youngest pre-late Pleistocene lacustrine unit here has been destroyed by gravel operations, but in 1991, excavations exposed gravelly foreset beds in a berm at an altitude of about 1417 m. This altitude corresponds to those of small berms on the north side of the subbasin (Figure 1, Table 1); surface soils on these berms are moderately developed with argillic horizons that are not present on the late Pleistocene deposits of Lake Columbus.

A deep pit on the north side of the subbasin exposes lacustrine sand and marl containing probable Bishop ash (sample 29068501, Tables 2, 3; collected by J. Whitney and P. Glancey, USGS) that are stratigraphically beneath late Pleistocene beach deposits of Lake Columbus (Figure 21A). The tephra layer is impure, and no unconformities or buried soils lie between it and the overlying late Pleistocene deposits. Thus, the tephra may have been reworked into much younger deposits and may not truly represent the age of the older lake unit.

In summary, deposits and berms at several locations around Columbus Salt Marsh indicate there had been at least four lake cycles that were older and higher than the late Pleistocene shoreline: the two oldest lakes rose in altitude to at least 1420 m, and one of these two rose to 1457 m; an intermediate-aged lake rose to about 1435 m; and a younger lake

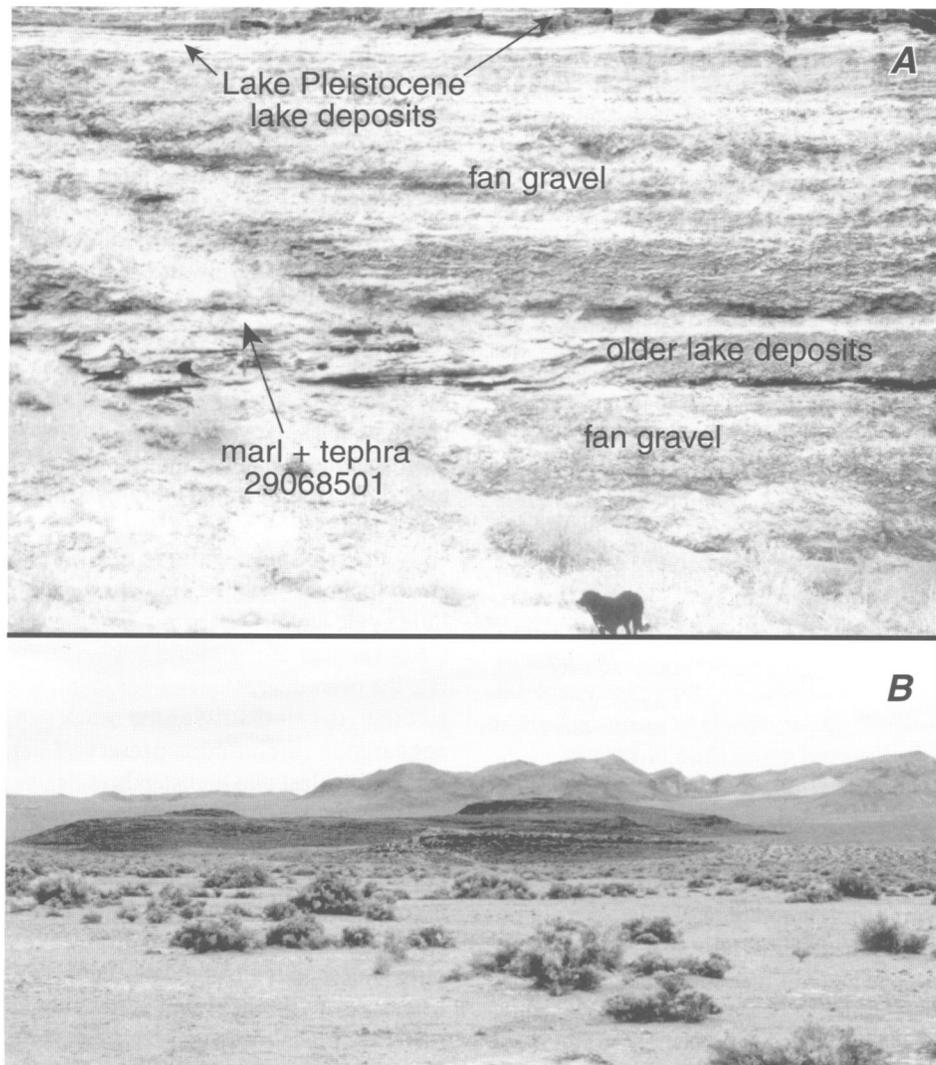


FIGURE 21.—Pre-late Pleistocene lacustrine features in Columbus Salt Marsh (see Figure 1). A, View of west side of deep pit on north side of valley; small dog and 1 m pick below tephra are for scale. Late Pleistocene lake gravel at top of pit overlies a sequence of debris-flow deposits that, in turn, overlie middle Pleistocene lake gravel containing probable Bishop ash (Tables 2, 3, no. 29068501) at bottom of pit. B, View north from borrow pit on southwest side of valley (see Figure 1) to shorelines (arrows) cut on basalt outcrops.

rose to 1417 m. One of the two oldest lakes probably occurred about 760 Ka.

**PLUVIAL LAKE CLAYTON.**—The floor of Clayton Valley has been cored numerous times by the USGS (Pantea et al., 1981) and by mining companies (reported in Kunasz, 1970; Davis, 1981). No exposures of lacustrine deposits of Pleistocene age have been found. Most of the wells bottomed in the so-called “ash aquifer,” a thick (as much as 10 m), coarse-grained tephra layer that lies at depths between about 100 and 300 m below the playa surface. This tephra layer contains dissolved lithium salts in a large brine pool, and it is these salts that are exploited by the mining companies. Sediments in the cores consist of alternating beds of sand, mud, gypsum, and halite, and include several coarse tephra layers and glass-rich intervals. The mud is interpreted to reflect deeper, freshwater conditions in the lake,

whereas the gypsum and halite beds are interpreted to reflect periods of brackish water and desiccation (Davis, 1981). In one core, Kunasz (1970) interpreted the absence of gypsum and halite below about 70 m to indicate freshwater conditions. In this core, this depth approximately corresponds to the interval including and below the ash aquifer. A sample of the ash aquifer obtained by Davis (1981) from a depth of 175 m in another core hole is tentatively identified as the Bishop ash (sample D77-2D, Table 3). In summary, sediment beneath Clayton Valley records a long history of intermittent lacustrine deposition, including one relatively freshwater lake at about 760 Ka.

**PLUVIAL LAKE RUSSELL (MONO BASIN).**—The Mono Basin is a structural depression that probably began forming about 4–3 Ma (Gilbert et al., 1968). Freshwater lacustrine sediments interbedded with volcanic flows deposited during this time

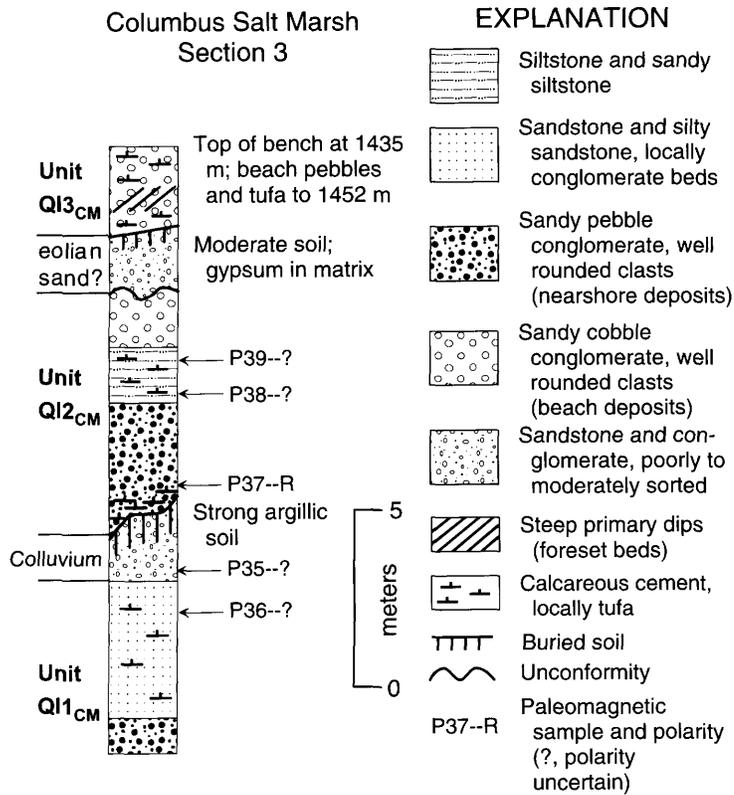


FIGURE 22.—Measured section above borrow pit on southwest side of Columbus Salt Marsh (see Figure 1, Table 1), above late Pleistocene shoreline.

crop out on the east side of the basin. These deposits are composed of diatomaceous sand and silt that contain abundant fossils, including molluscs and fish. Lake Russell has a well-known late Pleistocene history, as established by studies performed by Russell (1889), Putnam (1949), and Lajoie (1968). The highstand shoreline during the late Wisconsin was at an altitude of 2155 m; however, the last overflow of Lake Russell southward into Adobe and Owens Valleys (Figure 1) occurred at a highstand of about 2188 m. This lake cycle is thought to be equivalent to the Tahoe glaciation. Reheis et al. (2002) discussed the shoreline altitudes and changing drainage direction of Lake Russell since the late Pliocene.

Miller and Smith (1981) and Hubbs and Miller (1948) used fossils from the Mono Basin and modern fish populations in other areas (no fish presently live in Mono Lake) to show that fish had migrated southward into the Mono Basin from the Lahontan Basin, probably during the Pliocene. Fish later migrated southward from the Mono Basin into Owens Valley and Death Valley, probably using the overflow route through Adobe Valley (Figure 1). Russell (1889) hinted, and Hubbs and Miller (1948) proposed, that the earlier connection between the Lahontan and Mono Basins had been via the East Walker River and Aurora Valley over a sill at the northeast corner of Lake Russell that is presently at an altitude of 2237 m.

Recent discoveries around the north and east sides of the Mono Basin (Figure 1, Table 1) include (1) lacustrine deposits

near the former southern outlet of Lake Russell, representing at least one lake cycle that greatly exceeded the 2188 m high shoreline, (2) beach gravels on the north side at altitudes as high as 2268 m at one site and 2252 m at another site, and (3) an abandoned valley, now partially filled by a basalt flow, that lies north of the putative northern sill.

The lacustrine deposits near the southern outlet lie at an altitude of about 2205–2220 m and include two tephra layers within a coarsening-upward sequence of silt, sand, and beach gravel. Chemical analysis indicated that these tephra (samples EL-53-ML and EL-54-ML) are latest Pliocene in age (2.5–2.0 Ma; Table 3). A lake that at one time stood much higher than these deposits, however, is documented by beautifully rounded beach pebbles, large chunks of tufa-cemented beach rock, and snail coquina that are found on slopes as high as 2243 m in altitude directly above the tephra-bearing deposits. Several northeast-striking faults displace these beach-gravel remnants; locally the maximum altitude of the beach pebbles is 2277 m. Beach pebbles within a similar range of altitudes in areas with little evidence of Quaternary faulting (Dohrenwend, 1982b) on the north side of the Mono Basin (Figure 1, Table 1) corroborate the prior occurrence of very high levels of Lake Russell. In addition, the similarity of the beach pebbles and their outcrop appearance (including a preserved berm at one locality) to those of the last two highstands indicates that these deposits are Pleistocene in age. The landscape must have been very different when Lake Russell reached these altitudes because there is no present-day topographic barrier high enough to enclose a lake for several kilometers east and west of the outcrops near the southern outlet. Gilbert et al. (1968) reported numerous, closely spaced faults that have cut basalt flows from 3 Ma, and examination (this study) of aerial photographs has revealed evidence of recent faulting activity. It is likely that faulting acted to lower the terrain in this area, which eventually permitted Lake Russell to drain southward.

These old lacustrine deposits around the Mono Basin represent a lake that was high enough to have overflowed northward across the sill in the northeastern corner at its present altitude of 2237 m. It is difficult if not impossible to reconstruct pre-faulting altitudes in this tectonically active part of the basin (Dohrenwend, 1982b); however, the andesite-cored sill locally bears patches of subrounded pebble to cobble gravel, suggesting a former drainage way. A sample of this andesite (EL-KA-2) was dated by conventional K–Ar techniques at  $1.44 \pm 0.06$  Ma (E. McKee, USGS, in litt. to M.C.R., 1995) (Reheis et al., 2002).

North of the sill, the drainage is northward into the west-draining Mud Spring Canyon, which is a tributary to the East Walker River (Figure 1). Mud Spring Canyon appears to be an abandoned, underfit drainage; it carries water only intermittently, but its floor is as much as 300 m wide and is incised as much as 50 m below old alluvial surfaces. The alluvial deposits exposed in Mud Spring Canyon contain several thick, coarse tephra beds. Chemical analyses of glass in these beds (samples EL-35A-MS, EL-35B-MS, and EL-36-MS) indicate ages of 2.9–2.5 My (Tables 2, 3). The upper part of the canyon, near

the intersection of the northward drainage from the andesite sill, has been filled twice by basaltic eruptions and subsequently reincised by discharge from ancient Lake Russell during the early Pleistocene (Reheis et al., 2002).

The high beach gravels, drainage relations, and ages of lake sediments and volcanic flows on the east side of Mono Basin support the following scenario: an ancestral Lake Russell reached higher altitudes than its last overflow level (2188 m) during the late Pliocene and early Pleistocene. At least once during this time, the lake reached an altitude between 2237 m (the elevation of the sill) and 2277 m (the highest preserved beach gravel) and overflowed to the north and thence west down a precursor of Mud Spring Canyon into the East Walker River. Fish fossils (Miller and Smith, 1981) imply that a connection to the Lahontan Basin existed during the late Pliocene. The age of the andesite underlying the sill suggests that northward overflow also occurred after about 1.5 Ma. Thus, the Mono Basin periodically may have been a tributary to the Walker Lake basin in the late Pliocene and early to middle(?) Pleistocene (Reheis et al., 2002).

**PLUVIAL LAKE JONATHAN (KOBEB VALLEY).**—The large modern drainage basin of Lake Diamond includes several valleys to the southwest (Figure 1). When Lake Diamond fills and overflows, this drainage basin becomes a tributary to the Humboldt River and thus to Lake Lahontan (Tackman, 1993). Most of the drainage basin feeds first into Kobeh Valley, which lies just upstream of Diamond Valley and is separated from it by a very narrow, steep bedrock canyon called Devils Gate (Figure 23A). Lake sediments in Kobeh Valley (Figures 23B, 24) represent an internally drained lake that breached its sill at Devils Gate and became a tributary to Lake Diamond sometime after 670 Ka (Davis, 1987). We propose to name this former lake “Lake Jonathan” for Jonathan O. Davis, who discovered it two years before his untimely death. Lacustrine deposits in Kobeh Valley are extensively exposed in the eastern part of the valley near Lone Mountain, which formed an island in Lake Jonathan (Figures 1, 23B). Reconnaissance field work combined with data from Davis (1987) indicates a long and complex lacustrine history, which is worthy of a far more detailed investigation.

Two measured sections expose deposits of at least three lake units. In section 16, normally magnetized sediments of two of these lake units are separated by an unconformity and colluvium (Figures 24, 25). The upper lake unit contains the Rye Patch Dam ash bed (dated at 670 Ka) (AA-04, Tables 2, 3), which crops out in several other localities near Lone Mountain (samples EL-69-KV, shown in Figure 23C, and EL-70-KV, not in tables). Ostracodes in the ash bed are indicative of alkaline, moderately deep to deep lakes (R. Forester, USGS, in litt. to M.C.R., 1998). This lake unit was the last deposited before the sill was breached, and it is represented by several relatively well-preserved, carbonate-cemented berms (e.g., Figure 23B) in eastern Kobeh Valley. The lower lake unit contains an altered tephra layer that we believe is the same as that identified as a Bishop-like ash by Davis (1987); correlation to the Bishop ash is supported by the paleomagnetic data.

In section 18, three lake units are separated by unconformities. The two oldest units contain ostracodes that are indicative of alkaline, shallow to moderately deep lakes (R. Forester, USGS, in litt. to M.C.R., 1998). Of these two, the oldest unit is reversely magnetized, whereas the next younger, or middle, unit contains reversely magnetized samples near the base and normally magnetized samples above (Figure 25), suggesting that the unit spans the Matuyama–Brunhes boundary. Sample EL-81-KV taken from a tephra layer in the middle unit, however, is best correlated, on the basis of glass chemistry (Table 3), with one of the several tuffs of Taylor Canyon layers that erupted from Long Valley caldera 2.2–2.1 Ma (Sarna-Wojcicki et al., In review). This age assignment is supported by deposits that are unconformably beneath the youngest lake unit (dated at 0.67 Ma; see section 16, Figure 24) on the east side of Lone Mountain. This lake unit contains a tephra (sample EL-80-KV, Tables 2, 3) that correlates with the Huckleberry Ridge ash bed (dated at 2.1 Ma). If this correlation is accepted, then (1) the ~14 m of normal-magnetization sediment in the middle lake unit may have been deposited during the Reunion Normal Subchrons within the Matuyama Chron; (2) the lower lake unit in section 16 also may represent this time period, so the correlation to the Bishop ash bed is incorrect; and (3) the unconformity between these deposits and the youngest lake unit represents about 1.5 million years (My) rather than 100 Ky.

A third outcrop north of Lone Mountain (Figure 1, Table 1) exposes three deposits of beach gravel separated by unconformities and paleosols; the uppermost gravel belongs to the lake unit dated at 670 Ka. The development of paleosols on the lower two beach gravels is moderate (weak argillic horizons and stage II–III carbonate), and together they probably can account for no more than 200 Ky of subaerial exposure. These relationships suggest that these two lake units are no older than early Pleistocene, and that two or more lake units may be missing from section 18.

**OTHER BASINS IN CENTRAL NEVADA.**—Two independent basins in east-central Nevada held Lake Hubbs and Lake Newark during the latest Pleistocene at shoreline altitudes of about 1902 and 1848 m, respectively (Figure 1, Table 1). Mifflin and Wheat (1979) observed higher shorelines at the south ends of both lakes and attributed them to regional northward tilting; however, berms at similar altitudes on the north and east sides of both basins were located during field reconnaissance for this study in 1997, so northward tilting can be ruled out. Three levels of beach gravels that are increasingly indistinct, hence older, with altitude are preserved above the late Pleistocene shorelines of both lakes (Table 1). The highest levels are represented only by rounded beach gravel lagged on bedrock slopes. Relative preservation of berm morphology and properties of relict soils (Figure 26) indicate significant age differences among the lowest three shorelines (including that of the late Pleistocene) with preserved berm crests on the southeast side of Lake Newark. Soil properties, including solum thickness and pedogenic CaCO<sub>3</sub> content, suggest that the penultimate

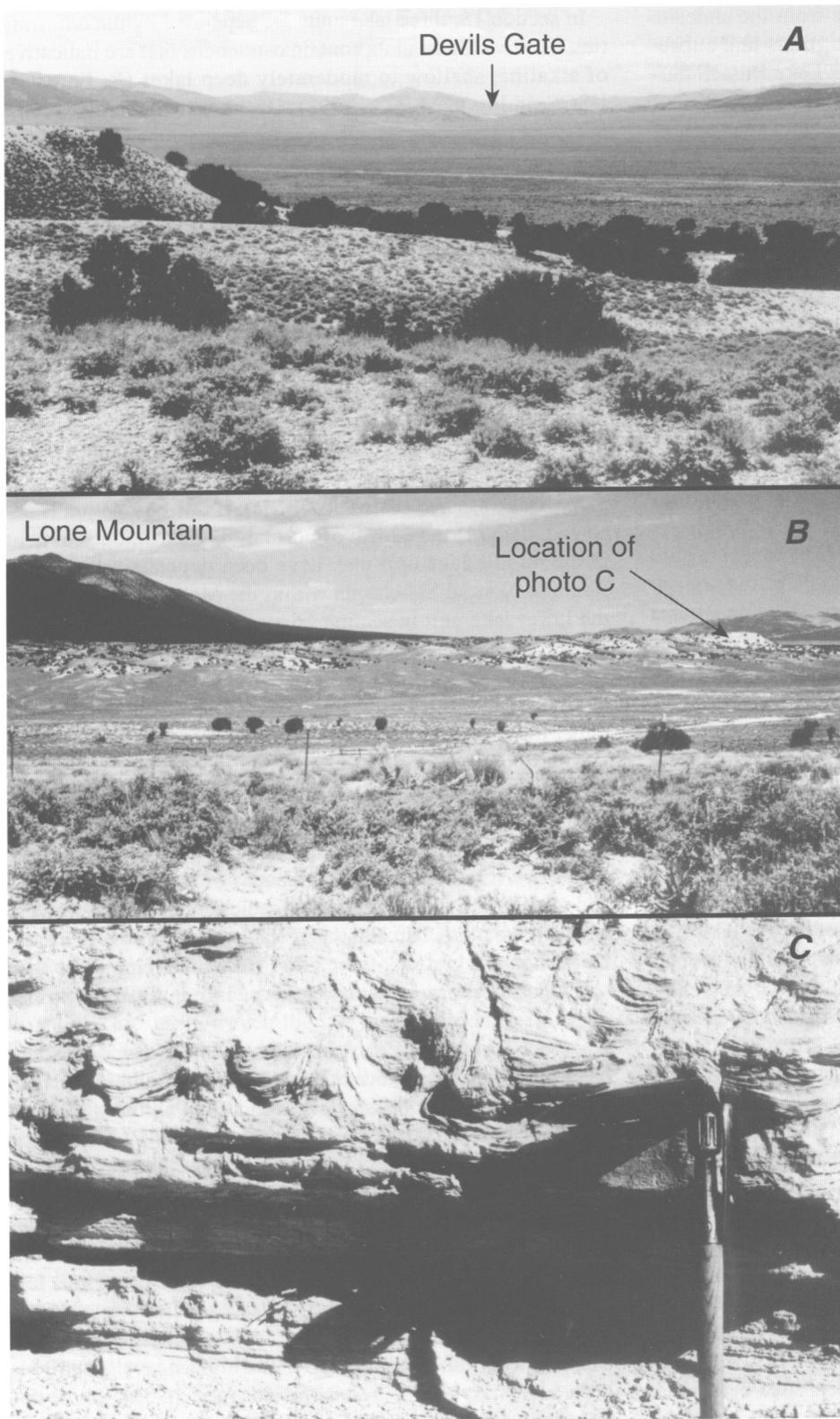


FIGURE 23.—Photographs of lacustrine deposits of Lake Jonathan in Kobeh Valley. A, View southeast from top of bench in B on Lone Mountain showing Devils Gate, the bedrock channel that formed when Lake Davis overtopped the divide between it and Lake Diamond. B, View northwest showing apron of pale-colored lake sediment capped by beach gravel as high as 1920 m flanking the “island” of Lone Mountain. C, Close-up of these sediments showing thick tephra layer with soft-sediment deformation (shovel is about 40 cm long); this layer (EL-69-KV) is identical in appearance to one in another outcrop identified as 670 Ka Rye Patch Dam ash (Tables 2, 3, no. AA-04 JOD) by Davis (1987).

shoreline probably occurred at least 100–50 Ka and the next older likely occurred at least 200 Ka by comparison to soils of known age in the Basin and Range area (e.g., Reheis et al., 1995). The soil chronosequence that formed on shorelines of

different ages in the Newark Basin has been studied in detail by Redwine (In prep.).

Several levels of well-preserved, nested shoreline features in Diamond Valley indicate highstands of pluvial Lake Diamond

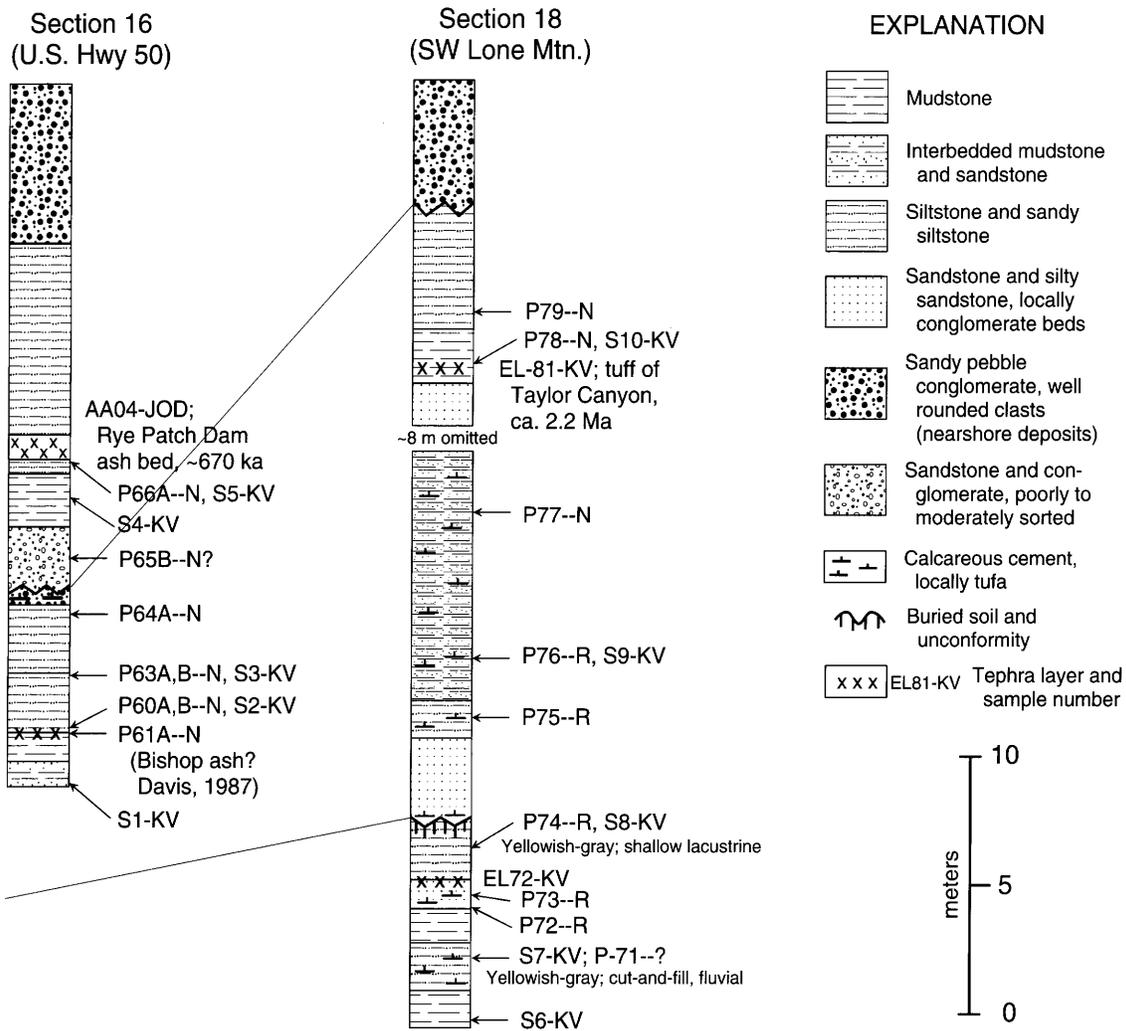


FIGURE 24.—Measured sections of lacustrine deposits of Lake Jonathan in Kobeh Valley (see Figure 1, Table 1). Symbols are the same as in Figure 9. Question mark (?) after N indicates polarity uncertain.

as much as 25 m above its late Pleistocene shoreline (Figure 1; Tackman, 1993). Relict soils indicate that the highest of these is likely several hundred thousand years old (Mifflin and Wheat, 1979); however, the decrease with time in the levels of pluvial Lake Diamond is likely the result of progressive erosion of the sill between Diamond Valley and Huntington Creek, a tributary to the Humboldt River.

Pine Valley, northwest of Diamond Valley, was an internally drained, fault-controlled basin with a long record of lacustrine sedimentation (Smith and Ketner, 1976; Gordon, 1990). During much of its history, probably spanning the late Pliocene and early Pleistocene, the lake was alternately alkaline and relatively fresh. Sometime after the deposition of the Lava Creek B ash bed (660 Ka), which lies near the top of the lake beds, the northern sill was breached and the valley began draining into the Humboldt River via Pine Valley Creek. Gordon (1990) inferred that Lake Pine was never a deep freshwater lake. His opinion was based upon the alkaline character of the sediments

and the reported absence of beach gravels. In field reconnaissance for the present paper, however, an approximately 10 m thick bed of well-rounded beach gravel, locally steeply bedded, was found at the top of the lacustrine sequence in the northeastern corner of the valley. We suggest that Pine Valley, like Kobeh Valley, was breached and integrated with the Humboldt River drainage when an exceptionally large lake spilled over a sill composed of easily eroded Tertiary tuff and sedimentary rocks at, or shortly after, 660 Ka.

### Discussion

#### AGES OF MIDDLE PLEISTOCENE SHORELINES IN THE WESTERN GREAT BASIN

The ages of deposits that mark the very high shorelines throughout the Lahontan Basin and in the basins of Lakes Columbus, Hubbs, and Newark can only be estimated because the units everywhere consist of gravel and sand that have not been directly dated.

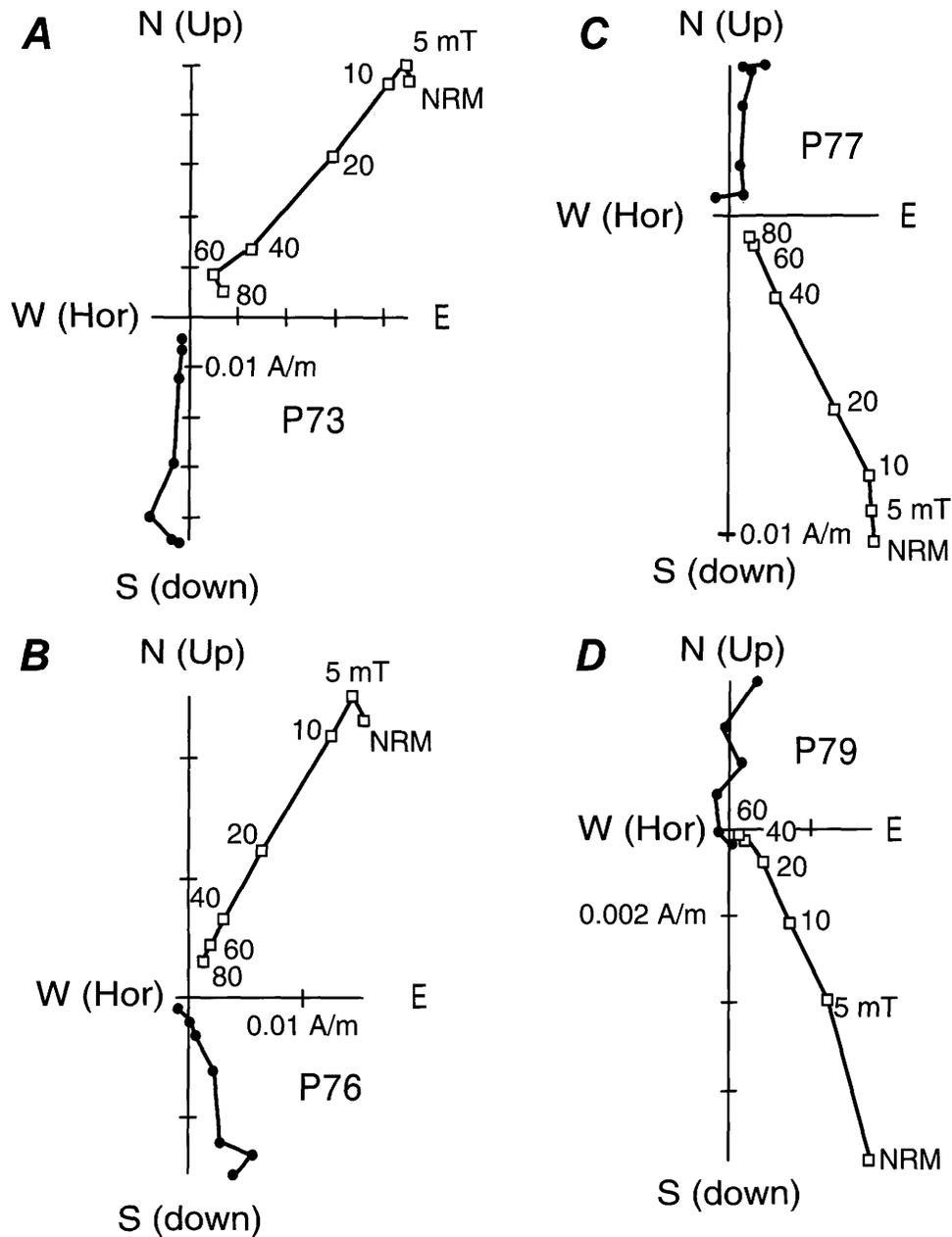


FIGURE 25.—A–D, Orthogonal demagnetization diagrams (method of Zijderveld, 1967) shown in stratigraphic order for specimens from section 18 in Kobeh Valley. A, reversed magnetization in sample P73 from the oldest exposed lake unit; B, reversed magnetization in sample P76 from the lower part of the middle lake unit; C, normal magnetization in sample P77 from the middle lake unit; D, normal magnetization in sample P78 from the upper part of the middle lake unit. This sample is from just above tephra EL-81-KV, correlated with ~2.2 Ma tephra of the tuff of Taylor Canyon (Table 3).

The lake deposits of McGee overlie the lake deposits of Campbell deposited about 1 Ma at three sites in the Walker Lake subbasin, and they overlie the lake deposits of Lone Tree deposited about 0.76 Ma (Figure 5). At Sunshine Amphitheater, two layers of fan gravel and three argillic paleosols intervene between the lake deposits of Campbell and the highest

beach gravel, an interval likely representing at least 200 Ky. These relationships and the very high lake level represented by the lake deposits of McGee suggest a correlation to marine oxygen-isotope stage (OIS) 16, one of the largest deviations toward glacial (and hence pluvial) conditions (Figure 18). We interpret the unit to be equivalent to the Rye Patch Alloformation

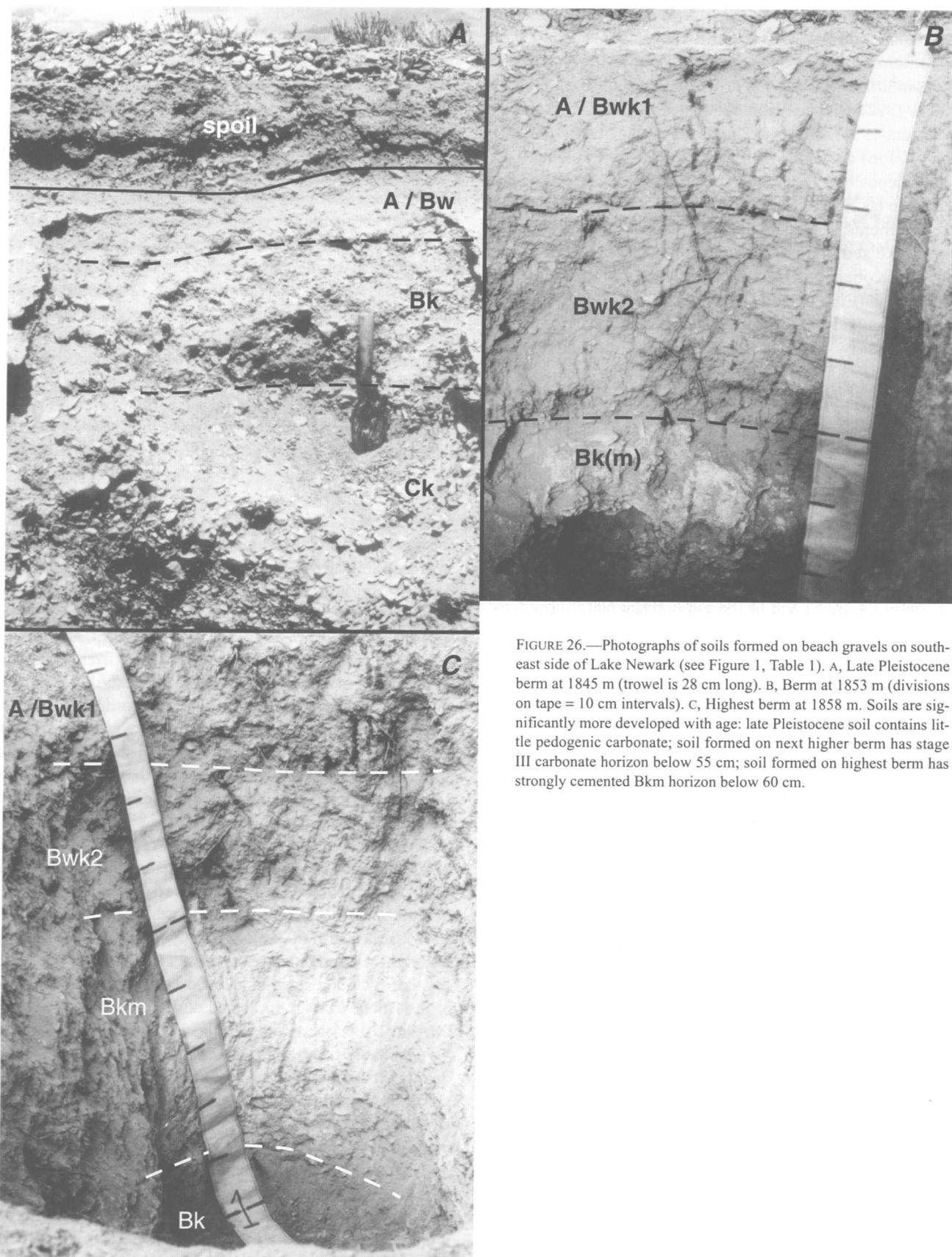


FIGURE 26.—Photographs of soils formed on beach gravels on south-east side of Lake Newark (see Figure 1, Table 1). A, Late Pleistocene berm at 1845 m (trowel is 28 cm long). B, Berm at 1853 m (divisions on tape = 10 cm intervals). C, Highest berm at 1858 m. Soils are significantly more developed with age: late Pleistocene soil contains little pedogenic carbonate; soil formed on next higher berm has stage III carbonate horizon below 55 cm; soil formed on highest berm has strongly cemented Bkm horizon below 60 cm.

deposited about 0.7–0.6 Ma (Reheis and Morrison, 1997) along the Humboldt River. At this site, sublacustrine deltaic deposits containing the Rye Patch Dam (~0.67 Ma; A. Sarna-Wojcicki, in litt. to M.C.R., 1997) and Lava Creek B (0.66 Ma; Izett et al., 1992) ash beds crop out at an altitude of about 1285 m (Morrison, 1991). If the lake deposits of McGee (at an altitude of 1400 m) correlate with the Rye Patch Alloformation, the deltaic deposits at Rye Patch Dam must represent low-level phases of the lake cycle. The correlation to OIS 16 is bolstered by lake sediments in Kobeh and Pine Valleys (Figure 1). The youngest lake sediments and highest beach gravels of Lake Jonathan in Kobeh Valley are dated at 0.67 Ma by the Rye Patch Dam ash (Figures 23C, 24; Davis, 1987). The youngest lake sediments and highest beach gravels in Pine Valley are dated at 0.66 Ma by the Lava Creek ash bed (Smith and Ketner, 1976; Gordon, 1980; and this study).

We infer, based upon the rare occurrence and poor preservation of lag beach gravel on bedrock, that the highest shoreline deposits of Lakes Columbus, Hubbs, and Newark also represent OIS 16 (Figure 18). From its degree of soil development, the highest shoreline of Lake Diamond (Mifflin and Wheat, 1979) also may have formed at this time, possibly as a result of overflow from Lake Jonathan (Tackman, 1993).

Beach deposits of the ~1370 m and ~1350 m high shorelines of Lake Lahontan (the upper and lower lake deposits of Thorne, respectively; Figure 5) and of the two intermediate shorelines of Lakes Columbus, Hubbs, and Newark, locally retain the forms of berms and wave-cut benches. In the Walker Lake sub-basin, these beach deposits are inset into older lake units. The relationships of these beach deposits and their morphologic preservation cause us to conclude that the upper and lower lake deposits of Thorne represent units that are younger than those correlated to the Rye Patch Alloformation but are as old or older than the last highstand represented by the upper part of the Eetza Alloformation, which is thought to be equivalent to OIS 6 (Morrison, 1991). Thus, these two sets of shorelines probably represent pluvial episodes corresponding to OIS 14 to perhaps as young as OIS 6 (~530–130 Ka). The upper lake deposits of Thorne and the higher of the two intermediate shorelines of the other lakes may be equivalent to OIS 12 (~430 Ka), a relatively large glacial episode in the marine record (Figure 18). This age assignment is consistent with the morphology of relict soils formed on these shorelines at the Thorne Bar site (Adams and Wesnousky, 1999) and at the south end of Lake Newark (Figure 26C).

The ~1350 m high shoreline is only represented in the Lahontan Basin by the lower lake deposits of Thorne (Figures 5, 18) at Thorne Bar and possibly along the Humboldt River, but other lake basins contain numerous remnants of a lower intermediate shoreline 7–17 m above the late Pleistocene highstand (Figure 1, Table 1). Properties of relict soils at Thorne Bar (Adams and Wesnousky, 1999) and in the basins of Lakes Columbus and Newark (Figure 26B) indicate ages from 100 to 50 Ka or earlier. Thus, these shorelines may represent pluvial

lakes associated with OIS 6 (an intense glacial episode at about 150–130 Ka) or possibly OIS 8 (a less intense glacial episode at about 250 Ka), but they are not likely to be as old as OIS 10 (~340 Ka; Figure 18). If the lower lake deposits of Thorne are as young as OIS 6, it seems that more remnants of this shoreline should have been found in the Lahontan Basin. Assignment of the 1350 m high shoreline of Lake Lahontan to OIS 6 also conflicts with Morrison's (1964, 1991) evidence that the highest Eetza shoreline is at about the same altitude as the 1330 m Sehoo shoreline; however, soil data of Adams and Wesnousky (1999) suggests that Lake Lahontan shorelines around the 1330 m level may all be Sehoo in age. Recently published uranium-series ages of tufa from the Pyramid Lake area of Lake Lahontan show that the lake achieved at least an intermediate level (~1207 m in altitude) almost continuously from about 400 to 170 Ka (Szabo and Bush, 1996) and may have intermittently stood much higher, but the timing and altitude of the highstands are unknown.

#### CAUSES OF VERY HIGH SHORELINES DURING THE EARLY AND MIDDLE PLEISTOCENE

The records of lakes in Nevada described herein stand in contrast to records presently available for lakes in the southwestern Great Basin and for Lake Bonneville in the eastern Great Basin; however, the records in the different regions are based upon different types of evidence. For example, interpretations of the records of Lakes Owens, Searles, and Bonneville depend largely upon stratigraphic evidence from cores and to a lesser extent from outcrops, whereas those of the present study depend upon shoreline deposits. The records of Lakes Owens and Searles show that these were fresh, overflowing lakes during periods that correspond with OIS 16, 12, 10, and 6 (Jannik et al., 1991; Smith et al., 1997). Flow-through lakes, however, do not leave adequately detailed evidence of changes in lake size because lake size is controlled by sill height. Oviatt et al. (1999) reinterpreted the middle Pleistocene record of the Bonneville Basin (east of the present study) using data from cores and concluded that four freshwater lakes were present during the Brunhes Chron. The oldest of these lakes just preceded the Lava Creek ash (660 Ka), and the younger three were inferred to have occurred during OIS 12, 6, and 2 (Oviatt et al., 1999). In contrast to Pleistocene lakes in northern Nevada, the largest of the Bonneville lakes formed during OIS 2. The large size of this late Pleistocene lake is not directly related to climate; it was probably caused by an increase in water volume from the capture of the Bear River drainage (Bouchard et al., 1998).

The descending bathtub-ring character of several Nevada shoreline sequences of this study suggests that pluvial periods became increasingly drier from the early-middle to the late Pleistocene. Climate, tectonics, drainage changes, and changes in moisture sources have probably interacted to produce the observed changes in pluvial lake levels in the western Great Basin, as discussed below, but their relative importance is difficult to determine and probably has changed with time.

Changes in the position of the jet stream induced by changing configurations of the Laurentide ice sheet could affect both precipitation and temperature in the western United States. Global circulation models show that the ice sheet induces splitting of the jet stream, and the movement of the two branches and their associated storm tracks appears to account for pluvial-lake fluctuations in the Basin and Range during the late Pleistocene (e.g., Thompson et al., 1993). Previous configurations (especially altitudes) of pre-late Pleistocene ice sheets are too poorly known to estimate their effects, and they may have differed little from that of the late Wisconsin (except in the area west of the Mississippi River; summarized in Hallberg, 1986).

Geologists have long believed that uplift of the Sierra Nevada since the late Pliocene, estimated to be about 1 km since 3 Ma and 300 m since 0.8 Ma (Huber, 1981; Winograd et al., 1985), has produced an increasing rain shadow to the east through time. In contrast, recent studies have suggested that the range was elevated before the middle Miocene and has since been decreasing in average elevation (Small and Anderson, 1995; Wernicke et al., 1996). Nevertheless, several lines of evidence indicate progressive warming and drying of at least the southern Great Basin during the last two million years. These include the depletion in deuterium content and the increase in  $\delta^{18}\text{O}$  content of ground water (Winograd et al., 1985, 1997), the decline in the water table (Winograd and Szabo, 1988), and the decrease in pluvial-lake size (this study). In addition, Whitney and Harrington (1993) used relict colluvial deposits in southern Nevada to infer that winter temperatures in the southern Great Basin were at least 1–3° C colder in the early and middle Pleistocene than in the late Pleistocene. The apparent discrepancy between the two views of Sierran uplift may be resolved by Small and Anderson's (1995) model. Their model suggests that geomorphic, rather than tectonic, uplift of the Sierra Nevada permitted 30–200 m of uplift per one million years during the Quaternary and that the uplift was in the maximum (as opposed to the average) altitude of slowly eroding parts of the Sierran crest. In addition, there is strong evidence that the Transverse and Cascade Ranges, to the south and north of the Sierra Nevada, respectively, also have increased in altitude during this period (Priest, 1990; Hildreth and Lanphere, 1994; Page et al., 1998; Spotila et al., 1998). Nevertheless, relative uplift of the western Cordillera does not account for the extremely high lake levels that we correlate with OIS 16, but it may help to explain the progressive decrease in lake levels since then.

Regional-scale lithospheric subsidence may have decreased the average altitudes in the northern Great Basin following uplift associated with emplacement of the plume head of the Yellowstone hot spot centered in northern Nevada (Parsons et al., 1994). This possible effect seems contradicted by recent interpretations of fossil flora that suggest elevations in Nevada were much higher at about 15 Ma but had decreased to about the same as the present by about 12 Ma (Wolfe et al., 1997).

More moisture may have crossed the Sierra Nevada in the early and early-middle Pleistocene because of the presence of Lake Clyde, a tectonically dammed lake that filled the Great

Valley of California (Sarna-Wojcicki, 1995). Pacific air masses that gave up moisture while passing over the Coast Ranges could have been recharged by water that evaporated from this large lake (30,000–50,000 km<sup>2</sup>). The added moisture could have increased the snow pack on the Sierra Nevada and on ranges in the Great Basin farther east. Lake Clyde overtopped its sill, rapidly incised its outlet, and drained shortly after 660 Ka (Sarna-Wojcicki, 1995). This moisture effect helps explain the high lake levels of OIS 16, but it does not account for the intermediate shoreline altitudes of pluvial Lakes Lahontan, Columbus, Newark, Hubbs, and possibly Gale that formed between OIS 16 and 2.

Drainage changes have altered the size of the Lahontan drainage basin through time. For example, Lake Russell probably discharged into the Walker River in the late Pliocene and early Pleistocene (Figure 1; Reheis and Morrison, 1997; Reheis et al., 2002). The addition of water from Lake Russell could help to account for high lake levels during the early Pleistocene in the Walker Lake subbasin, if it were not integrated with the Lahontan Basin to the north during part of this period.

Other lake basins that are now tributaries to Lake Lahontan were previously isolated. Smith and Ketner (1976) showed that Pine Valley (PV, Figure 1), presently a tributary to the Humboldt River, was internally drained until sometime after about 660 Ka (following deposition of the Lava Creek B ash bed). Davis (1987) suggested that the lake in Kobeh Valley (Lake Jonathan) was internally drained until sometime after about 670 Ka (following deposition of the Rye Patch Dam ash bed). Recent field work (this study) confirms this proposal and suggests that Lakes Jonathan and Diamond (Figure 1) became integrated with each other and with the Humboldt River when Lake Jonathan spilled over its eastern sill shortly after 670 Ka. The sudden appearance of endemic ostracodes (sample S13-LT, Figure 15) in lake deposits of Lone Tree at Lone Tree Mine could represent a rapid influx of water from a long-lived, stable lake not previously part of the drainage basin (R. Forester, USGS, in litt. to M.C.R., 1998). The newly discovered highest shorelines of Lakes Hubbs and Newark (Table 1) are very close to modern sill levels between these two basins and between the Newark and Lahontan Basins (Figure 18); thus, it is possible that these lakes were temporarily tributaries to Lake Lahontan during this old (OIS 16?) lake cycle. Beach gravel at elevations 3–7 m higher than the late Pleistocene shoreline of Lake Gale, and at the same altitude as its present northern sill (Figure 1, Table 1), indicate that this lake once discharged northward into the Lake Franklin basin, as previously suggested by Hubbs et al. (1974). In addition, other pluvial lakes in east-central Nevada that were isolated during the late Pleistocene, such as Lakes Gilbert, Franklin, and Clover (Figure 1; Mifflin and Wheat, 1979), could have potentially discharged into the Lahontan Basin if their water levels were about 10–40 m above their late Pleistocene levels (estimated from modern topography and not accounting for changes caused by faulting and sedimentation). These three basins as well as the Lake Gale basin presently contain relict fish populations that indicate former

drainage connections with the Lahontan Basin via the Humboldt River, as discussed below (Hubbs and Miller, 1948). Gravel pits north of the northeastern corner of Lake Clover expose thick deposits of probable beach gravel that indicate the lake level was as much as 32 m above the late Pleistocene highstand (Table 1). In addition, gravel pits on the west side of Wells, Nevada, expose a 5–10 m thick sequence of deltaic gravel and sand beds, including steeply dipping foreset beds. These beds lie directly north of the lowest sill around the Lake Clover basin and are interpreted to indicate overflow of the Lake Gale–Lake Franklin–Lake Clover chain of lakes into a small basin around Wells that is now the headwaters of the Humboldt River (Reheis, 1999). Other overflows and basin connections are also possible (Figure 1).

#### IMPLICATIONS FOR MIGRATION OF AQUATIC SPECIES IN THE WESTERN GREAT BASIN

The evidence presented in this paper for connections between presently disjunct lake basins permits geological and chronological constraints to be placed on the Pliocene and Quaternary dispersion of fish and molluscs in the western Great Basin. The pioneering work of Hubbs and Miller (1948) and subsequent refinements by Hubbs et al. (1974), Miller and Smith (1981), and Smith et al. (2002) established that many of these isolated basins contain (or once contained) species of relict fish that are related to each other, to species in the modern Lahontan Basin, and to species in the Columbia River basin to the north and the Owens Lake–Death Valley area to the south. Similar studies of springsnails (Hershler and Sada, 2002) and leeches (Hovingh, 1997) have suggested similar connections, although many of the migrations are probably much older than the period of time discussed in this paper. Research conducted in the last 20 years on material from fossil localities has shown that many modern species of fish and springsnails are very similar to ancestral species that were widely distributed in western North America during the Pliocene. As a result, speciation previously attributed to rapid evolution since about 12 Ka (Hubbs and Miller, 1948) is now more commonly attributed to inheritance from widespread Tertiary populations followed by extinctions and intermittent population-mixing caused by wet–dry climatic cycles and tectonic disruptions during the Pleistocene (e.g., Miller and Smith, 1981; Taylor and Smith, 1981; Taylor, 1985; Minckley et al., 1986; Hershler and Sada, 2002; Smith et al., 2002).

This paper documents large, previously unknown lakes in the western Great Basin that were intermittently connected during the early and middle Pleistocene. This long lacustrine history may allow the observed divergence between some species to be averaged over half a million years rather than over several thousand years, thereby greatly reducing the apparent discrepancy in evolutionary rates. At the least, this new information provides alternative hypotheses about rates of evolution from independent evidence, as urged by Smith et al. (2002). In some cases, these older Pleistocene lakes may require revision of pre-

vious conclusions that were based upon incorrect age assignments. For example, Taylor and Smith (1981) reported on fossil snails and fish from an outcrop in the Mopung Hills in the Lahontan Basin. They noted that the fish were probably ancestral to Lahontan forms but were unlike known Pliocene fossils from the Honey Lake area; therefore, they postulated that a barrier had existed between the two subbasins. These lacustrine deposits in the Mopung Hills had been assigned a Pliocene age by Willden and Speed (1974); lacking chronologic dating, these authors assumed incorrectly that indurated lacustrine deposits older than the late Pleistocene Lake Lahontan sediments must be Pliocene in age! Similar deposits previously mapped as Pliocene at McGee Wash and Sunshine Amphitheater (Greene et al., 1991) are now known to represent early to middle Pleistocene deposits of Lake Lahontan.

**PLIOCENE AND EARLY PLEISTOCENE CONNECTIONS.**—Late Miocene to latest Pliocene lacustrine deposits that fill the present divide between Rhodes and Columbus Salt Marshes (Figures 1, 20) reflect the presence of a former waterway. This connection could have allowed fish to migrate from the Lahontan Basin into Fish Lake Valley, where a relict population of a Lahontan tui chub, *Siphateles bicolor obesus*, survived until historic settlement of the valley (Hubbs and Miller, 1948). Thus, this fish could have migrated into Fish Lake Valley no later than about 2 Ma, after which movement along the Huntoon Valley fault system disrupted the ancient lake basin. *Siphateles b. obesus* and *Rhinichthys osculus lariversi* Lugaski, 1972 (a speckled dace related to the Lahontan dace; Smith et al., 2002), are found in the basin of Lake Toiyabe, in northern Big Smoky Valley, and may have arrived by the same route. Alternatively, Hubbs and Miller (1948) postulated that these fish could have migrated southward into Big Smoky Valley from Grass Valley (pluvial Lake Gilbert, Figure 1) by diversion of tributary streams in the divide area between these two valleys. The modern distribution of a springsnail (*Pyrgulopsis gibba* Hershler, 1995) in the Lahontan Basin, Grass Valley, and Big Smoky Valley supports the latter route (Hershler and Sada, 2002).

The combination of high remnants of lacustrine deposits containing Lake Lahontan-related fish fossils (Miller and Smith, 1981), drainage relationships, and ages of sediments and flows on the east side of the Mono Basin support the interpretation that the basin was a tributary northward to the Walker Lake basin (Figure 1) in the late Pliocene and early to middle(?) Pleistocene (Reheis et al., 2002). Sometime after 1.3 Ma (the age of basalt filling a channel that carried lake discharge northward), this outlet was abandoned and highstands of Lake Russell began to overflow to the south, permitting fish to move into the Owens River drainage. The creation of the new outlet probably was caused by intense faulting in the area of the southern outlet, as evidenced by mapping studies conducted during this study. The relatively youthful appearance of many of the fault scarps suggests that this faulting may have followed the eruption of the Bishop ash (760 Ka) (Sarna-Wojcicki et al., 1991) from Long Valley caldera (Bailey et al., 1976); several studies

have concluded that the rates of vertical slip along fault zones in the area increased markedly after this eruption (dePolo, 1989; Gillespie, 1991; Reheis and Sawyer, 1997). A deep core taken on the floor of Owens (dry) Lake indicates that *Siphates bicolor*, *Prosopium* sp. (whitefish), and *Oncorhynchus* cf. *clarki* (trout) were present in Owens Lake by 730 Ka (Firby et al., 1997); however, fossils identified as *Chasmistes* (lake sucker), similar to *C. batrachops* Cope, 1883, from localities in Oregon and the Snake River Plain, were reported in sediments of early Pleistocene age near China Lake, south of Owens Lake (Miller and Smith, 1981). These fossils suggest that some fish were spread widely along the east slope of the Sierra Nevada by the late Pliocene (Reheis et al., 2002). Three species of springsnails in Owens Valley are most closely related to a Lahontan species (Hershler and Sada, 2002); they may have arrived by migration via the Mono Basin, as discussed above. Another species (*Pyrgulopsis wongi* Hershler, 1995) lives in several isolated basins along the eastern side of the Sierra Nevada south of the Carson River (Figure 1), suggesting the occurrence of a widespread pre-Quaternary population that was subsequently isolated by tectonic disruptions.

**MIDDLE PLEISTOCENE CONNECTIONS.**—The implications of Lake Lahontan having a shoreline at an altitude of 1400 m, herein estimated to have occurred about 650 Ka (within OIS 16), are staggering (Figure 1). For example, such a lake would have (1) inundated Granite Springs and Kumiva Valleys, (2) backed up the Truckee and Carson Rivers to submerge all or part of present-day Reno and Carson City, Nevada, (3) backed up the Humboldt River at least to present-day Battle Mountain, and (4) extended 60 km southeast from Walker Lake to Rhodes Salt Marsh. If allowances are made for local tectonics and for sedimentation in the last half million years, the lake also would have flooded into Dixie and Fairview Valleys and would have inundated many other flat-lying valleys whose floors are now only 5–30 m above the 1400 m level.

Such projections allow specific hypotheses to be proposed and tested. For example, Hubbs and Miller (1948) postulated an “early pluvial” connection between Lake Dixie and Lake Lahontan (Figure 1) on the basis of a subspecies of *S. b. obesus* that inhabits a present-day spring in Pleasant Valley, between Dixie Valley and Grass Valley (an arm of Lake Lahontan). The modern distribution of the springsnail *P. gibba* also supports this connection (Hershler and Sada, 2002). As shown in Figure 1, the 1400 m level of Lake Lahontan probably would have flooded Dixie, Fairview, and Pleasant Valleys (the present lowest sill height is only 8 m above this lake level; Reheis and Morrison, 1997), providing easy access for migrating fish. An enigmatic outcrop in eastern Fairview Valley provides supporting evidence for such a connection. At this site, possible beach gravel extends up to an altitude of 1384 m; this gravel rests unconformably on fine-grained lacustrine deposits containing tephra of probable early Pliocene age (samples EL-59-FV and EL-66-FV, Tables 2, 3). Further searches should be made in Dixie and Fairview Valleys for better sites to confirm their postulated connection to Lake Lahontan.

It is also likely that Lake Lahontan, while at its 1400 m highstand about 650 Ka, flooded Granite Springs and Kumiva Valleys. These valleys are located within a large “island” in the center of the Lahontan Basin, and each held a small, isolated pluvial lake during the Seho highstand of Lake Lahontan (Figure 1; Mifflin and Wheat, 1979). No search for deposits of the 1400 m highstand has been done in this internally drained area; however, pre-late Pleistocene inundation is supported by the existence of leeches (*Erpobdella* sp.) in present-day springs within the “island” that are identical to species in springs of Eagle Lake, Madeline Plains, and Winnemucca Lake (P. Hovingh, Utah Museum of Natural History, in litt. to M.C.R., 1997) within the Lahontan Basin. The springsnail *Pyrgulopsis gibba* also lives in both the Lahontan and Granite Springs Basins (Hershler and Sada, 2002).

Several basins in central Nevada show evidence of much higher lake levels in the past. Results of the present study combined with previous research show that two of these basins, Kobeh Valley (Davis, 1987; Tackman, 1993) and Pine Valley (Smith and Ketner, 1976), were internally drained basins containing pluvial lakes until at least about 670 and 660 Ka, respectively, and that they subsequently integrated with the Lahontan Basin. It is likely that shortly after 660 Ka, very high stands of Lake Jonathan (Kobeh Valley), and perhaps of Lake Pine (Pine Valley), triggered overflows that caused the integration of these drainage basins with the Lahontan Basin. If so, fish presently living in these valleys, including populations of *S. b. obesus* and *R. osculus* (Hubbs et al., 1974), may not have arrived until after 660 Ka.

Hubbs et al. (1974) proposed that Lakes Hubbs and Newark may have once been connected to the Humboldt River (Figure 1) by overflow from Lake Hubbs to Lake Newark through Beck Pass and thence from Lake Newark northward to Huntington Creek. Their best evidence for overflow of Lake Newark came from the presence of two subspecies of *S. bicolor* in modern springs of Newark Valley; no fish were found in Long Valley (Lake Hubbs). They observed what they considered to be wave-cut terraces nearly up to the height of the sill (1891 m in altitude) at the north end of Newark Valley. Although Mifflin and Wheat (1979) reported no shorelines this high, field work for the present study found definite beach gravel as high as 1887–1890 m in altitude at the north end of Newark Valley, only 1–4 m below the modern divide (Table 1); there is also a large drainage channel leading north into Huntington Creek that begins just below the summit. Beach gravel is preserved at least as high as about 1927 m in Long Valley, which is 25 m above the late Pleistocene shoreline of Lake Hubbs, and possibly as high as 1940 m, which is about 6 m below the modern sill at Beck Pass. The highest shorelines of Lake Hubbs and Lake Newark may have formed at the same time as those of the 1400 m highstand of Lake Lahontan (Figure 1) and of Lake Jonathan and Lake Pine, i.e., at about 650 Ka (Figure 18). The highest shoreline of Lake Newark is so close to the present northern divide that it is very likely that the lake overflowed northward into Huntington Creek at this time, providing a migration route

for the fish presently in Newark Valley. We speculate that Lake Hubbs may have overflowed into Lake Newark at the same time. These hypotheses can be tested by more detailed field work and mapping.

We further speculate that other isolated fish-bearing basins in central and eastern Nevada could have been populated by fish and springsnails during pre-late Pleistocene overflows (Figure 1). These basins held Lakes Gilbert (Grass Valley: *R. osculus*, *P. gibba*), Gale (Butte Valley: *Relictus solitarius* Hubbs and Miller, 1972), Franklin (Ruby Valley: *R. solitarius*, *Pyrgulopsis leporina* Hershler, 1998), and Clover (*R. osculus* and *S. bicolor*) (Hubbs et al., 1974; Hershler and Sada, 2002; Smith et al., 2002). We acknowledge, however, that some of the fish species—especially *R. solitarius*—are so different from their nearest relatives in the Lahontan Basin that they could have resulted from divergence from fish that were widely distributed across Nevada in the Pliocene, when conditions were much wetter and drainage basins were configured differently (Forster, 1991). The modern divide between Grass Valley and Crescent Valley (part of the Lahontan drainage basin) is 36 m above the late Pleistocene shoreline of Lake Gilbert (Figure 1; Mifflin and Wheat, 1979). As noted by Hubbs et al. (1974), the altitude of this divide has probably been affected by faulting. Lakes Gale, Franklin, and Clover form a chain of lakes with very low divides that are less than 15 m above their late Pleistocene shorelines (Figure 1). Both Hubbs et al. (1974) and Mifflin and Wheat (1979) noted the presence of a channel leading north from the present divide between Butte and Ruby Valleys; reconnaissance for the present study found beach gravels at altitudes at and below the altitude of the lip of this channel in northern Butte Valley (Figure 1, Table 1). These authors explained that overflow from Lake Gale to Lake Franklin in pre-late Pleistocene time enabled the same fish to inhabit these two lakes. The divide between Ruby and Clover Valleys is even lower, and it seems very likely that Lake Franklin also overflowed into Lake Clover, although Hubbs et al. (1974) found no evidence of a connecting channel and thought that such an overflow had not occurred because of the disparity in fish species between Ruby and Clover Valleys. Nevertheless, *R. solitarius*, which apparently evolved from a Lake Lahontan-type dace (Hubbs et al., 1974), had to have reached Ruby and Butte Valleys by some means, and the obvious route was by discharge from Lake Franklin to Lake Clover and thence northward into the Humboldt River. Recent discovery of probable beach gravel that lies 32 m above the late Pleistocene shoreline of Lake Clover as well as deltaic deposits at Wells, just north of the present lowest sill of Lake Clover (Table 1), suggests that a discharge had occurred. Such a connection is also supported by the occurrence of the springsnail *P. leporina* in both Ruby Valley and the upper Humboldt River drainage (Hershler and Sada, 2002).

### Summary

The large study area and the amount of detail presented in this paper is dauntingly complex. In the following summary of results, we present a speculative but coherent framework of hypotheses that provides context for the results and a springboard for future integrative studies to test the hypotheses. We encourage other researchers to pursue these tests.

During the Pliocene to middle Pleistocene, pluvial lakes in the western Great Basin repeatedly rose to levels much higher than those of the well-documented later Pleistocene. Early migrations of aquatic species were facilitated by connections among Pliocene lakes, which were subsequently disrupted by tectonic movements. The geologic evidence for these Pliocene connections supports recent work summarized by Smith et al. (2002) and by Hershler and Sada (2002), indicating that many of the modern distributions of aquatic species result from pre-Quaternary dispersions.

The parallel histories of Pliocene lakes in Rhodes Salt Marsh, Clayton Valley, and Fish Lake Valley, combined with the lack of sills or very low sills between Columbus Salt Marsh and Clayton, Fish Lake, and Big Smoky Valleys, support the interpretation that these lakes were interconnected during the Pliocene. In addition, we infer that a Miocene to Pliocene lake basin that at least included Rhodes and Columbus Salt Marshes was disrupted by faulting and (or) compression. The timing of these connections indicates that fish and possibly springsnails must have migrated into Fish Lake Valley from the north before about 2 Ma. The populations of fish and springsnails in northern Big Smoky Valley may have arrived by the same route or across a higher divide from Grass Valley (Lake Gilbert) to the north (Hubbs and Miller, 1948), or they may be relict from older, more widespread ancestral populations (e.g., Taylor, 1985; Minckley et al., 1986).

The combination of high remnants of lacustrine deposits containing Lake Lahontan-related fish fossils (Miller and Smith, 1981), drainage relationships, and ages of sediments and flows on the east side of the Mono Basin indicate that the Mono Basin periodically was a tributary to the Walker River in the late Pliocene and early Pleistocene, permitting Lake Lahontan fish to enter the Mono Basin. Some of these fish then migrated southward into the Owens River drainage when a new, lower outlet opened sometime after 1.3 Ma and possibly as recently as after 760 Ka. Some fish, however, may have already reached the area south of Owens Lake before the early Pleistocene (Miller and Smith, 1981).

Several outcrops in the Lahontan Basin document highstands of a lake that rose far above the Seho and Eetza(?) shorelines during the early and middle Pleistocene. A conservative correlation among all the known sites yields a total of seven lacustrine units whose shorelines exceeded that of the Seho lake; three of the units postdate the lake unit containing a tephra provisionally correlated to the Bishop ash bed dated from 0.76 Ma, and three predate the tephra-containing unit but are younger than 2.6 Ma. The Walker Lake subbasin became integrated with the northern Lahontan subbasins probably by 1 Ma (lake deposits of Campbell) but possibly as recently as about 650 Ka (lake deposits of McGee). The youngest three units represent middle Pleistocene shorelines stepped progressively downward with time. The lake deposits of McGee, representing the highest Lake Lahontan shoreline preserved at an altitude of 1400 m, is correlated with the Rye Patch Dam Alloformation from 670 to 630? Ka (Morrison, 1991) and with marine OIS 16. The younger two shorelines, at altitudes of about 1370 and 1350 m, are tentatively correlated with OIS 12 (~430 Ka) and OIS 10 (~340 Ka) or younger glacial stages, respectively.

Similar records of undated shorelines descending from an early-middle Pleistocene highstand are preserved in the basins of Lakes Columbus-Rennie, Hubbs, and Newark. Very high stands also were achieved shortly after about 660 Ka by Lake Jonathan and Lake Pine. The geographic distribution of these lakes indicate that the causes of the very high stands were not limited in their effects to western Nevada; how far east the higher lake levels of middle Pleistocene age can be found is unknown, but they have not been reported in the Bonneville Basin of Utah (Oviatt et al., 1999). Complex interactions among climate, tectonics, drainage changes, and moisture sources are responsible for the observed differences in pluvial lake levels in the western Great Basin. These interactions could be tested by global circulation models.

At about 650 Ka, pluvial lakes in Nevada reached such high levels that numerous interbasin thresholds were likely over-

topped. In the cases of Lake Jonathan and Lake Pine, these overflows caused the basins to become permanently or periodically part of the Lahontan drainage basin. In other cases, such as Granite Springs and Dixie Valleys, Lakes Hubbs and Newark, and perhaps simultaneously Lakes Gilbert, Gale, Franklin, and Clover, the overflows were temporary. These connections provided potential migration routes for relict populations of Lake Lahontan-type fishes and springsnails that presently reside in internally drained basins, especially those species and subspecies that apparently have diverged little from their modern relatives in the Lahontan Basin. This scenario presents a startling vision of a western Great Basin in which climatic and tectonic effects conspired to integrate presently isolated basins into one enormous drainage system during at least one brief period during the Quaternary. Much work remains to be done to test this hypothetical vision.

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# Pleistocene Lakes and Paleoclimates (0 to 200 Ka) in Death Valley, California

*Tim K. Lowenstein*

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## ABSTRACT

The existence of an ancient lake in Death Valley, California, named Lake Manly by geologists in the early part of the twentieth century, was suggested on the basis of shoreline features (gravel deposits, erosional terraces, and carbonate tufas) and basin-center muds and evaporites. Radiocarbon dating of black lacustrine muds and uranium-series dates on shoreline tufas later established that permanent lakes occurred in Death Valley during at least two different periods: marine oxygen isotope stage 2 (26 thousand to about 10 thousand years ago (Ka)) and marine oxygen isotope stage 5e/6 (>200 to ~120 Ka).

The sources of inflow water to Death Valley during wet pluvial periods were the Amargosa River, the Owens River system, and the Mojave River. The timing of spillover from the Owens River system via Panamint Basin into Death Valley is still uncertain; inflow from the Mojave River is interpreted to have occurred during the last 18 Ky, but more precise timing and the significance of the Mojave River inflow is unknown.

A borehole core (DV93-1) taken from Badwater Basin, Death Valley, in 1993, is composed of interbedded salts and muds. Core DV93-1 contains a 186 m long, 200 thousand years (Ky) record of closed-basin paleoenvironments and paleoclimates, which is interpreted on the basis of sedimentology, ostracode assemblages, homogenization temperatures of fluid inclusions in halite. The lacustrine sediments in core DV93-1 correlate with dated shoreline tufa. The 200 Ky paleoclimate record is dominated by two cycles of dry and/or warm conditions followed by wet and cold conditions that occurred on a 100 Ky time scale. Of significance are the major lacustrine phases of 35–10 Ka and 186–120 Ka (marine oxygen isotope stages 2 and 5e/6, respectively), which represent dramatically colder and wetter conditions than those of modern Death Valley. Of the two major lake periods, the penultimate glacial lakes were deeper and lasted far longer than those of the last glacial.

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## Previous Work on the Ancient Lakes of Death Valley

The first published evidence of an ancient lake in Death Valley, California, is from Noble (1926), who briefly described strandlines along a basalt hill in southern Death Valley (Shoreline Butte) and in gravel deposits at Mormon Point (Figure 1). These former shorelines were, according to Noble (1926), 122 to 153 m, respectively, above the low point of Death Valley. The ancient lake in Death Valley was named Lake Manly by Means (1932) for William Manly, who traveled through Death Valley in 1849—and survived. Blackwelder (1933) described further evidence of former Lake Manly, including the mud deposits underlying the modern surface salt crust in the center of Death Valley, and at least 12 erosional terraces on Shoreline Butte that were up to 95 m above sea level and contained rounded gravels and carbonate coatings. Less pronounced terraces from several locations on the southwest and eastern margins of Death Valley (Park Village and Mormon Point, respectively) also were described by Blackwelder (1933), as well as two localities where small tufas were interpreted as possible shoreline deposits of a former lake.

Blackwelder (1933, 1954) speculated that Lake Manly existed during a glacial period. The poor preservation of shoreline features compared with the well-documented features from Lake Bonneville and Mono Lake led him to conclude that Lake Manly existed during the Tahoe glaciation (early Wisconsin, now dated at ~74 to ~49 thousand years ago (Ka)) and that a shallower lake also may have existed during the late Wisconsin Tioga glacial (dated at ~30 to ~12 Ka (Phillips et al., 1990; Phillips et al., 1996)). Blackwelder (1933) suggested that Lake Manly was a relatively short-lived lake because of the relative paucity of tufa and the poor development of erosional shoreline features in Death Valley.

Hunt and Mabey (1966) followed previous workers when they concluded that Lake Manly had been synchronous with Wisconsin (Tahoe and Tioga) glaciation in the Sierra Nevada, and they added several more observations to the growing list of shoreline features. The lacustrine shoreline and near-shore

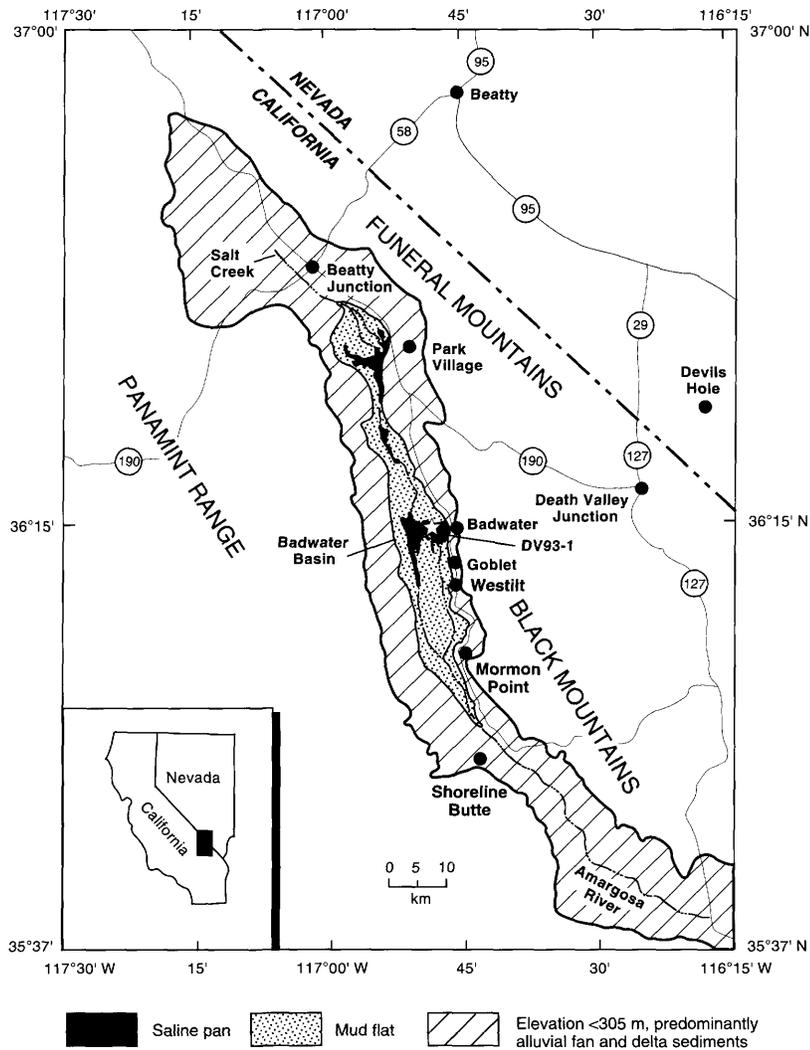


FIGURE 1.—Map of Death Valley, California, and location of core DV93-1 (indicated by the white star).

features described by Hunt and Mabey (1966) included shingled gravels along the north and east sides of Death Valley that were up to 116 m above sea level; a large gravel bar composed of well-sorted and crossbedded gravels, near Beatty Junction at 46 m above sea level; terraces near Park Village at elevations between sea level and 46 m above sea level; calcite-cemented gravels along the Black Mountains between Badwater and Mormon Point, most commonly between sea level and 61 m above sea level; and numerous horizontal shoreline features of Shoreline Butte.

Hooke (1972) found important new information on the ancient lakes in Death Valley from borehole cores taken in the center of Badwater Basin and from shoreline carbonate tufas plastered on the Black Mountains. Hooke (1972) was the first to publish quantitative information on the timing of the ancient lakes in Death Valley, which he derived from radiocarbon dating of organic carbon from the Badwater Basin cores. The Badwater Basin cores contained brown mud, 3–15 m thick, overlying 1–2 m of olive green mud, which graded into black mud below. The black muds were interpreted as lake deposits

that were never subaerially exposed (Hooke, 1972). Radiocarbon dates from two samples near the top of the black mud interval were 11,900 yr and 12,980 yr. A date of 21,500 yr was obtained from lower in the black mud interval. Hooke (1972), therefore, proposed that a perennial lake existed in Death Valley from about 26 to 10.5 Ka. Radiocarbon dates from the basin-center lacustrine muds led Hooke (1972) to interpret the shorelines 90 m above sea level as latest Wisconsin in age, 11–10 Ka, and he named the youngest shoreline features the Blackwelder stand of Lake Manly. Hooke (1972) also studied carbonate tufas from various locations in the Black Mountains. He tentatively inferred the presence of three generations of tufas on the basis of their coloration and weathering characteristics: latest Wisconsin (Blackwelder stand), early Wisconsin, and pre-Wisconsin.

Later work on dating the Black Mountain tufas by Hooke and Lively (1979) and by Hooke and Dorn (1992) has led to new interpretations of the Blackwelder stand. Hooke and Lively (1979) dated 34 tufas by uranium-series (U-series) methods. Although there were problems with the possible loss

of uranium from samples, and also possible  $^{230}\text{Th}$  contamination, a majority of the dates fell between 225 and 135 Ka, which led Hooke and Lively (1979) and Hooke and Dorn (1992) to conclude that the Blackwelder stand was much older than previously thought and likely coincided with Illinoian glaciations and marine oxygen isotope stage 6. In addition, two tufas from the high shorelines of neighboring Panamint Valley (Figure 2) were dated by Hooke and Lively (1979). They, too, were apparently Illinoian in age,  $138 \pm 7$  Ka and  $137 \pm 4$  Ka, although loss of uranium and  $^{230}\text{Th}$  contamination may have affected the samples. Finally, Dorn (1989) and Dorn et al. (1989) performed cation-ratio dating of desert varnish and concluded that the high Blackwelder stand receded 130–120 Ka.

Dorn et al. (1990) used radiocarbon dating of rock varnish to estimate the beginning of the recession of the latest Pleistocene lake in Death Valley. They obtained dates of 12,970 yr from Mormon Point (3 m above sea level) and 12,630 yr from Park Service Housing, Park Village (5 m below sea level) (Dorn et al., 1990). These dates were consistent with the radiocarbon dates obtained by Hooke (1972) for the existence of a perennial lake in Death Valley between 26 and 10 Ka.

Most recently, Meek (1997) carefully measured the shoreline elevations at Shoreline Butte and Mormon Point. The prominent 94.7 m bench at Shoreline Butte was interpreted as an Illinoian-age (marine oxygen isotope stage 6) shoreline, marking a lake 1606 km<sup>2</sup> in area and having a volume of 176 km<sup>3</sup>. Meek (1997) interpreted the shorelines around 5 m above sea level as late Wisconsin in age (marine oxygen isotope stage 2). The highest shoreline in Death Valley, 135.4 m above sea level at Shoreline Butte, was interpreted by Meek (1997) as being older than marine oxygen isotope stage 6. Meek (1997) discussed the difficulties involved in correlating shorelines from different localities because the timing and magnitude of faulting are unknown. For example, the highest shoreline features at Mormon Point (104–113 m) and the uppermost shoreline at Shoreline Butte (135.4 m) may represent different lake phases or they may represent the same lake phase with faulting of approximately 26 m between locations (Meek, 1997).

D.E. Anderson and Wells (1997) and Anderson (1998) investigated late Wisconsin-age lake sediments from 10 shallow cores taken in southern Death Valley. On the basis of sedimentary textures and accelerator mass spectrometry (AMS) radiocarbon ages, Anderson (1998) identified three late Pleistocene highstands at ~26, ~18, and ~12 Ka, which are in complete agreement with the work of Hooke (1972).

Lake Manly was fed by inflow from the Amargosa River. This river currently drains areas to the east of Death Valley in southwestern Nevada and is a source of inflow water into the southern end of Death Valley. In the Pliocene and Pleistocene, Lake Tecopa, with an estimated area of 235 km<sup>2</sup>, may have been the terminal lake of the Amargosa River drainage (Figure 2) (Morrison, 1991). Correlation of tephra layers indicates the breaching of Lake Tecopa may have occurred between 170 and

150 Ka (Morrison, 1991). After that time, the Amargosa River flowed directly into Death Valley.

Additional inflow sources that may have supplied water to Death Valley during wet pluvial periods were (1) the Owens River system to the west of Death Valley, which receives water from the Sierra Nevada, and (2) the Mojave River from the south, which receives the drainage from the San Bernardino Mountains (Figure 2) (see for example, Blackwelder, 1933, 1954; Smith, 1979, 1984; Smith and Pratt, 1957; Jannik et al., 1991; Brown and Rosen, 1995). The Owens River system derived waters from the Sierra Nevada and eventually reached Death Valley via a system of lakes and spillways, namely Owens Lake, China Lake, Searles Lake, Panamint Lake (Lake Gale), and finally Death Valley (Lake Manly) via Wingate Pass in southwestern Death Valley (Gale, 1914; Blackwelder, 1954; Smith and Pratt, 1957; Smith, 1979, 1984; Jannik et al., 1991). The inferred connection between Panamint Lake and Lake Manly at Wingate Pass is controversial because evidence of erosion by spillover flow from Panamint Lake into Death Valley is equivocal. Hooke (1972) interpreted four hills composed of gravels as delta deposits, implying they were formed by water spillover from Panamint Lake. Tufa deposits, along with erosional benches and shallow-water gravel deposits, have been described by R.S.U. Smith (1978) from various locations in Panamint Valley between elevations of 502 and 627 m above sea level. Some of these shoreline features are at or above the elevation of Wingate Pass (605 m), which is strong evidence for spillover into Death Valley, ignoring the effects of faulting. Fitzpatrick and Bischoff (1993) obtained U-series dates on samples from the high shorelines of Panamint Lake but argued that the dates may be unreliable because of post-depositional mobilization of uranium. They concluded that the shoreline features are between 300 and 30 Ka in age but probably do not represent late Pleistocene marine oxygen isotope stage 2 (Fitzpatrick and Bischoff, 1993). Their isochron plots suggest ages between 95 and 55 Ka; therefore, although water clearly entered Death Valley via spillover from Panamint Lake, the timing of that spillover is still uncertain.

Inflow of water from the Mojave River into the south end of Death Valley was discussed by Brown and Rosen (1995), who concluded that Lake Manly may have received inflow from the Mojave drainage area only in the latest Pleistocene. This conclusion was based on the age of Pleistocene Lake Mojave (now Silver Lake playa near Baker, California) to the south of Death Valley (younger than 22 Ka) and on the supposition that for water to overflow into Death Valley from the Mohave River drainage area, Lake Mojave itself must have been at or above a spillover level (Figure 2). This interpretation is supported by work on the Manix Basin by Meek (1989; pers. comm., 1996). From the study of the sediments at Afton Canyon, near Lake Manix, Meek (1989; pers. comm., 1996) concluded that Lake Manix was the terminal lake in the Mojave River system for most of the Pleistocene until Afton Canyon was eroded sometime after 18 Ka. At that point, waters from the Mojave River

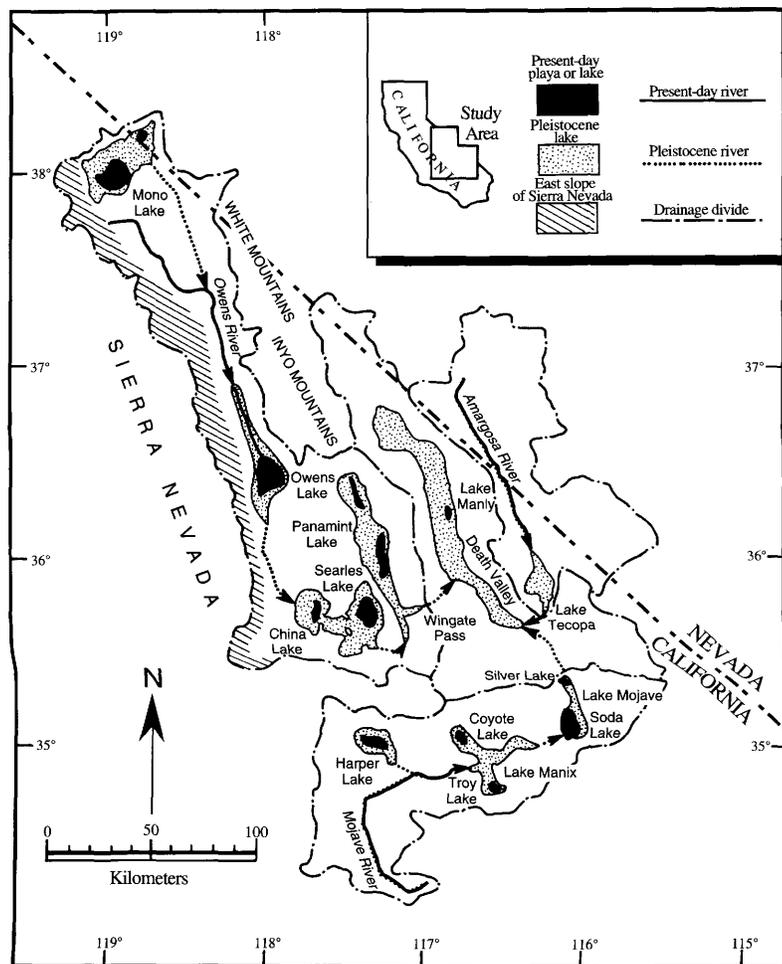


FIGURE 2.—Map of pluvial lakes, modern lakes and playas, Pleistocene drainage patterns, and modern drainages of the Owens River, Amargosa River, and Mojave River systems. Modified from Blackwelder (1954), Smith (1984), Jannik et al. (1991), and Brown and Rosen (1995).

reached the Silver Lake and Soda Lake playas. During exceptionally high levels of Silver Lake (Lake Mojave), water may have overflowed into the southern end of Death Valley. There are no features reported from Death Valley indicating inflow of large amounts of water at approximately 18 Ka, but this period does coincide with a wet period in Death Valley when the basin contained a perennial lake (see "Sedimentology," below).

Additional information on the timing of inflow waters from the Mojave River into the southern end of Death Valley comes from studies of Lake Dumont conducted by K.C. Anderson and Wells (1996, 1997). The Dumont Basin (10 km<sup>2</sup>) is a small playa located between Silver Lake playa and the southern arm of the Amargosa River (Figure 2). K.C. Anderson and Wells (1996, 1997) found lacustrine sediments in two 13 m long cores taken in Dumont Basin. They identified Lake Dumont I (25.3–30 Ka) and Lake Dumont II (18–19.8 Ka) on the basis of radiocarbon dates obtained from ostracode-bearing lacustrine muds. K.C. Anderson and Wells (1996) concluded that Lake Dumont II broke through its sill sometime after 18 Ka, which established a direct connection between the Mojave River, the

Amargosa River, and Death Valley. That date coincides with the timing of the erosion of Afton Canyon upstream in the Mojave River system (Meek, 1989; pers. comm., 1996). It is not known whether Lake Dumont I overflowed into Death Valley between 30 and 25 Ka.

#### Analysis and Interpretation of Data from Core DV93-1 from Death Valley

A 6.4 cm diameter core, DV93-1, was drilled to a depth of 185.5 m through Badwater Basin, Death Valley, during April and May of 1993 (Figure 1). The drill site was near the center of the saline pan, 3.2 km northwest of Badwater Springs. The core is composed of interbedded salt and mud. Virtually all salt layers were completely recovered, but retrieval of the mud intervals was about 60 percent successful. The core records the 200 Ky record of closed-basin paleoenvironments and paleoclimates in Death Valley, as interpreted on the basis of sedimentology, ostracode species, fluid-inclusion homogenization temperatures in halite, saline mineralogy, and correlation with shoreline tufa.

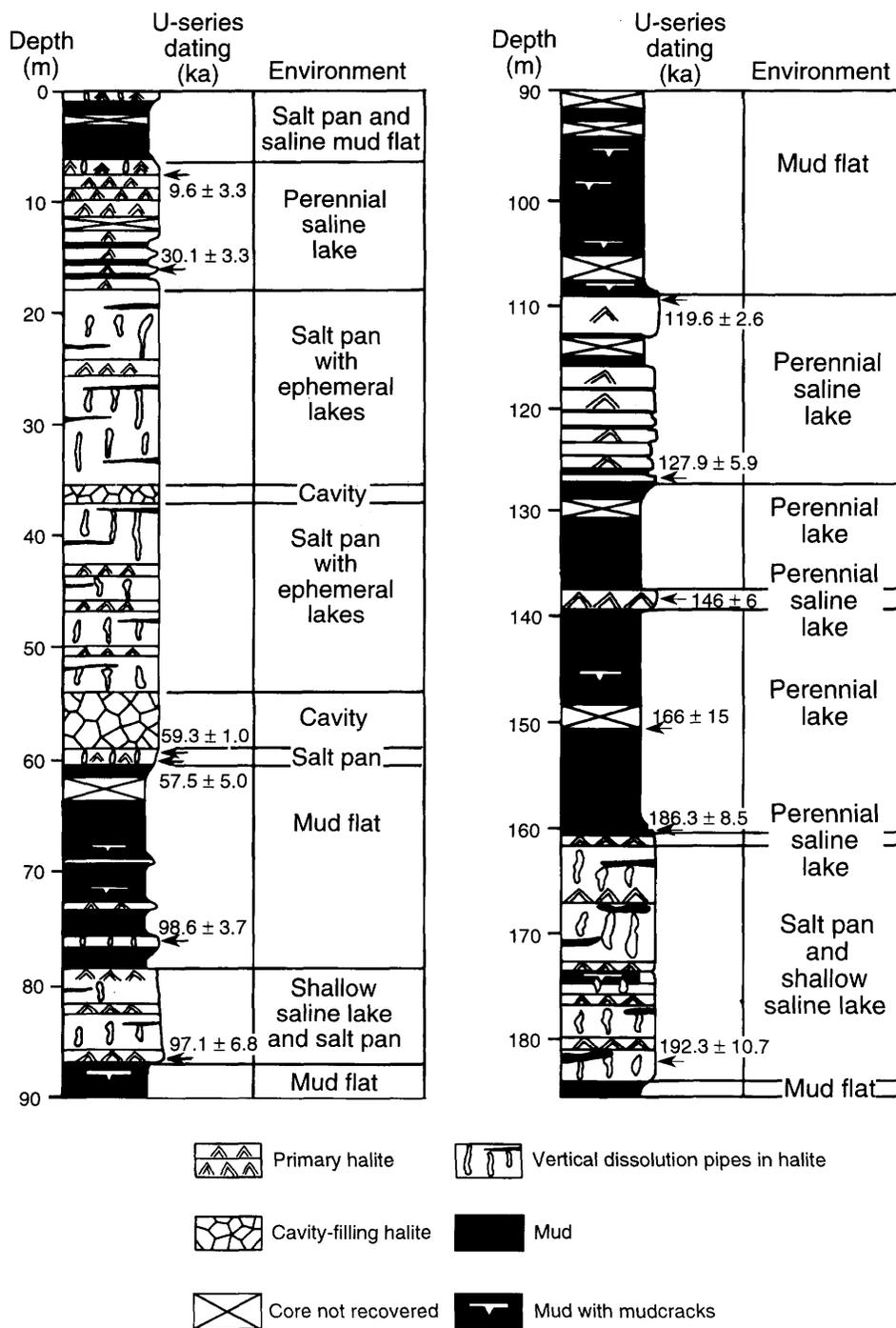


FIGURE 3.—Stratigraphic column, Core DV93-1, with uranium-series ages, sediment types, and interpreted depositional environments.

DATING CORE DV93-1.—The core was dated using the  $^{230}\text{Th}/^{234}\text{U}$  method, which determines the time uranium was incorporated into a sample (Luo and Ku, 1991; Ku et al., 1998). The total dissolution isochron technique was used to account for initial detrital  $^{230}\text{Th}$  in the samples (Luo and Ku, 1991). Samples from 12 stratigraphic intervals were dated (Figure 3).

The samples contained preserved primary halite as well as incorporated clay, carbonate (predominantly calcite), and sulfate minerals (mainly gypsum or glauberite,  $\text{CaSO}_4 \cdot \text{Na}_2\text{SO}_4$ ). Authigenic  $^{230}\text{Th}/^{234}\text{U}$  and  $^{234}\text{U}/^{238}\text{U}$  ratios used in calculating the age of a halite sample were determined from linear plots (isochrons) of  $^{230}\text{Th}/^{232}\text{Th}$  versus  $^{234}\text{U}/^{232}\text{Th}$  and of  $^{234}\text{U}/^{232}\text{Th}$  versus

$^{238}\text{U}/^{232}\text{Th}$  of a series of subsamples taken from each of the 12 stratigraphic intervals. These activity ratios were counted using alpha particle spectrometry (Ku et al., 1998). The given age errors are one standard deviation, which were derived from counting statistics and the fitting of isochrons. The age errors are less than 11 percent, except for the uppermost sample from 7.7 m, where the large error results from the relatively large amount of detrital  $^{230}\text{Th}$  initially in this relatively young sample. The reliability of the dating technique can be seen from the general increase in age down the core. Two samples from around 60 m (Figure 3) with very close ages, but with very different amounts of detrital material, and hence different  $^{230}\text{Th}/^{232}\text{Th}$  ratios, supports the validity of the isochron approach. All dates discussed that were not obtained directly from the U-series isochron method were calculated by interpolation, assuming constant accumulation rates for each sediment interval. Sedimentation rates averaged over the entire 186 m of core DV93-1 are 1 m/1 Ky (thousand years). Salts, predominantly halite, were deposited rapidly, 1.7–3.8 m/1 Ky, whereas muds accumulated more slowly, at rates of 0.4–1.0 m/1 Ky.

Carbonate shoreline tufas from the east side of Death Valley, between Badwater Springs and Mormon Point were carefully chosen to avoid samples with impurities, weathering rinds, extensive cements, or recrystallization textures (see "Shoreline Carbonate Tufas," below). Samples were cleaned and dissolved, and  $^{238}\text{U}$ ,  $^{234}\text{U}$ ,  $^{232}\text{Th}$ , and  $^{230}\text{Th}$  were counted by alpha particle spectrometry (Ku et al., 1998). The ages of tufas, along with one standard deviation errors derived from counting statistics, are shown in Figure 4C. For most samples, the high activity ratios of  $^{230}\text{Th}/^{232}\text{Th}$ , greater than 15, suggest that the ages of samples should be close to the time of tufa formation (Ku et al., 1998).

**SEDIMENTOLOGY.**—Paleoenvironments present in Death Valley over the past 200 Ky were interpreted by comparing sedimentary structures and petrographic features described from modern closed-basin sediments with those observed in core DV93-1 (Figures 3, 4A) (Hardie et al., 1978; Lowenstein and Hardie, 1985; Smoot and Lowenstein, 1991; Roberts et al., 1994; Li et al., 1996). The cored sediments contain a record of closed-basin paleoenvironments ranging from hot, dry mudflats, similar to the modern floor of Death Valley, to temperate climate, deep perennial lakes.

Disrupted brown muds overlain by a 0.25 m thick surface halite crust (0–7.7 m) indicate Death Valley has been a mudflat and saline pan during the last 10 Ky (Figures 3, 4A). Further details are lacking because most sedimentary structures from this interval were destroyed during coring.

A perennial saline lake existed in Death Valley for an ~25 Ky period, from 10 to 35 Ka (core depths of 7.7–18 m) (Li et al., 1996). Interbedded mud and halite cycles accumulated during the early perennial lake stage, followed by interlayered thenardite ( $\text{Na}_2\text{SO}_4$ ) and mud. A cap of chevron halite formed during the latest lake stage. These deposits record a generally wet climate, with fluctuating lake levels and salinities. The lack

of syndimentary dissolution features in evaporite layers indicates that accumulated salts were permanently protected from dilute flood waters by the saline lake, which suggests that lakes existed more or less continually, without drying out, for 25 Ky. The mud layers are structureless, contain rare ostracodes, and are black in color but change to gray green after exposure to air. Halite textures include cumulate settle-out layers and bottom-grown crusts, which are interlayered with black muds (Li et al., 1996). Thenardite layers from 10 to 13 m are apparently diagenetic in origin but may have first formed as mirabilite ( $\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$ ), as observed in the winter in Great Salt Lake and Owens Lake (Spencer et al., 1984; Spencer et al., 1985a; Spencer et al., 1985b; Smith et al., 1987). The age of the thenardite is ~22 to ~16 Ka in core DV93-1. This age coincides with the last glacial maximum and suggests that  $\text{Na}_2\text{SO}_4$  crystallized as mirabilite during winter cold water conditions, probably at temperatures below ~10° C (Smith et al., 1987). Halite from the uppermost saline lake interval (7.7–10 m) contains chevrons, raft textures, and pisoids. These are interpreted to have accumulated in a shallow, perennial lake that ultimately dried out about 10 Ka (Li et al., 1996).

Saline-pan evaporites present from 18 to 60 m indicate that Death Valley was commonly desiccated between ~35 to ~60 Ka, but it did receive enough inflow water to maintain shallow saline lakes at times and to supply the solutes required to accumulate salts rapidly, at rates of 1.7 m/1 Ky (Figures 3, 4A) (Li et al., 1996). Saline-pan halites consist of poorly bedded halite, with little preservation of primary depositional textures. A distinctive feature of halite layers is a vertical pipework fabric cemented with halite, which signifies multiple episodes of subaerial exposure, dissolution of surficial halite by dilute floodwaters, and later cementation of cavities by shallow groundwater brines. Five thin halite intervals between 43 and 52 m (Figure 4A) (~50–54 Ka), which carry primary features such as chevrons and rafts, indicate that shallow saline lakes existed in Death Valley during this time.

Clayey silts, some massive and some with mudcracks and sand-patch textures, which are diagnostic of deposition on dry mudflats, are the dominant sediment type from 60.5 to 109 m (Figures 3, 4A) (60–120 Ka) (Smoot and Lowenstein, 1991; Roberts et al., 1994; Smoot and Castens-Seidell, 1994; Li et al., 1996). Sand patches are wind-blown or water-deposited sediments, which filled depressions in efflorescent crusts on the mudflat surface (Smoot and Castens-Seidell, 1994). Later flooding dissolved the efflorescent salt crusts, which caused collapse of the overlying sediments and produced internal fractures, faulting, and rotation of sand patches. Saline minerals consist of crystals of halite, glauberite ( $\text{CaSO}_4 \cdot \text{Na}_2\text{SO}_4$ ), and gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ) that formed during early diagenetic displacive growth from groundwater brines. Interbedded remnants of saline-pan halite and a total lack of lacustrine fossils, such as diatoms and ostracodes, reinforce the interpretation that these muds were from mudflats, not perennial-lake deposits. One halite interval, interpreted to have been deposited in shal-

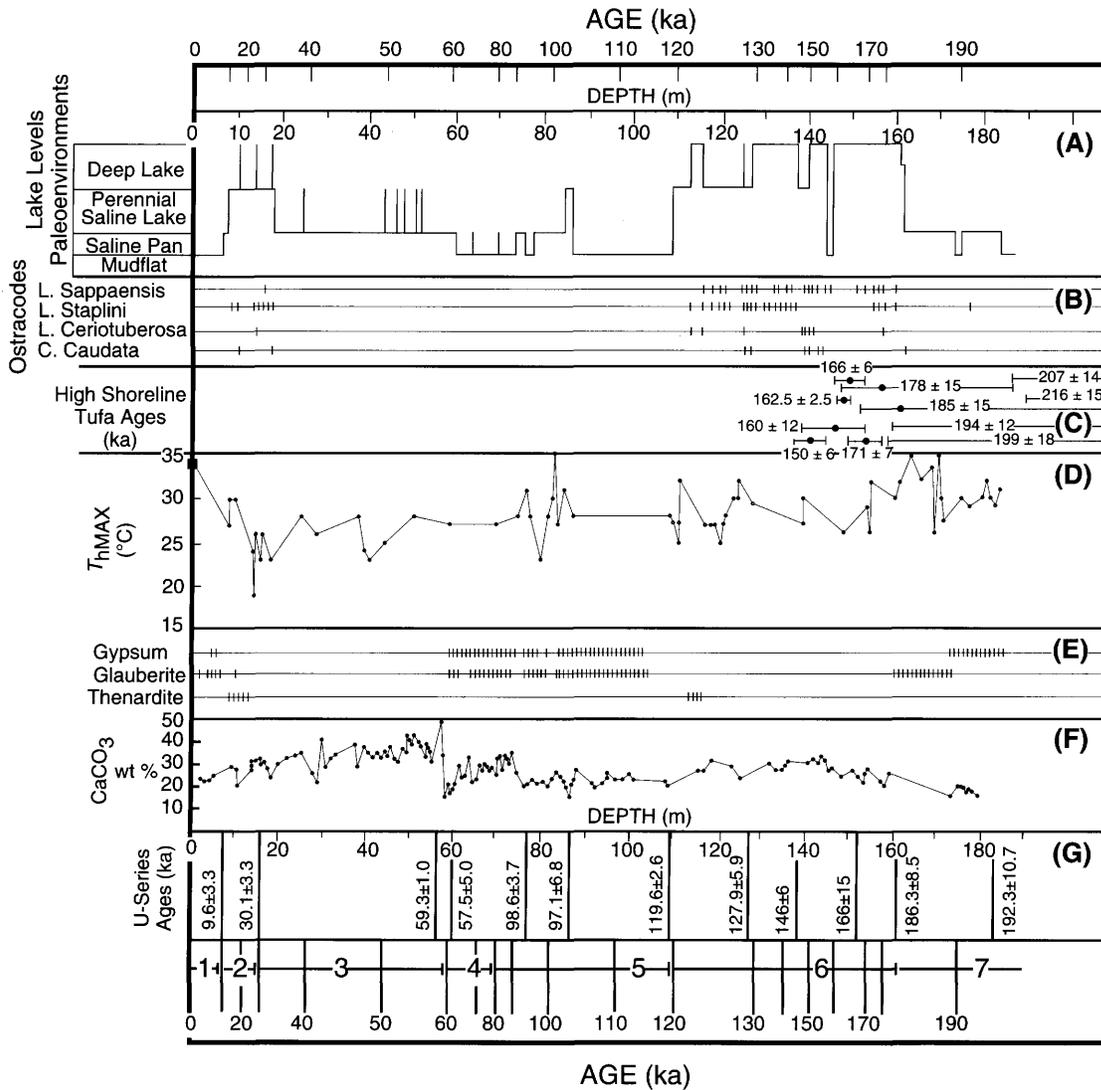


FIGURE 4.—Paleoclimate record, core DV93-1, during the last 200 Ky. A, Lake levels and paleoenvironments, based on relative ranking, from driest to wettest: mudflat, saline pan, perennial saline lake, and deep lake. The deepest lakes are interpreted from the occurrence of ostracode species *Candona caudata* and *Limnocythere ceriotuberosa* (R.M. Forester, pers. comm., 1995). B, Ostracodes. C, Uranium-series ages of high-shoreline (about 90 m above sea level) carbonate tufas, Black Mountains, Death Valley. D, Maximum homogenization temperatures of fluid inclusions in halite ( $T_{hMAX}$ ). E, Sulfate minerals, determined by x-ray diffraction analysis of bulk samples. F, Weight percent calcite, determined by x-ray diffraction analysis of the  $>1 \mu\text{m}$  size insoluble fraction of the core. G, Uranium-series ages, interpolated ages, and marine oxygen isotope stages.

low saline lake and saline-pan settings, occurs from 78 to 87 m (Figure 3). Uranium-series dates from the top and bottom of the interval are 98.6 Ka and 97.1 Ka, respectively, which suggests rapid evaporite accumulation.

Perennial-lake sediments were deposited during a 66 Ky period, between 186 and 120 Ka (Figures 3, 4A). Dark lacustrine muds (core depth of 127–161 m) were overlain by saline-lake halites (core depth of 109–127 m), which were interlayered with muds (Roberts et al., 1994, 1997). The perennial-lake muds were massive to vaguely layered and dark gray when first exposed to air, but they changed color to gray green over time.

Halite layers at 152 m (166 Ka) and at 137.5 to 139.5 m (146 Ka) indicate high salinities and probable shallower lake waters occurred during these intervals. Perennial-lake halites are generally clear and lack dense, fluid-inclusion banding; they have sorted cumulate textures produced by crystallization at the air-brine interface as rafts, skeletal crystals, and cubes (Roberts et al., 1994; Roberts and Spencer, 1995). It is likely that lake levels and water salinities commonly fluctuated over the entire 66 Ky lacustrine phase (Roberts et al., 1997). The upper 18 m of the perennial-lake succession (109–127 m) consist of interlayered subaqueous halite (settle-out cumulates or vertical crystal

fabrics formed by slow crystallization at the brine bottom) and mud that record two major shallowing events between 120 and 128 Ka, and final desiccation at 120 Ka.

The bottom 25 m of the core, 186 to 192 Ka (core depth of 161–186 m) is predominantly layered halite and mud that formed in saline pan and shallow saline lake environments. The halite layers contain primary fluid-inclusion banded-chevron textures and cumulate settle-out layers that crystallized at the bottom and top of a shallow saline lake (Roberts and Spencer, 1995). Vertical pipework fabrics, cemented with halite, indicate exposure of salt layers to dilute floodwaters above the water table, which produced the diagnostic vertical pipes (Roberts et al., 1994). The lowest one meter of the core is composed of mudcracked silty mud and is interpreted as a mudflat deposit.

**OSTRACODES.**—Ostracodes from core DV93-1 provide information on the lower limits of water salinities of the two long-lived perennial lakes in Death Valley during the last glacial, 35–10 Ka, and the penultimate glacial, 186–120 Ka (marine oxygen isotope stages 2 and 5e/6, respectively) (Figure 4B). Perennial-lake muds contain ostracode species *Candona caudata* Kaufman, 1900, *Limnocythere ceriotuberosa* Delorme, 1967, *L. sappaensis* Staplin, 1963, and *L. staplini* Gutentag and Benson, 1962, which, although not abundant, indicate that the salinity of the Death Valley lakes in which the ostracodes lived was typically below 10,000 parts per million and at times was less than 3000 parts per million for the salinity sensitive species *C. caudata* (Forester, 1983, 1987). Such lower-salinity lake phases are inferred from ostracode occurrences at 10, 14, and 18 m (approximately 16, 25, and 34 Ka, respectively) for the last glacial lake and 113–116, 125–126, 138–143, 157, and 162 m (approximately 121–123, 127–129, 146–154, 179, and 186 Ka, respectively) for the long-lived penultimate glacial lake. Unfortunately, information on the last glacial lake is incomplete because muds from depths of 9–14 m (~12–25 Ka) were partially lost during coring.

**FLUID-INCLUSION PALEOTEMPERATURES.**—The paleotemperature component of the Death Valley climate record was obtained from homogenization temperatures of fluid inclusions in subaqueously formed halites from core DV93-1, which record brine temperatures during salt precipitation (Goldstein and Reynolds, 1994; Roberts and Spencer, 1995; Roberts et al., 1997; Lowenstein et al., 1998) (Figure 4D). Shallow saline lake temperatures, in turn, correlate closely with air temperatures in modern settings (Carpelan, 1958; Hammer, 1986; Roberts and Spencer, 1995; Roberts et al., 1997; Lowenstein et al., 1998). Crystals of halite with textures diagnostic of crystallization in a lacustrine environment (cumulates, chevrons, bottom-grown crusts) and with initially one-phase liquid inclusions were chilled in a freezer at temperatures of  $-5^{\circ}\text{C}$  to  $-20^{\circ}\text{C}$  to nucleate vapor bubbles without freezing the inclusions (Roberts and Spencer, 1995). These crystals, now with abundant two-phase liquid-vapor inclusions, were slowly heated to the temperature at which the vapor phase disappeared and the fluid inclusions “homogenized” back to one liquid phase. The temperatures of

homogenization record the original brine temperatures at which the crystal grew in the Death Valley saline lakes. Maximum homogenization temperatures of fluid inclusions in halite ( $T_{\text{hMAX}}$ ) were used as a record of maximum brine temperature and maximum air temperature during halite crystallization. This method was used by Roberts and Spencer (1995) and Lowenstein et al. (1998) for the precipitation of halite from Death Valley in 1993. Halites in 66 stratigraphic intervals of core DV93-1, from depths of 0 to 183.5 m (0–192 Ka) have fluid-inclusion homogenization temperatures commonly below the modern  $T_{\text{hMAX}}$  of  $34^{\circ}\text{C}$  (maximum brine and air temperature during halite precipitation, late April and early May, 1993) (Roberts et al., 1997; Lowenstein et al., 1998). Lacustrine halites deposited during the last glacial period, 35–10 Ka, have low fluid-inclusion maximum homogenization temperatures ( $T_{\text{hMAX}} = 19\text{--}30^{\circ}\text{C}$ ), which suggests brine temperatures were  $\sim 4\text{--}15^{\circ}\text{C}$  below modern late April and May values. Ephemeral saline lake halites precipitated from 60 to 35 Ka have  $T_{\text{hMAX}}$  between  $23^{\circ}\text{C}$  and  $28^{\circ}\text{C}$ , which are  $6\text{--}11^{\circ}\text{C}$  below the modern  $T_{\text{hMAX}}$  values. A relatively low temperature interval,  $10^{\circ}\text{C}$  below the modern, existed  $\sim 50$  to  $\sim 47$  Ka. Limited data from fluid inclusions in two halite intervals,  $\sim 92$  and  $\sim 80$  Ka in age, suggest generally cool conditions,  $6\text{--}7^{\circ}\text{C}$  below modern late April to May temperatures. Relatively higher  $T_{\text{hMAX}}$  values, to  $34^{\circ}\text{C}$  and  $35^{\circ}\text{C}$  in halite dated as  $\sim 100$  Ka and to  $32^{\circ}\text{C}$  in halite dated as 120 Ka, may record climate regimes more similar to the modern. These temperature, however, are still below modern mid-summer temperatures in Death Valley (average air temperatures in Death Valley are  $39^{\circ}\text{C}$  in July and  $37^{\circ}\text{C}$  in August; average maximum air temperatures are  $46^{\circ}\text{C}$  in July and  $45^{\circ}\text{C}$  in August).

Generally colder conditions are recorded in most fluid inclusions in halite for the 186–120 Ka perennial-lake sequence, where  $T_{\text{hMAX}}$  values range from  $25^{\circ}\text{C}$  to  $32^{\circ}\text{C}$ , but only 3 of 22 stratigraphic intervals have  $T_{\text{hMAX}}$  greater than  $30^{\circ}\text{C}$  (Roberts et al., 1997). A combination of homogenization temperatures of fluid inclusions in halite and petrographic evidence of possible pseudomorphs of hydrohalite ( $\text{NaCl}\cdot 2\text{H}_2\text{O}$ ) suggest that temperatures in the perennial lakes may have dropped below  $0^{\circ}\text{C}$  at times and that temperatures during this period probably averaged  $10\text{--}15^{\circ}\text{C}$  below the modern (Roberts et al., 1997). In the bottom 20 m of core DV93-1 (164–184 m, 186–192 Ka), homogenization temperatures are relatively high. Of 19 stratigraphic intervals analyzed, 14 have  $T_{\text{hMAX}}$  values greater than or equal to  $30^{\circ}\text{C}$ , which is similar to those obtained from halite precipitated in modern Death Valley in late April and early May.

**SALINE MINERALOGY.**—Chemically precipitated minerals (sulfates and carbonates) in the Death Valley core provide information on Pleistocene water inflow sources and climate (Figure 4E,F) (Li et al., 1997). Abundant glauberite ( $\text{CaSO}_4\cdot\text{Na}_2\text{SO}_4$ ) and gypsum ( $\text{CaSO}_4\cdot 2\text{H}_2\text{O}$ ) and relatively small amounts of calcite (13%–35% of the  $>1\ \mu\text{m}$  size insoluble fraction) are associated with dry periods (mudflat deposits of 120–60 Ka and

10–0 Ka and saline-pan sediments of 192–186 Ka). In contrast, scarce  $\text{CaSO}_4$ -bearing minerals but relatively abundant calcite (20%–50% of the  $>1 \mu\text{m}$  size insoluble fraction) are associated with halite and mud layers from wetter periods (186–120 Ka, 60–10 Ka). Different mixing ratios of inflow waters between wet and dry periods are interpreted to be responsible for the relationship between mineral assemblages and climate.

Modern Death Valley, which is representative of ancient dry periods, is characterized by Na-Cl- $\text{SO}_4$  brines that are produced by mixing two basic types of inflow waters (Li et al., 1997): (1) Na- $\text{HCO}_3$ -rich and Na-Cl- $\text{SO}_4$ - $\text{HCO}_3$ -rich meteoric waters from the Amargosa River, from springs, and from groundwaters from northern and central Death Valley; and (2) Na-Ca-Cl-rich springs and groundwaters from southern Death Valley, possibly related to volcanism, hydrothermal activity, and a 15 km deep magma body (de Voogd et al., 1986; Serpa et al., 1988; Li et al., 1997). During dry periods, relatively abundant Ca-rich spring inflow removes  $\text{HCO}_3$  as calcite during the early stages of brine evolution (Jones, 1966; Hardie et al., 1978; Li et al., 1997). Further evaporative concentration produces gypsum and glauberite from the remaining Ca. During wetter periods, increased discharge of meteoric  $\text{HCO}_3$ -rich Amargosa River water and basin-margin spring waters removes most Ca from the brine via precipitation of calcite, and, with low calcium concentrations,  $\text{CaSO}_4$ -minerals are not abundantly formed during further evaporative concentration. Such Ca-poor, Na-Cl- $\text{SO}_4$ -rich brines precipitate thenardite ( $\text{Na}_2\text{SO}_4$ ) during later stages of brine evolution.

**SHORELINE CARBONATE TUFAS.**—Shoreline carbonate tufas provide information on the depths of Pleistocene lakes in Death Valley (Figure 4C). Shoreline tufas, most prominent approximately 90 m above sea level, form horizontal terraces encrusting bedrock and gravel on the eastern side of Death Valley (Black Mountains, between Badwater Springs and Mormon Point) (see “Previous Work on the Ancient Lakes in Death Valley”; see also Hooke, 1972). Tufas were collected from locations previously described by Hooke (1972), including, from north to south, Badwater, Goblet, Westilt, and Mormon Point (see Figure 1 for locations) (Ku et al., 1998). Relatively fresh hand-samples of tufas are porous and fine-grained with massive or radiating fabrics. In thin section, tufas commonly form crusts around tubular molds, which are up to several millimeters in length and range in diameter from tens of microns to about 1 mm. The tubular molds are surrounded by coatings composed of dark micrite, and then calcite microspar, which may have a radial fabric. These textures probably represent carbonate precipitation around plant material, such as green algae and moss. A second petrographic texture exhibited by tufas consists of clusters of dark micrite, tens of microns in diameter, organized into millimeter-scale “bundles of grapes” similar in appearance to the “arborescent shrubs” of Demicco and Hardie (1994). Yet a third tufa fabric consists of bladed calcite crystals, up to 1 mm long, grown from thin carbonate crusts. The calcite crystals have upward-radiating growth fabrics, with the

number of calcite crystals decreasing away from the original growth substrate. This fabric is interpreted to have formed by direct chemical precipitation of calcite. Elemental mapping of samples for Mg and Sr using an electron microprobe indicates that chemical zonation of these elements coincides with textural and mineralogical (calcite and minor aragonite) zones in the tufas, which confirms their unrecrystallized primary origin. The above petrographic and geochemical studies indicate that the tufas selected for dating have not recrystallized nor have they undergone major later cementation, both of which could complicate interpretation of age dates (Benson et al., 1990; Ku et al., 1998).

Eleven samples of tufa from the 90 m shoreline were dated by U-series methods. Of the 11 samples, 7 are 185–150 Ka, which closely agrees with the results (200–120 Ka) obtained by Hooke and Lively (1979) and Hooke and Dorn (1992) on samples from the same locations and the same general elevations. The dates also correlate with perennial lake sediments observed in core DV93-1 from 186 to 128 Ka; thus they serve as an independent check confirming the reliability of the dating methods. These tufas indicate lake depths of up to 335 m, if faulting is ignored and if 130–160 m of basinal sediments are added to reach equivalent-age lacustrine sediments in core DV93-1. Four high-shoreline tufas, from 73 to 90 m above sea level, dated between 194 and 216 Ka, are older than any sediments from core DV93-1. These oldest tufas suggest the existence of yet a third perennial lake stage in Death Valley at approximately 200 Ka, which is consistent with earlier age-dating (Hooke and Lively, 1979; Hooke and Dorn, 1992).

### Summary and Conclusions

The 200 Ky paleoclimate record of Death Valley from core DV93-1 is dominated by two dry and/or warm and wet/cold cycles that occurred on a 100 Ky time scale (Figure 4A,D). These cycles began with mudflat deposits (192 Ka to bottom of core, and 120–60 Ka). Wetter conditions, colder climates, or both, produced greater effective moisture, with saline-pan and ephemeral-saline-lake sediments (192–186 Ka, 60–35 Ka) overlying the mudflat sediments. Eventually, enough water was supplied to Death Valley to sustain perennial lakes, fluctuating from fresh to saline (186–120 Ka, 35–10 Ka, respectively). The perennial-lake phase ended, the lakes desiccated (120 and 10 Ka), and dry conditions led to the accumulation of mudflat deposits, completing the cycle. Of particular importance are the major lacustrine phases from 35 to 10 Ka and from 186 to 120 Ka (marine oxygen isotope stages 2 and 5e/6, respectively), which represent markedly colder and wetter conditions than those in modern Death Valley. Of the two perennial-lake periods, the penultimate glacial lake was deeper and lasted far longer than the last glacial lake.

In summary, the Death Valley climate record is divided into six periods (Figure 4). (1) From 192 to 186 Ka, the climate was dry, dominated by saline pans and shallow ephemeral

lakes. Inflow and evaporation were sufficient to allow the rapid accumulation of 25 m of salt in 6 Ky.  $T_{hMAX}$  values are 30° C or greater for 14 of 19 stratigraphic intervals, indicating that temperatures were similar to the modern late April to early May  $T_{hMAX}$  values. (2) The climate from 186 to 120 Ka was relatively cool to cold, with abundant inflow to continually maintain a series of fluctuating perennial lakes, at times greater than 300 m deep and having a salinity less than 3000 parts per million. Temperatures during this period probably averaged 10°–15° C below the modern. If the effects of faulting are ignored, the ages of high-shoreline tufa indicate that Death Valley at that time commonly had lakes hundreds of meters deep. During the latest phase of this 66 Ky lacustrine period, from 128 to 120 Ka, reduced inflow or more saline inflow produced hypersaline conditions, which ultimately led to basin desiccation at 120 Ka. Slightly higher fluid-inclusion temperatures ( $T_{hMAX} = 32^{\circ}$  C), comparable to the modern late April to early May  $T_{hMAX}$ , mark the terminal lake stage at 120 Ka. (3) From 120 to 60 Ka, a dry period dominated by mudflat environments prevailed. Limited data from fluid inclusions in two halite intervals suggest generally cool conditions, 6°–7° C below modern late April to May temperatures, ~92 and ~80 Ka; however,  $T_{hMAX}$  from 10 halite intervals around 100 Ka are close to the modern late April to early May values, which suggests a warm climate but still cooler than the modern at 100 Ka. (4) From 60 to 35 Ka, the climate was cold, with moderate aridity; saline pans dominated, but there was enough inflow to accumulate thick salts relatively rapidly and to maintain shallow saline lakes approximately 54–50 Ka. Homogenization temperatures ( $T_{hMAX}$  between 23° C and 28° C) are 6°–11° C below the modern late April to May values. A relatively low temperature interval, 10° C below the modern, existed ~50 to

~47 Ka. (5) From 35 to 10 Ka, the climate was cold and wet; plentiful inflow fed a perennial lake that was commonly saline but at times became up to 90 m deep (Dorn et al., 1990) with salinities less than 3000 parts per million. Overall, for this 25 Ky period, fluid inclusion  $T_{hMAX}$  data suggest brine temperatures were 4°–15° C below modern late April to May values. During the latest lake phase, from 15 to 11 Ka,  $T_{hMAX}$  values of halites were only 4° C below modern values, whereas  $T_{hMAX}$  values decreased to 7° C below the modern late April to May temperatures in halites from ~11 to ~10 Ka, signifying cooler temperatures during this period. (6) From 10 to 0 Ka, dry arid conditions featured mudflat and/or saline-pan environments, minor inflow of meteoric waters, and a water table normally below the surface.

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# Bonneville Basin Lacustrine History: The Contributions of G.K. Gilbert and Ernst Antevs

*Charles G. Oviatt*

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## ABSTRACT

The careful observations and eloquent writings of Grove Karl Gilbert in the late 1800s laid the framework for most subsequent studies of lacustrine history in the Bonneville Basin. By the time of the 1942 symposium on the glacial and postglacial history of the Great Basin, his work had been largely unchallenged by the scientific community. Ernst Antevs, who participated in that symposium, reinterpreted some of Gilbert's observations and contributed both a global perspective and a hypothesis involving atmospheric circulation to studies of Lake Bonneville and other Great Basin Quaternary lakes. Fifty years after the 1942 symposium, the contributions of Gilbert and Antevs are still at the core of state-of-the-art research on Great Basin Quaternary lakes.

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## Introduction

Systematic studies of ancient lakes in the Bonneville Basin began with the work of Grove Karl Gilbert, who published his monograph on Lake Bonneville in 1890. By the time of the 1942 symposium on the glacial and postglacial history of the Great Basin, Gilbert's reconstruction of the lake's history had been reinterpreted by only a few people (Sack, 1989). Ernst Antevs, who contributed to the 1942 symposium, was one of those few. In subsequent decades, many new chronologies and hypotheses about the lake have been proposed. This paper is a brief review of the knowledge of the Lake Bonneville basin as of 1942, with emphasis on the contributions of G.K. Gilbert and Ernst Antevs, and a critique of those contributions from the perspective of the late 1990s.

ACKNOWLEDGMENTS.—Ellis Yochelson and an anonymous reviewer provided useful suggestions for improving the manuscript. I am grateful to all my friends, colleagues, professors,

and students, from whom I have learned about Lake Bonneville and the Great Basin. I dedicate this paper, however, to the one person who has taught me more than all the others and who continues to inspire me with his intelligence, curiosity, knowledge, and good humor—Don Currey.

## G.K. Gilbert

Lakes began forming in the Bonneville Basin during the Miocene with the initiation of tectonic extension in the region (Miller, 1997). Gilbert (1890) noted a few exposures of Tertiary lake deposits in the Bonneville Basin, but very little was known about them at the time. Based on the meager evidence he had available, Gilbert made an insightful comment concerning the Tertiary history of the basin. He thought it was "possible that the Bonneville Basin continuously held a lake which, as the land rose and fell unequally, was expanded and contracted, now in one direction, now in another" (Gilbert, 1890:101). Later studies have confirmed this general statement, but a detailed history of Tertiary (primarily Neogene) lakes is just beginning to emerge (Miller, 1997; Thompson et al., 1997; Davis, 2002).

Gilbert's great contributions were the careful study of sedimentary deposits and shorelines of Lake Bonneville and the proposal of hypotheses to explain its history. Gilbert (1890) reported geomorphic and stratigraphic evidence that suggested Lake Bonneville had risen twice to high levels in the late Pleistocene after a long period of low lakes and alluvial-fan deposition on piedmont slopes. His conclusions were based on his interpretation of sediments deposited on the bottom of Lake Bonneville (the Bonneville beds). Two of his study sites were along the Old River Bed, and one was near the town of Leamington, in west-central Utah (Figure 1). Gilbert defined the stratigraphic units at these sites by measuring the sediment layers, which he then traced or correlated from outcrop to outcrop throughout the basin. Gilbert argued that the shorelines of the ancient lake and the stratigraphy of the offshore deposits together tell the story of rising and falling lake levels.

OLD RIVER BED.—The Old River Bed is an abandoned river valley cut into the Bonneville beds. Gilbert demonstrated that it

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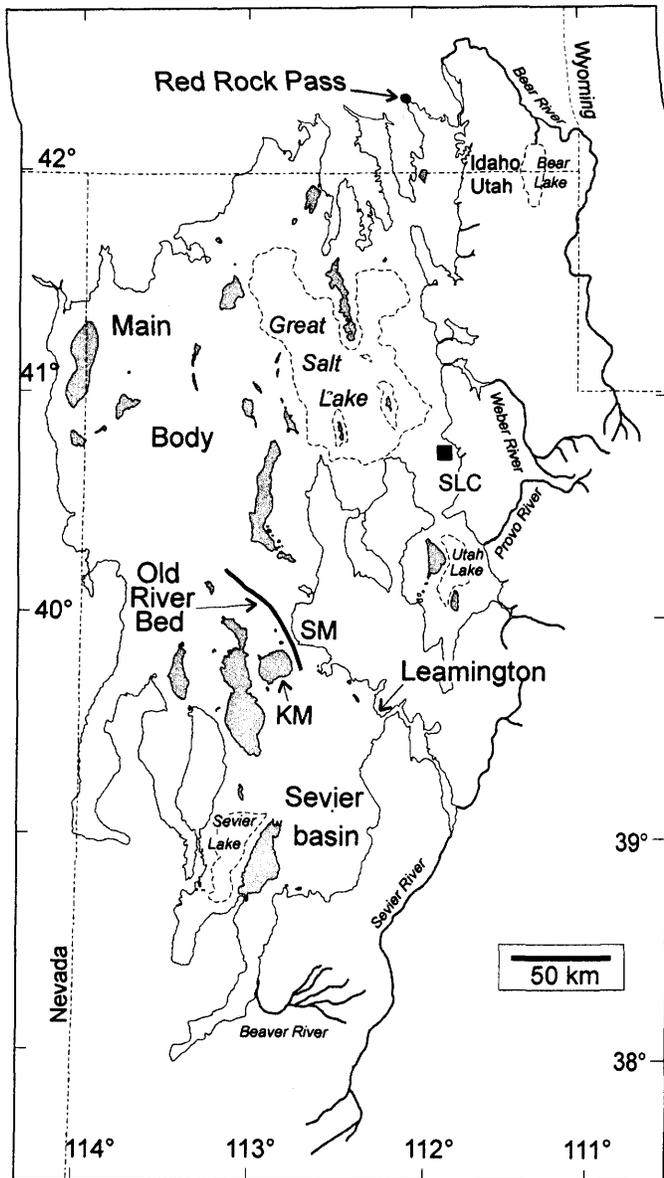


FIGURE 1.—Map of Lake Bonneville at its highest stage, the Bonneville shoreline. SLC = Salt Lake City. Arrows point to the areas at Old River Bed and Leamington illustrated in Figures 2 and 4, respectively. A heavy line marks the Old River Bed strait, which is a narrow constriction between Keg Mountain (KM) to the west and the Simpson Mountains (SM) to the east.

was formed during the regressive (falling) phase of the lake by a river that flowed from the Sevier Basin in the south to the Great Salt Lake basin in the north (Figures 1, 2). The exposures of the Bonneville beds and the shorelines along the Old River Bed are some of the finest in the basin, and Gilbert took advantage of this by studying them for a total of about two weeks during several different trips in 1879 and 1880 (Hunt, 1982; Oviatt and McCoy, 1988).

Gilbert measured and described stratigraphic sections of the Bonneville beds at two sites at the Old River Bed. The Lower

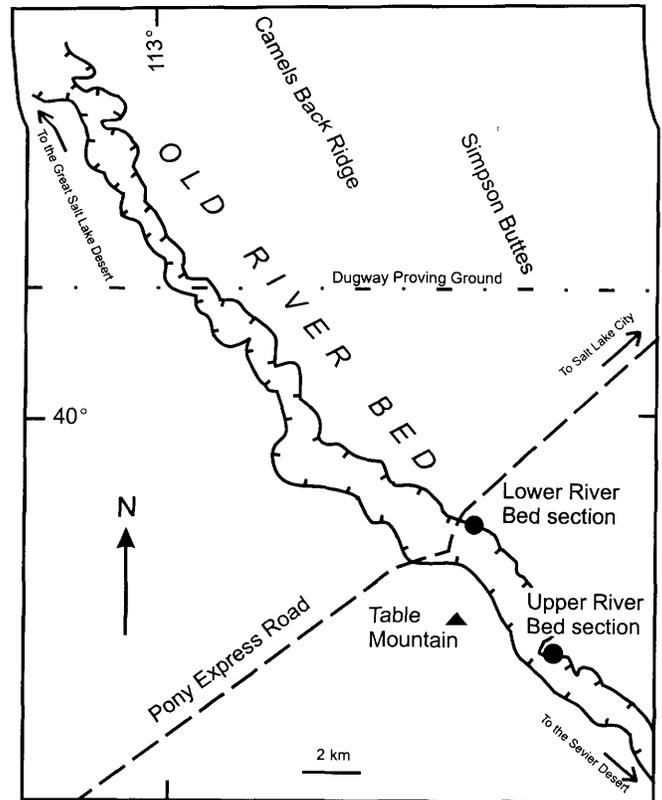


FIGURE 2.—Map of the Old River Bed in the vicinity of Gilbert's Lower and Upper River Bed sections.

River Bed section was located approximately where the Overland Stage, or Pony Express, Road crossed the Old River Bed (Figure 2). At this section, Gilbert defined two stratigraphic units, the Yellow Clay and the White Marl. Because both of these units are fine grained, he interpreted them as deep-water deposits. The Yellow Clay was the thicker of the two and occurred below the White Marl, so he concluded that it was deposited during a relatively long period of deep-lake conditions, called the Yellow Clay Epoch, prior to the White Marl Epoch (Figure 3).

The White Marl was deposited during the most recent deep-water period and included the time of formation of the prominent Bonneville, Provo, and Stansbury shorelines. A thin sand unit containing gastropod shells separates the Yellow Clay from the White Marl. Gilbert interpreted the base of this sand as marking an unconformity, or period of time when the lake was below the level of the section and was not depositing sediments there. In his interpretation, the sand and gastropods were deposited as the lake rose during the White Marl Epoch. Gilbert referred to the Lower River Bed section as a typical section of the Bonneville beds, which therefore recorded the major events in the history of the lake (Figure 3).

Gilbert's Upper River Bed section displayed the Yellow Clay, the White Marl, and several other stratigraphic units. The Yellow Clay and the White Marl are overlain at this section by an

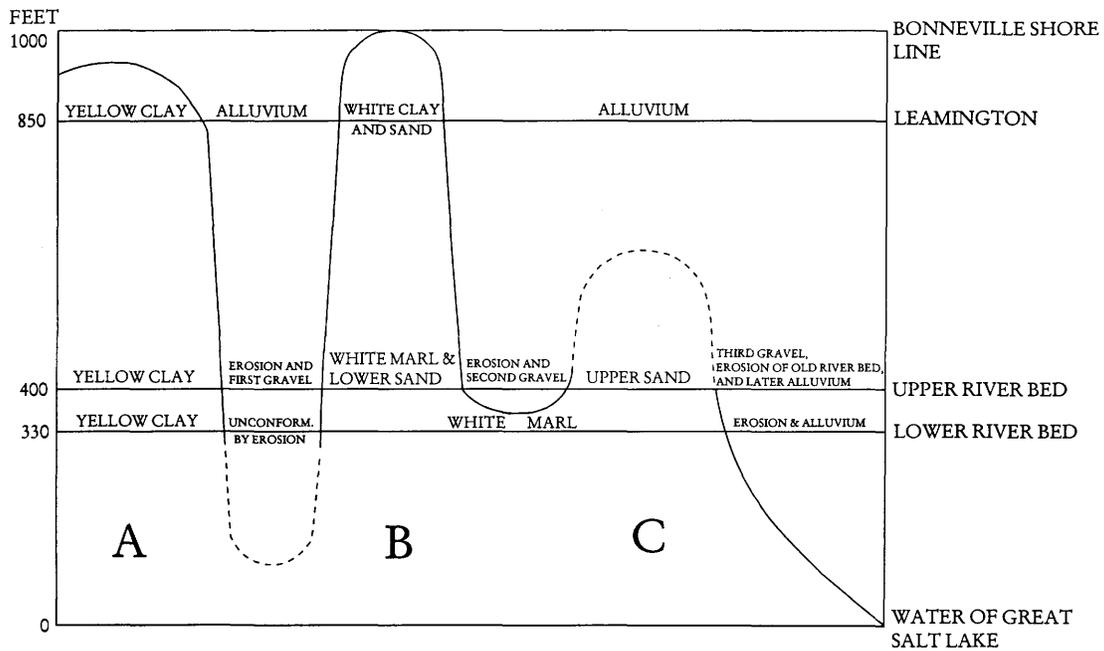


FIGURE 3.—Modification of “Diagram of Lake Oscillations inferred from Deposits and Erosions” from Gilbert (1890, fig. 30). The horizontal axis can be read as time, with a variable scale, or as vertical distance (also with variable scale) in each of the three stratigraphic sections (Lower River Bed, Upper River Bed, and Leamington). The White Clay at Leamington is equivalent to the White Marl. Letters A, B, and C represent the three lake highstands interpreted by Gilbert (A = Yellow Clay Epoch; B = White Marl Epoch; C = minor regressive-phase fluctuation).

additional sand unit, termed the Upper Sand, which Gilbert considered as representing a short-lived, minor rise in lake level (Figure 3).

Of primary importance in Gilbert’s interpretation of the Upper River Bed section was a gravel unit, which he referred to as the First Gravel. The First Gravel is more than 15 m thick along the east side of the exposures at the Upper River Bed section (Figure 4), but it thins abruptly to the west to less than 1 m, thus leading Gilbert to refer to the gravel as a “wedge” in his field notes (Hunt, 1982:128).

Gilbert called the First Gravel a “bar” in his field notes and described large quantities of tufa cementing the gravel (Hunt, 1982:128), thus indicating that he regarded the gravel as having been deposited in a lake environment. In United States Geographical Survey (USGS) Monograph 1, Gilbert (1890:195) wrote that “the form of the [gravel mass] described, the associated tufa, and the preponderance of boulders of local derivation, indicate shore action, but it is possible that an interlacustrine [that is, between the Yellow Clay and White Marl Epochs] river was the agent of transportation.” References in other places in his monograph to thick alluvial deposits at this horizon suggest that by the time Monograph 1 was published Gilbert had decided that the First Gravel at the Upper River Bed section was alluvial rather than lacustrine gravel, despite the field evidence he had observed that the gravel had a lacustrine origin.

Regardless of whether the First Gravel was interpreted as alluvial or lacustrine, it indicated to Gilbert that the lake fell to a low level relative to the deep-lake intervals of the Yellow Clay and White Marl Epochs (Figure 3). The tops of both River Bed sections represented the final regression of the lake and local deposition of alluvium.

LEAMINGTON.—The section at Leamington, Utah, is approximately 140 m higher in altitude than the Old River Bed sections, and it is close to the Bonneville shoreline (Figure 1). At Leamington, Gilbert noted stratigraphic units that he correlated with the Yellow Clay and White Marl. They were thicker and sandier than at the Old River Bed. Because Leamington is located at the mouth of the Sevier River where it enters the Sevier Desert, the river delivered large volumes of fine-grained sediment (silt, sand) to the lake margin in this area (Figure 5). Gilbert interpreted gravel between the Yellow Clay and the White Marl (e.g., White Clay in Figure 3) as alluvium, and he correlated this gravel with the unconformity at the Lower River Bed section and with the First Gravel at the Upper River Bed section. Leamington is too high in altitude to record events after the lake fell from the Bonneville shoreline (Figure 3).

GILBERT’S CONCLUSIONS.—By combining the stratigraphic evidence from the Old River Bed and Leamington sections with information from the shorelines and other geologic evidence in the basin, Gilbert deduced a lake history illustrated in Figure 6.

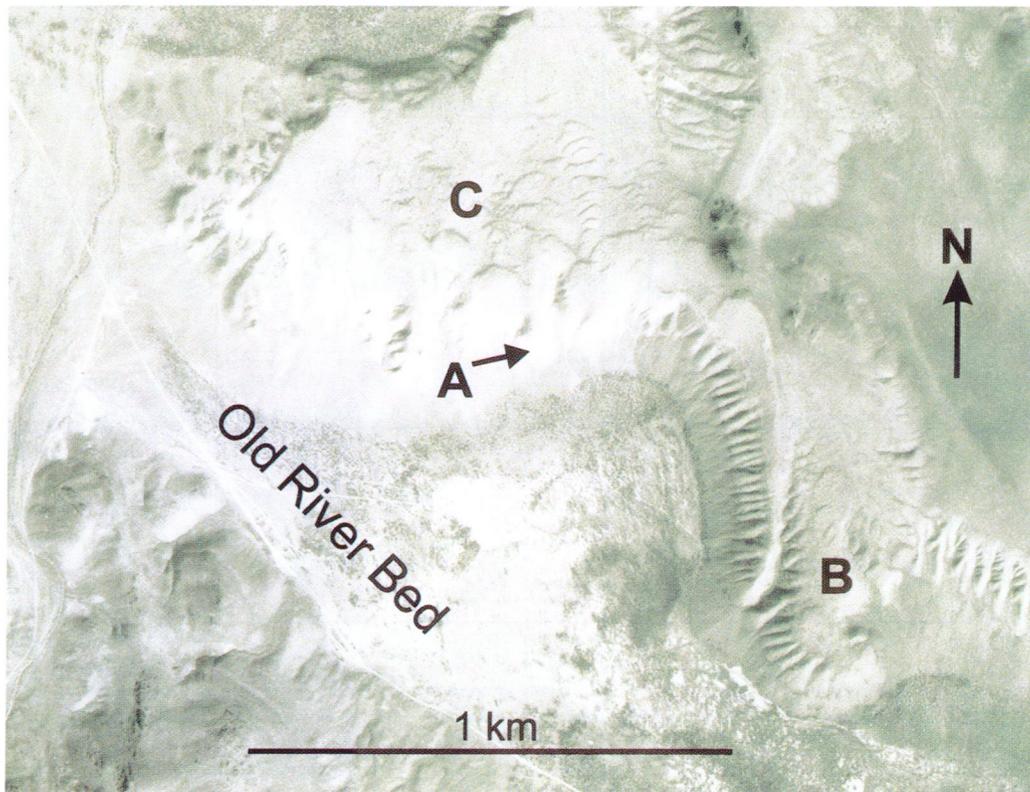


FIGURE 4.—Aerial photograph of Gilbert's Upper River Bed section and surrounding area. A = Yellow Clay and White Marl exposed in the section described by Gilbert (1890); B = lacustrine gravel spit composed of Gilbert's First Gravel (note the eastward-recurved distal end of the spit; longshore current direction was from the north); C = eolian sand dunes composed of Gilbert's Upper Sand.

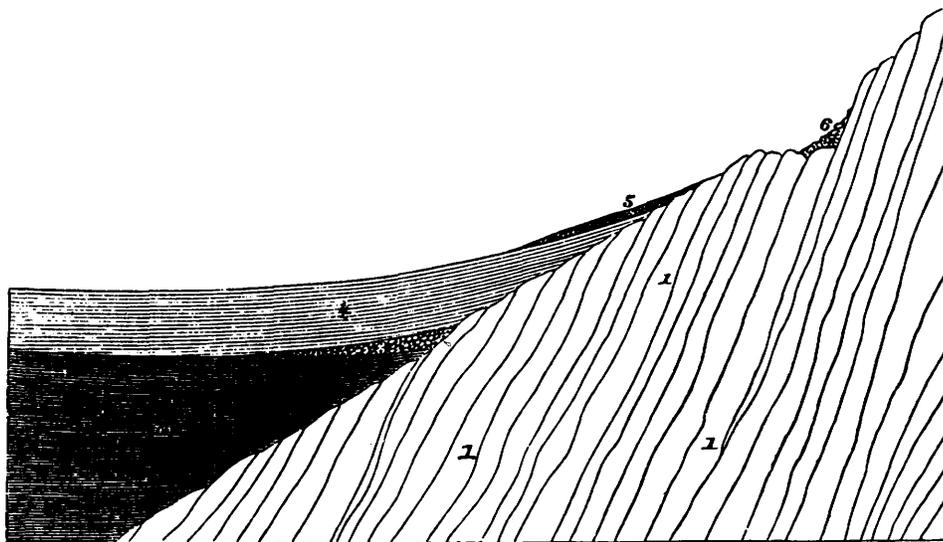


FIGURE 5.—Gilbert's (1890) fig. 28, about which he stated, "Section showing succession of Lacustrine and Alluvial Deposits at Leamington, Utah. 1. Paleozoic sandstone. 2. The Yellow Clay (Lower Bonneville). 3. Wedge of alluvial gravel. 4. The White Marl [White Clay of Figure 3] (Upper Bonneville). 5. Recent alluvial gravel. 6. Bonneville shore notch, with recent talus."

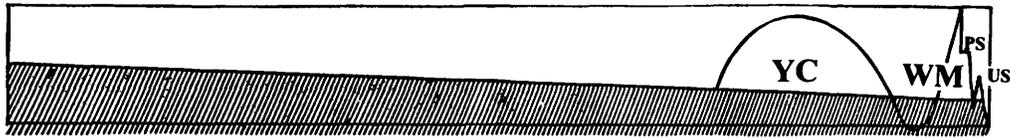


FIGURE 6.—Modified from Gilbert's (1890) fig. 34, about which he stated, "The upper and lower horizontal lines represent the horizons of the Bonneville shore and the surface of Great Salt Lake. Horizontal distances represent time, counted from left to right. The curve represents the height of the oscillating water surface, and the shaded area indicates ignorance." Gilbert's curve shows the Yellow Clay Epoch (YC), the White Marl Epoch (WM), the Provo shoreline (PS), and the regressive-phase fluctuation he deduced from the Upper Sand at the Upper River Bed section (US).

The Yellow Clay Epoch occurred after a long period of shallow lakes and alluvial-fan deposition in the basin. By Gilbert's estimate, the Yellow Clay lake did not overflow, and it persisted much longer than the White Marl lake. Gilbert's interpretation of the First Gravel at the Upper River Bed section and the gravel at Leamington as alluvium led him to conclude there had been a profound lake-level lowering between the Yellow Clay and the White Marl Epochs (Figure 6). This idea strongly influenced Antevs and most later workers.

According to Gilbert, the White Marl Epoch included the rise to overflow at Red Rock Pass, Idaho (Figure 1), and the formation of the Bonneville shoreline. Catastrophic failure of the alluvial-fan dam at Red Rock Pass resulted in the Bonneville Flood and the subsequent formation of the Provo shoreline. A minor rise in lake level during the regression from the Provo shoreline at about the altitude of the Upper River Bed section deposited the Upper Sand; the lake subsequently dropped to levels near that of the modern Great Salt Lake. Gilbert apparently thought the Stansbury shoreline formed during the regressive phase of Lake Bonneville, that is, later than the formation of the Provo shoreline, although he did not explicitly state this in his monograph. This reconstructed history was the starting point for the work of Ernst Antevs.

**Ernst Antevs**

During the first half of the twentieth century, Ernst Antevs published a number of papers concerning Lake Bonneville and Great Basin Quaternary history. He also contributed to the 1942 symposium. Antevs was convinced that lake fluctuations in the Bonneville Basin were correlated with growth and decay of Northern Hemisphere ice sheets and mountain glaciers. Despite the lack of direct evidence for the ages of either the glacial or lacustrine deposits, he presented careful arguments for ways in which they simultaneously varied in size during the late Pleistocene (Figure 7). Evidence from the mouths of Little Cottonwood and Bells Canyons in the Wasatch Mountains near Salt Lake City indicated that Lake Bonneville reached its highest level, the Bonneville shoreline, shortly after the glaciers in those canyons reached their maximum down-valley extent (Antevs, 1948), so that correlation with mountain glaciers in the Sierra Nevada and ice sheets in Canada was likely.

Antevs spent less time in the field examining the stratigraphic sections at the Old River Bed and Leamington than did Gilbert, but he reinterpreted Gilbert's descriptions at the three primary sections, focusing especially on those at the Old River Bed. Antevs thought the Yellow Clay Epoch was correlated with an old period of glaciation in the Rocky Mountains and Sierra Nevada (Bull Lake and Tahoe glaciations, respectively), and he did not include it in his discussion of Lake Bonneville history in his symposium paper (Figure 7) (Antevs, 1948). His interpretation of the depositional environment of the Yellow Clay as having been a deep lake was essentially the same as Gilbert's.

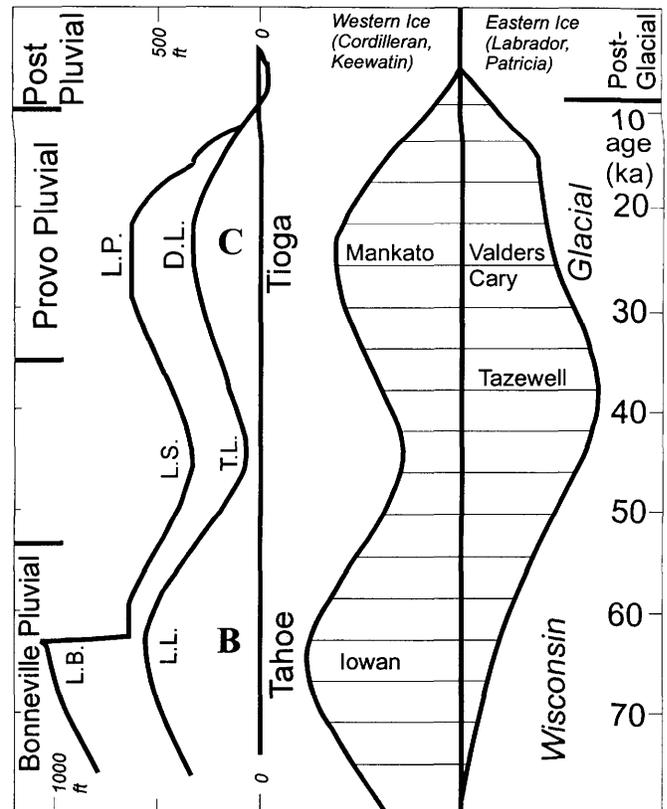


FIGURE 7.—Fluctuations of Lake Bonneville (L.B.), Lake Lahontan (L.L.) in western Nevada, and Northern Hemisphere ice sheets (modified from Antevs, 1948:171). D.L. = Dendritic Lake; L.P. = Lake Provo; L.S. = Lake Stansbury; T.L. = Thinolite Lake. Letters B and C represent lake highstands and correlations with Gilbert's interpretations of Lake Bonneville history (see Figure 3).

Antevs regarded the regressive-phase lake rise, which Gilbert had deduced from the Upper Sand at the Upper River Bed section, as a major event in the history of the lake. He suggested that during this event the lake reoccupied the Provo shoreline and overflowed for a second time at Red Rock Pass, Idaho. In addition, Antevs thought the Stansbury shoreline formed during the interval between the two Provo occupations. He then correlated fluctuations of Lake Bonneville with fluctuations of Lake Lahontan in western Nevada, and with the Cordilleran and Laurentide ice sheets (Figure 7).

Antevs (1948) argued that during the late Pleistocene the large North American ice sheets, particularly the Cordilleran ice sheet, attained a size large enough to deflect the polar front far to the south of its mean position in historic time. As a consequence, frequent storms carried moisture from the Pacific Ocean across the Sierra Nevada to the Great Basin to create the large pluvial lakes. Thus, the filling and emptying of the lake basins were correlated with the expansion and contraction of the Northern Hemisphere ice sheets. He also thought that the astronomical hypothesis of climate change formulated by Milutin Milankovitch was probably valid (Antevs, 1938). Added to this was his fundamental belief that major climatic events had to be global in extent (e.g., Antevs, 1955). Accordingly, he was eager to find correlative climatic events across North America and in northern Europe.

#### Late Twentieth Century Views

Machette and Scott (1988) and Sack (1989) have reviewed how interpretations of Lake Bonneville have changed during the second half of the twentieth century. In this paper, I focus only on current interpretations of the work of Gilbert and Antevs.

With a few possible exceptions, all the lake sediments observed by Gilbert, including the Yellow Clay and the White Marl, are now recognized to have been deposited during a single major lake cycle between about 30 thousand years (Ky) before present (B.P.) and 10 Ky B.P. (Scott et al., 1983; Oviatt, 1987; Oviatt et al., 1994). This is the Bonneville lake cycle, or Lake Bonneville. Some Pleistocene lake cycles older than 30

Ky B.P. have been given separate names (e.g., Cutler Dam, Little Valley, Pokes Point; Figure 8).

Massive shoreline deposits, erosional shorelines, deltas, and offshore sediments are prominent in the Bonneville Basin. Most of these were almost certainly produced during the Bonneville lake cycle. In a refinement of Gilbert's initial work, prominent shorelines named and mapped by him have been dated and linked to the offshore deposits, and an accurate radiocarbon chronology has been established that can now be used in many ways as a predictive model (Figure 9) (Oviatt et al., 1992; Oviatt, 1997). The major shorelines have been mapped with precision (Currey, 1982), and Currey (1990) has shown how the extensive knowledge about the Bonneville Basin serves as a prime example of the landforms and processes typical of semi-desert basins.

In addition to the accumulation of abundant numerical-age data and numerous other advances in understanding the Bonneville lake cycle, Gilbert's sections at the Old River Bed and Leamington have been reinterpreted. The Yellow Clay is now recognized to be a shallow lacustrine deposit; it consists essentially of fine-grained deltaic sediment deposited early in the rise of Lake Bonneville (Oviatt, 1987). During deposition of the Yellow Clay the Sevier River flowed across the flat floor of the Sevier Desert, through the Old River Bed strait, and transported sand, silt, and clay to the margin of the rising lake in the Great Salt Lake basin ("Main Body" in Figure 1). In light of this interpretation, Gilbert's dilemma with explaining why the Yellow Clay is so much thicker and contains so much more silt and sand than the White Marl (Gilbert, 1890:200–209), is resolved—the Yellow Clay and the White Marl were deposited in different depositional environments and should not be expected to look similar. Although deposits similar to the Yellow Clay are present at many localities in the basin, they represent disconnected shallow-water depositional environments near the mouths of large rivers rather than a single, widespread, deep-water lake deposit. In contrast, the White Marl is the basin-wide stratigraphic unit that records the deep-water, or offshore, history of Lake Bonneville (Oviatt, 1997).

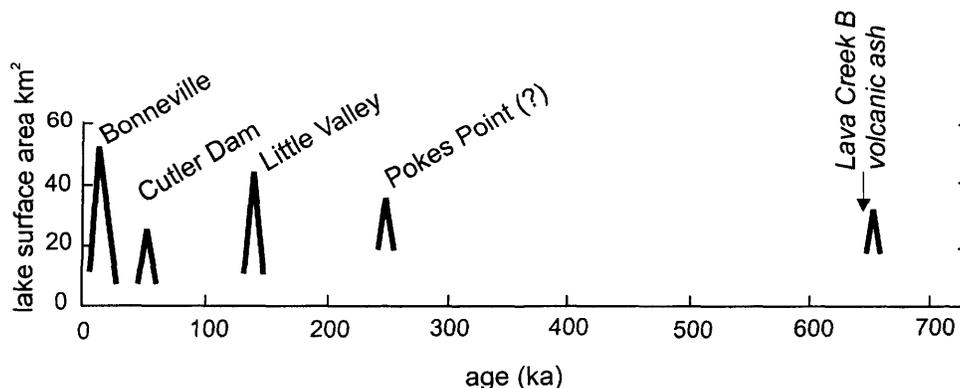


FIGURE 8.—Schematic diagram of middle and late Pleistocene lake cycles in the Bonneville Basin. Modified from Machette and Scott (1988, fig. 3) and Oviatt and Miller (1997, fig. 2).

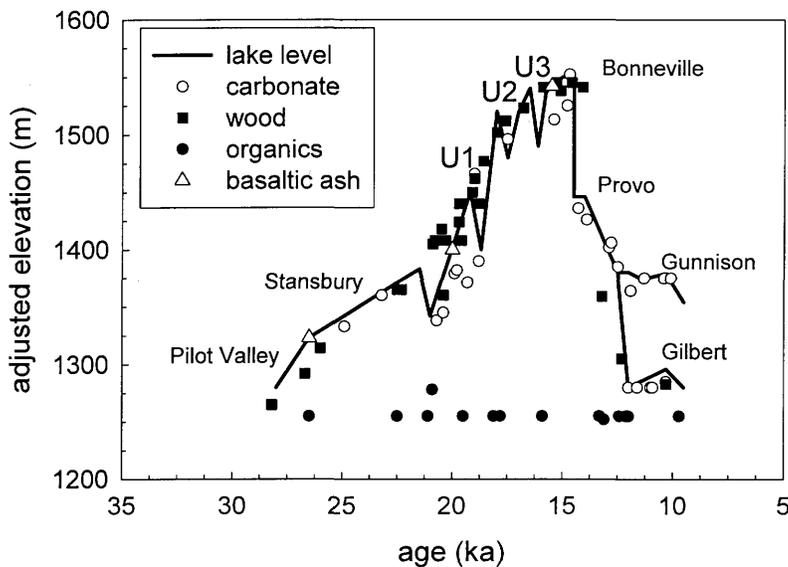


FIGURE 9.—Chronology of Lake Bonneville fluctuations, modified from Oviatt et al. (1992), Oviatt (1997), and Oviatt and Miller (1997). Elevations have been adjusted for isostatic rebound. U1, U2, and U3 are transgressive-phase fluctuations (Oviatt, 1997). Radiocarbon ages were obtained for disseminated organic carbon, wood or charcoal, carbonate (shell or tufa), and basaltic ashes.

Figure 4 is an aerial photograph of the area around Gilbert's Upper River Bed section. It shows the prominent recurved lacustrine spit composed of Gilbert's First Gravel, which he had decided might be alluvium. The spit was deposited by long-shore currents in Lake Bonneville after deposition of the Yellow Clay as the lake began to rise, following formation of the Stansbury shoreline (Figure 9); it does not represent river deposition during a lowstand between two high lake stands, as Gilbert suggested in his monograph. At the Lower River Bed section the unconformity between the Yellow Clay and the White Marl, which Gilbert and Antevs interpreted as representing a long period of erosion and alluvial deposition, represents a short period (possibly less than 500 years) when the lake level fell about 45 m and the Stansbury shoreline formed (Oviatt, 1987; Oviatt et al., 1990). The gravel wedge between the Yellow Clay and the White Marl at Leamington, which Gilbert interpreted as alluvium, is now interpreted as lacustrine gravel deposited during a fluctuation in lake level during the transgressive phase of the lake (U2 in Figure 9; Oviatt et al., 1994).

Figure 4 also shows well-developed eolian sand dunes composed of Gilbert's Upper Sand. Although Gilbert recognized that the surface of this sand "may have gained or lost [thickness] by the action of the wind, which throws its surface into waves, and has caused it to bury at the north the exposure of the lower formations" (Gilbert, 1890:196), he thought that the lower part of the sand was lacustrine. Because no features of lacustrine origin have been found in the sand, his interpretation of a minor lake rise, and Antevs' suggestion of a second transgression to the Provo shoreline, are unlikely.

Despite these changes in interpretation of Gilbert's stratigraphic sections, which are the results of building on his work and the work of others and the availability of superior technology for field and laboratory investigations, Gilbert laid the groundwork for all subsequent research on Lake Bonneville. Most of his observations from his horseback trips into the

desert were highly accurate, even if some of his interpretations have been replaced by alternative hypotheses. It is clear that he thoroughly understood the lake beyond the context of his own century, and many of his conclusions have not been improved upon even after 100 years of subsequent research. One of Gilbert's many long-lasting contributions to science was to demonstrate that paleoclimatic information can be obtained from studies of ancient lake deposits.

Antevs also made his mark on Great Basin paleoclimate research. Modern research has demonstrated empirically the general validity of Antevs' conviction that the major climate changes that resulted in large pluvial lakes were global in scope. Although the details of his correlations with Lake Lahontan and with glacial events have not survived scientific tests, the urge to find global connections persists today. With refinements in glacial chronologies and modeling, including the realization that the Laurentide ice sheet was even more influential than he thought, Antevs' general hypothesis that ice sheets diverted storm tracks into the Great Basin to feed the large pluvial lakes is well supported by computer simulations and field data (COHMAP members, 1988; Kutzbach et al., 1993; Thompson et al., 1993).

### Future Work

Since the days of Gilbert and Antevs, scientific advancements have resulted in major changes in interpretations, but the solid foundation laid by Gilbert and the refinements made by Antevs half a century later are still at the heart of our knowledge of Lake Bonneville and late Pleistocene climate change in the Great Basin (e.g., Oviatt, 1997; Benson, 1997). Despite many advances in understanding the history of Lake Bonneville and Great Salt Lake, a number of important questions remain only partially answered. These include questions about the timing and duration of regression from the Provo shoreline and the

age of the Provo shoreline itself; the timing and character of the initial rise of Lake Bonneville between about 30 and 20 Ky B.P.; the chronology of fluctuations of Great Salt Lake during the last 10 Ky; the precise relationships between Lake Bonneville and Great Salt Lake and climate, including the relative importance of temperature and precipitation or other variables in

determining lake size; and the details of pre-Bonneville lake cycles and their connections to global climate. These questions and others are being pursued in the Bonneville Basin, and, thanks in part to the powerful early contributions of Gilbert and Antevs, reliable answers are likely to be forthcoming in the near future.

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# Fluvial Linkages in Lake Bonneville Subbasin Integration

*Dorothy Sack*

“... and so lakes developed in nearly all the basins. Of these lakes the great majority overflowed into adjacent basins ...”

E. Blackwelder (1948:12)

## ABSTRACT

Several late Pleistocene lakes in the Great Basin, including Lake Bonneville, consisted of component subbasins that were united into a single large lake only when water levels were high enough to breach the subbasins' thresholds. During the last deep-lake cycle, but before and after their period of integration with the major water body, isolated closed-basin lakes existed in many of those subbasins. This study focuses on two of Lake Bonneville's seven major subbasins, Puddle Valley and Tule Valley, because they display distinctive geomorphic and sedimentologic evidence of the subbasin integration process. In both cases, Lake Bonneville burst through material at the dividing threshold, and water poured into the adjoining subbasin as a fluvial current of high discharge. Where the jet spread out onto the subbasin's piedmont, it deposited a gravel expansion bar over which gravel was transported in large-scale subaqueous bedforms. Fluvial braid bars in their initial stage of development provide a good analogue for the general form of the inflow bars and help identify the fluvial processes of inflow-bar formation. Details of the geomorphology and sedimentology of the inflow bars reflect the site-specific conditions under which they formed. The ability to recognize inflow bars in the geomorphic and stratigraphic record will help researchers identify subbasin integration events and will, therefore, contribute to improved accuracy in reconstructing the geomorphic and paleoclimatic history of other paleolake basins.

## Introduction

For more than a century, scientists have periodically published comprehensive inventories of late Pleistocene lakes in western North America (e.g., Russell, 1885, 1896; Meinzer,

1922; Hubbs and Miller, 1948; Snyder et al., 1964; Mifflin and Wheat, 1979; Williams and Bedinger, 1984). Although these inventories have been compiled for various specific physiographic or political boundaries, each included all or a large part of the Great Basin. Information provided about Great Basin paleolakes in that literature ranged from their approximate locations and relative extent, as delineated on small-scale maps; to measurements of various lake attributes, such as depth and area; to observations regarding possible overflow episodes for the predominantly closed-basin lakes. Not surprisingly, those contributions emphasized the maximum extent of the paleolakes and any associated overflow that made the lakes tributary to lower closed-basin lakes, or to the sea, via long, connecting stream courses. The emphasis on maximum lake size, however, obscured the fact that, like most large modern lakes (Sly, 1978), several late Pleistocene lakes in the Great Basin were assemblages of subbasins united into a single lake only during periods of relatively high water levels (Table 1). Many of the lacustrine

TABLE 1.—Examples of Great Basin paleolakes that consisted of component subbasins.

Paleolake	Open-basin		Reference
	Location	interval	
Lake Bonneville	UT, NV, ID	Yes	Gilbert, 1890
Lake Lahontan	NV	No	Russell, 1885
Lake Chewaucan	OR	No	Waring, 1908; Allison, 1945
Fort Rock Lake	OR	?	Waring, 1908; Allison, 1979
Lake Alkali	OR	No	Waring, 1908
Lake Warner	OR	?	Waring, 1908, 1909; Weide, 1974
Lake Malheur	OR	No	Russell, 1903; Waring, 1909
Lake Alvord	OR	?	Waring, 1909
Lake Surprise	CA, NV	No	Russell, 1884
Lake Searles	CA	No*	Gale, 1915
Lake Panamint	CA	No*	Smith, 1976
Little Mojave Lake	CA	No	Thompson, 1929
Lake Mojave	CA	No	Thompson, 1929

\*Overflowed to another closed-basin lake by means of a long fluvial connection.

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subbasins that constituted arms or embayments of a major lake at its higher levels contained independent closed-basin lakes before and after their interval of integration.

In order to reconstruct accurate paleohydrologic and paleoclimatic models for such a region of closed-basin lakes, it is important to distinguish those water-level fluctuations controlled primarily by geomorphic factors from those induced more directly by climatic variables. A shoreline that is well represented in the geomorphic or stratigraphic record, for example, is not necessarily the result of static climatic conditions; nor does a change in lake level always indicate a climatically induced shift in effective moisture (Sack, 1994c). In addition to climatic factors that affect lake hydrology, geomorphic factors influencing lake hydrography are also reflected in the lake's shoreline record. Variations in lake size that create multiple shorelines may be the result of changes in drainage basin area caused by such factors as tectonism, volcanism, mass movement, stream diversion, or overflow of upstream lake basins. If the geomorphically induced water-level change is rapid, a vertical zone mostly devoid of shoreline evidence, i.e., a null zone, may result (Sack, 1990, 1995). It is also possible that a well-developed shoreline in a closed-basin lake marks the elevation of an intrabasin threshold rather than an interval of climatic equilibrium (Eardley et al., 1957; Benson, 1978; Currey and Oviatt, 1985; Benson and Paillet, 1989). For example, when, under conditions of increasing effective moisture, the water level in one subbasin reaches the elevation of an intra-basin sill, it may remain essentially at that elevation until overflow fills the adjoining closed basin to the threshold level and a single integrated closed-basin lake is formed. The coalescing of subbasin lakes into a single water body by successive overflows from one subbasin to another can create in the confluent lake basin a complex set of shoreline evidence and can result in the amalgamated lake basin having not just a single lake-level chronology but, rather, a complicated assemblage of subbasin chronologies (Davis, 1982). Properly allocating the contributions to paleolake-level changes influenced primarily by geomorphic factors versus those responding directly to climatic variables leads to a more accurate reconstruction of a paleolake basin's climatic and geomorphic history.

At its maximum extent, Lake Bonneville was the largest of the standing water bodies that accumulated in the Great Basin during the late Pleistocene (Figure 1). The Bonneville lacustral cycle lasted from about 30 thousand years ago (Ka) to 12 Ka (Figure 2) (Oviatt et al., 1992), but considerable shoreline and sediment evidence of it remains visible in the landscape (Sack, 1992). The white marl, for example, is a distinctive Lake Bonneville marker bed that was deposited widely around the basin during the deeper phases of Lake Bonneville spanning an interval of at least 8 thousand years (Ky) (Gilbert, 1890; Oviatt, 1987). The most prominent of the relict Lake Bonneville shorelines are the Stansbury, Bonneville, and Provo. The Stansbury shoreline was formed between about 22 and 20 Ka, during the transgressive phase of Lake Bonneville (Currey et al., 1983;

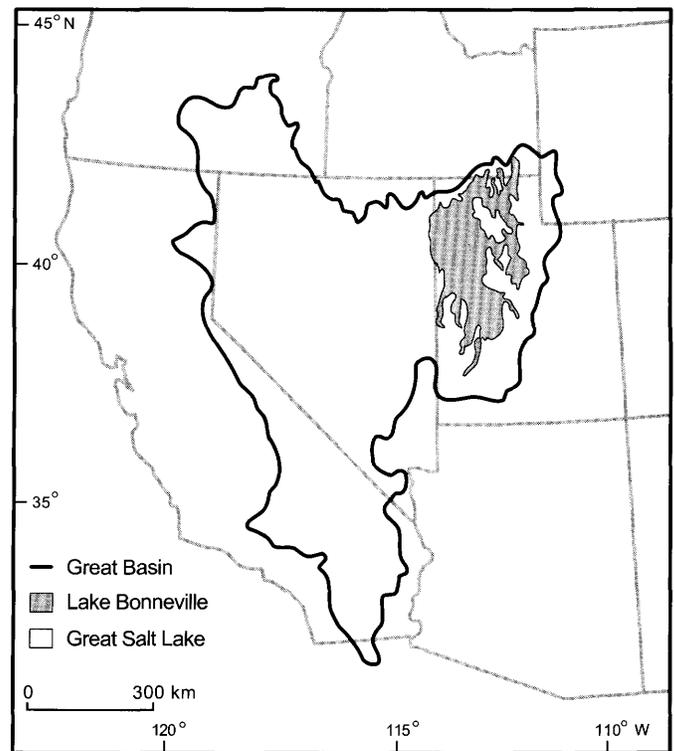


FIGURE 1.—Map showing Lake Bonneville at its greatest extent relative to the Great Basin.

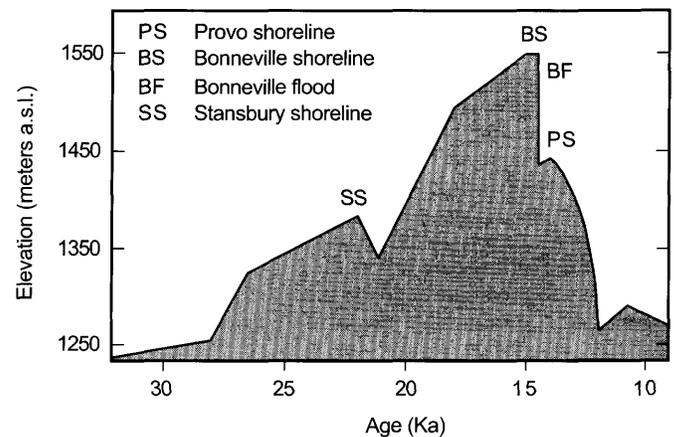


FIGURE 2.—Generalized hydrograph of Lake Bonneville (after Burr and Currey, 1988; Oviatt et al., 1992).

Oviatt et al., 1990). After Stansbury shoreline time, the lake continued rising until it reached the lowest point on its drainage divide, perhaps as late as 15 Ka (Oviatt et al., 1992). With its upper limit constrained by this external threshold, the lake constructed the Bonneville shoreline (Gilbert, 1890). Bonneville shoreline time ended about 14.5 Ka when failure of material at the threshold triggered the Bonneville Flood (Gilbert, 1890; Malde, 1968; Oviatt et al., 1992; O'Connor, 1993). The lake re-

stabilized at the level of a bedrock sill about 110 m below the Bonneville shoreline, and the conspicuous Provo shoreline was created during a period of a few hundred years while the lake was controlled by this lower external threshold (Gilbert, 1890; Burr and Currey, 1988; Oviatt et al., 1992). Closed-basin conditions finally resumed when Lake Bonneville regressed from the Provo shoreline because of climatic reasons, with the lake cycle ending roughly 2 Ky later (Oviatt et al., 1992).

The Bonneville lake basin consists of seven major closed subbasins each of which was integrated into the megalake for a different period of time (Figure 3; Table 2). Lake Bonneville originated in the lowest subbasin, that of Great Salt Lake. Rush Valley was part of the Great Salt Lake basin at the start of the Bonneville lacustral cycle but was isolated from it after Bonneville shoreline time because of the barricading effect of the Stockton Bar complex, which Lake Bonneville had built across their connecting strait (Gilbert, 1890). Integration of the Great

TABLE 2.—The major Lake Bonneville subbasins and selected characteristics.

Subbasin	Approximate modern threshold elevation (m)	Mode of integration
Great Salt Lake	Lowest basin	Origination basin
Great Salt Lake Desert	1285	Spillover from Lake Bonneville
Puddle Valley	1362	Spillover from Lake Bonneville
Sevier Desert	1399	Overflow to Lake Bonneville
Tule Valley	1446	Spillover from Lake Bonneville
Cedar Valley	1507	Overflow to Lake Bonneville (?)
Rush Valley	1585	Origination basin, isolated later

Salt Lake Desert, Puddle Valley, and Tule Valley occurred when transgressing Lake Bonneville spilled over successively higher thresholds into those adjacent subbasins (Currey, 1980; Currey and Oviatt, 1985; Sack, 1990). Although Currey and Oviatt (1985) maintained that Cedar Valley was also integrated by spillover from Lake Bonneville, overflow may actually have

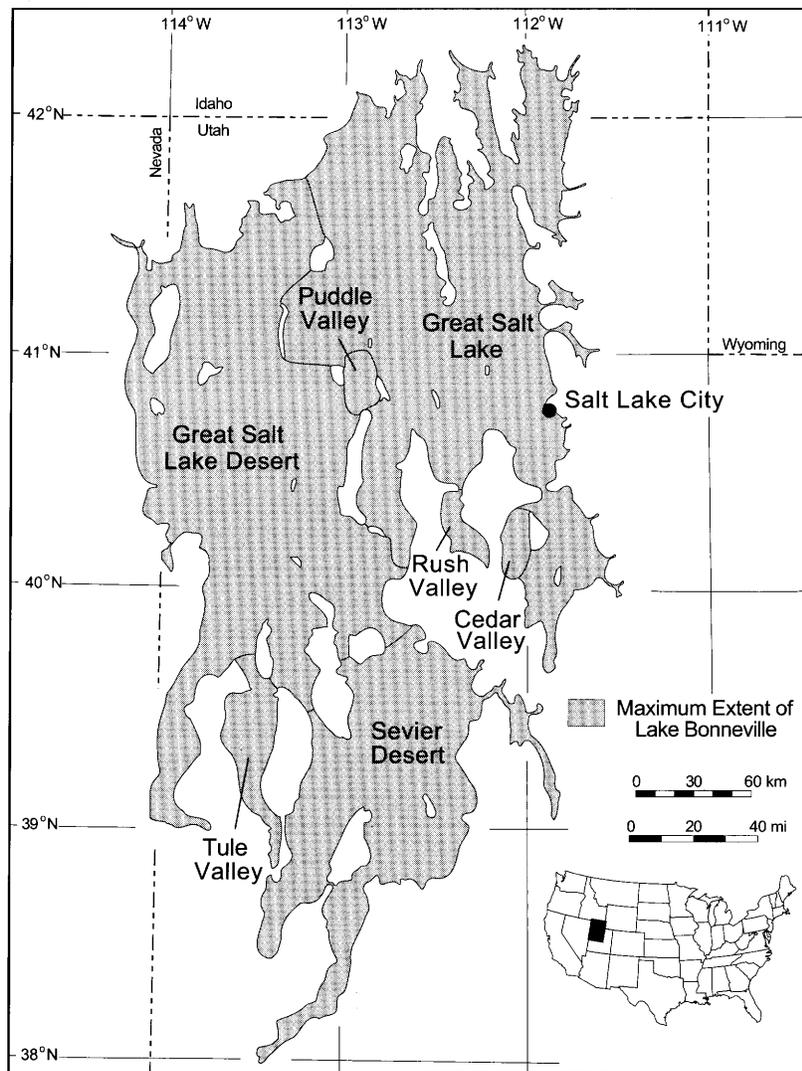


FIGURE 3.—Map showing the seven major subbasins of Lake Bonneville.

been from the high Cedar Valley lake basin, which has a relatively small capacity, into Lake Bonneville. On the other hand, it seems clear that the Sevier Desert basin initially drained northward over the lowest point on its divide into Lake Bonneville by means of a river channel tens of kilometers long (Currey et al., 1983; Oviatt and McCoy, 1988). Lake Bonneville eventually transgressed well above that threshold, converting the connecting river bed into a strait and the Sevier Desert tributary basin into its Sevier Desert arm.

Regardless of the direction of overflow, spillover from one subbasin to an adjacent one is essentially a fluvial process. Even if both basins initially contain independent closed lakes, differences in such variables as elevation, relief, hypsometry, precipitation, surface runoff, and ground-water budgets will cause the water bodies to rise at different rates (Benson, 1978; Benson and Mifflin, 1986). The first one to overtop their connecting sill will discharge a current of water flowing downslope by the force of gravity toward the base level of the receiving basin. Depending upon specific geomorphic and hydrologic circumstances, this fluvial current may occupy a long or short channel, flow on a continuous or intermittent basis, and have a total existence of brief or extensive duration.

In both the Puddle Valley and Tule Valley subbasins of Lake Bonneville, a well-exposed example of a distinctive depositional landform created during integrating inflow is found adjacent to the subbasin threshold (Currey, 1980; Currey and Oviatt, 1985; Sack, 1990). Combined with the results of valley-wide investigations, a comprehensive analysis of the geomorphology, sedimentology, and morphostratigraphy of these features, referred to in this paper as inflow bars, provides insights into the nature of the subbasin integration process and the timing of Lake Bonneville's integration of the two valleys. Results of this investigation, moreover, are useful beyond the Bonneville Basin. Recognizing similar evidence in the geomorphic and stratigraphic record of other Quaternary and perhaps even pre-Quaternary lake basins will help researchers to identify subbasin integration events and, thereby, to reconstruct more accurately the geomorphology, chronology, and paleoclimate of other paleolake basins.

### Previous Work

The fact that climate is not the only variable affecting the size of closed-basin lakes has been recognized in several previous paleolake studies. More than a century ago Gilbert (1890:262) emphasized the significance of "topographic configuration" as well as "meteorologic conditions" with regard to changing lake levels. Stream diversion is probably the most frequently mentioned nonclimatic influence on closed-basin lake levels (e.g., Gilbert, 1890; Bright, 1963; King, 1978; Davis, 1982; Benson and Paillet, 1989). In their report on late Pleistocene lakes in Nevada, however, Mifflin and Wheat (1979) stressed the importance of recognizing episodes of external drainage in a lake's history because pluvial hydrologic

indexes calculated for shorelines controlled by external thresholds are only minimum estimates, which limits their usefulness in making interbasin hydrologic comparisons. Smith and Street-Perrott (1983:192) noted that the size, shape, and hydrologic regime of a lake basin, and therefore the position of its water plane, may change as the result of various nonclimatic processes, including tectonism, volcanism, landsliding, sediment infilling, stream capture, and the cutting of an external outlet. Such alterations can make interpreting the paleoclimatic signal from closed-basin lakes especially challenging (Street-Perrott and Harrison, 1985).

The Great Basin paleolake literature contains some discussion of the nature of constituent subbasins and intrabasin sills and their role in lake history. The second largest late Pleistocene lake in the Great Basin, Lake Lahontan, has thus far been studied more intensively from the subbasin perspective than any other Great Basin paleolake, probably because even when portrayed at its largest extent it maintains the strong appearance of discrete water bodies separated by narrow straits. The importance of the subbasin nature of Lake Lahontan was first identified by Russell (1885), who recognized that various component basins would have been united or isolated at different lake levels. In another early work, Jones (1925:37) observed that the Lake Lahontan intrabasin sills consist of alluvium, and he examined precipitation differences among the "subsidiary basins." Later, those subbasin lakes that would expand mainly by direct inflow from perennial tributary streams were distinguished from those without perennial streams, which would rise instead by spillover from adjoining subbasins (Benson, 1978). More recently, Benson and Paillet (1989) used seven major Lake Lahontan subbasins to demonstrate the influence of topography on lake level. They concluded that total lake-surface area is a better indicator of climate change than lake level or volume. Since the late 1970s, subbasin events and sill elevations have figured prominently in efforts to reconstruct the chronology of Lake Lahontan (Benson, 1978, 1991; King, 1978; Davis, 1982, 1983; Thompson et al., 1986; Benson and Thompson, 1987; Benson et al., 1992). It was in this period that Davis (1982:54) summarized so well the importance of component basins to reconstructing the chronology of a paleolake: "there is no 'Lahontan chronology'; there is a complex family of chronologies, which are fewer when the water is high, and more numerous when it is low."

Gilbert (1890) briefly mentioned constituent subbasins and intrabasin sills in his extensive monograph on Lake Bonneville. Gilbert (1890:20) observed that, because of coalescence of expanding lakes, the number of independent endoreic drainage basins in the entire Great Basin decreased during the late Pleistocene lake epoch, with Lake Bonneville becoming the largest of the "confluent lakes." Desiccation at the end of the lake cycle left the Lake Bonneville basin redivided into numerous, independent closed basins (Gilbert, 1890). According to Gilbert (1890:186), the strongly developed geomorphic characteristics of one of the lake's most conspicuous closed-basin-phase

shorelines, the Stansbury, suggest that it was controlled “by an outflow or its equivalent” rather than by climatic equilibrium. He considered the possibility that sill-controlled inflow to a component subbasin “might have served as a regulator, causing the oscillating lake to linger at a particular level each time it rose” (Gilbert, 1890:186–187).

In a 1957 paper, Eardley et al. (pages 1155–1164) presented some hypotheses regarding Lake Bonneville subbasins and shorelines. Those authors emphasized the notion that the expansion of Lake Bonneville into a subbasin increased the lake’s surface area, resulting in greater evaporation from the lake. If precipitation surplus over evaporation was modest during the lake’s transgressive phase, which they believed was generally the case, expansion in surface area by subbasin integration would create a temporary balance between precipitation and evaporation, and a water-level stillstand would result. The longest stillstand, and hence the best shoreline evidence, would be associated with the largest and most arid receiving basins. During the regressive phase, with precipitation slightly less than evaporation, abandonment of a subbasin would cause a sudden decrease in evaporation from the lake surface. The resulting temporary balance between precipitation and evaporation would again cause a stillstand in lake level. Eardley et al. (1957) used sill and shoreline elevation data to reject Gilbert’s (1890) suggestion that the Stansbury shoreline of Lake Bonneville was controlled by an intrabasin sill. On the other hand, they hypothesized that the stillstand that created the Gilbert shoreline of Great Salt Lake was caused by Great Salt Lake spilling over its threshold into the Great Salt Lake Desert.

More recent publications that mention Lake Bonneville subbasins and interior sills identify the landforms created by inflow. In a study of the coastal geomorphology near Great Salt Lake, Currey (1980) suggested that during the regressive phase of the last deep-lake cycle inflow from the desiccating Lake Bonneville briefly maintained a lake in the Puddle Valley subbasin. According to Currey (1980:76), a low-level shoreline marks the small Lake Puddle, and a “lobate, steep-fronted delta” indicates the point of high-velocity inflow. A subsequent analysis of shoreline evidence, however, describes rapid filling of Puddle Valley by Lake Bonneville inflow during the transgressive phase of the lake cycle and concludes that the low-level Puddle Valley shoreline was formed by an independent Lake Puddle that existed during the regressive phase of the lake cycle after the subbasin lost its surface connection with Lake Bonneville (Sack, 1995). Shoreline evidence supporting the existence of an isolated Lake Puddle during the transgressive phase of the last lake cycle, before Lake Bonneville integration, has not been reported.

In their outline of the fluctuations of Lake Bonneville, Currey and Oviatt (1985) included probable transgressive-phase stillstands caused by the lake spilling into the Cedar Valley and Tule Valley subbasins. Those authors attributed a scoured zone close to the Cedar Valley threshold to high-velocity inflow, but they were unable to identify a shoreline in Lake Bonneville that

resulted from that inflow event. Currey and Oviatt (1985:11) found inflow into Tule Valley to be “clearly marked by a bed-load delta,” and they tentatively assigned a particular, unnamed Lake Bonneville shoreline to the associated stillstand. Sack (1990, 1994a, 1994b) later suggested that the Tule Valley inflow “delta” may be a compound feature, and she attributed the 29 m high Tule Valley null zone, a basinwide sector of the piedmont that lacks substantial shoreline evidence, to rapid inflow from Lake Bonneville. She also reported on the existence during the last lake cycle of an isolated Lake Tule both before and after the subbasin’s interval of integration with Lake Bonneville.

## Data and Interpretation

### PUDDLE VALLEY

**GENERAL SETTING.**—Puddle Valley is located about 100 km west of Salt Lake City, Utah (Figure 3). It is bordered by the Lakeside Mountains to the east, Cedar Mountains to the south, Grassy Mountains to the west, and by smaller ridges and knolls to the north (Figure 4). The 400 km<sup>2</sup> closed drainage basin is entirely surrounded by (inset into) the Bonneville Basin. Specifically, it adjoins the Great Salt Lake subbasin, which lies to

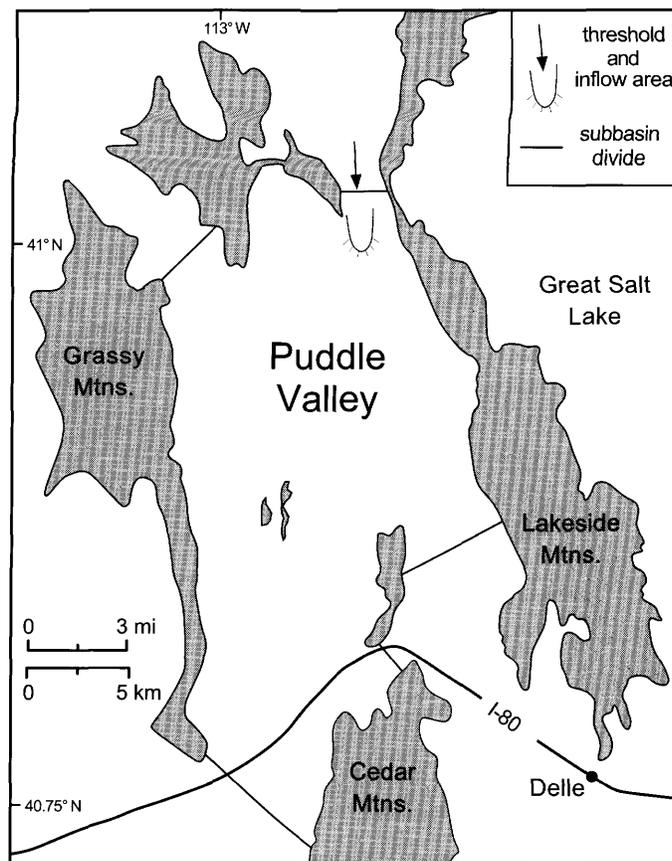


FIGURE 4.—Regional map of Puddle Valley.

the north, east, and southeast, and the Great Salt Lake Desert subbasin, which lies to the west and southwest. Elevations in the subbasin range from 1316 m on the valley floor to 2019 m at the highest peak in the Lakeside Mountains. There is no naturally occurring perennial or intermittent surface water in Puddle Valley today.

The lowest point on the Puddle Valley drainage divide, i.e., its threshold, lies in an unnamed pass in the northeastern part of the valley (Figure 4). A paved highway to Lakeside, Utah, extends through the pass. The pass has an approximate elevation of 1362 m, which is below the modern local elevations of the Bonneville (1625 m), Provo (1501 m), and Stansbury (1380 m) shorelines and above the post-Bonneville Lake Puddle level (1338 m) (Currey, 1982; Sack, 1995). On the Puddle Valley (south) side of the threshold, the pass area consists of a north-south-trending, trough-shaped valley, which is about 1.2 km long and 0.5 km wide (Figure 5). The sides of the trough consist mostly of Lake Bonneville shoreline deposits, which locally have been reworked into alluvial fans; eolian, fluvial, and



FIGURE 5.—Aerial photograph of the Puddle Valley threshold area, including the unnamed pass (P), Lake Bonneville shoreline deposits (S), the trough-like depression (T), and the inflow bar (IB).

alluvial-fan sediments dominate the floor of the trough. The floor of the confined trough slopes about  $0.7^\circ$  toward Puddle Valley, but the modern topography is locally irregular primarily because of eolian action.

**INTEGRATION INTERVAL.**—The approximate duration of Puddle Valley's integration into the Bonneville lacustrine system can be estimated by plotting the rebound-corrected elevation of the Puddle Valley threshold on a detailed hydrograph of Lake Bonneville. The following formula is used to convert modern Bonneville Basin elevations to their values prior to hydro-isostatic rebound (Currey and Oviatt, 1985):

$$Z_a = Z_r - \frac{(Z_r - 1200)}{(Z_b - 1200)}(Z_b - 1552), \quad (\text{Equation 1})$$

where  $Z_a$  is the adjusted rebound-free (estimated original) elevation,  $Z_r$  is a given rebounded (present) elevation,  $Z_b$  is the local modern elevation of the Bonneville shoreline, 1552 is the rebound-free elevation of the Bonneville shoreline, and 1200 is an empirical constant (all elevations are in meters). For the Puddle Valley threshold, 1362 m and 1625 m are used in Equation 1 for  $Z_r$  and  $Z_b$ , respectively. Plotting the resulting  $Z_a$  (1334 m) on the Lake Bonneville hydrograph of Oviatt et al. (1992) yielded an estimate of 25.8 to 12.2 Ka for the interval of Puddle Valley integration (Figure 6). The latter value is a minimum-limiting age estimate because some hydro-isostatic rebound had already occurred by this stage of Lake Bonneville (Currey and Burr, 1988); the elevation of the pass at the time of re-isolation would have been somewhat higher than 1334 m.

**GEOMORPHOLOGY AND SEDIMENTOLOGY OF THE INFLOW BAR.**—The depositional landform that marks the inflow of Lake Bonneville into Puddle Valley (Currey, 1980) lies immediately south of the Puddle Valley threshold area, just beyond the southern end of the trough-shaped valley (Figures 4, 5, 7). Field work and the interpretation of aerial photographs reveal that the inflow landform is a large-scale, tongue-shaped bar on

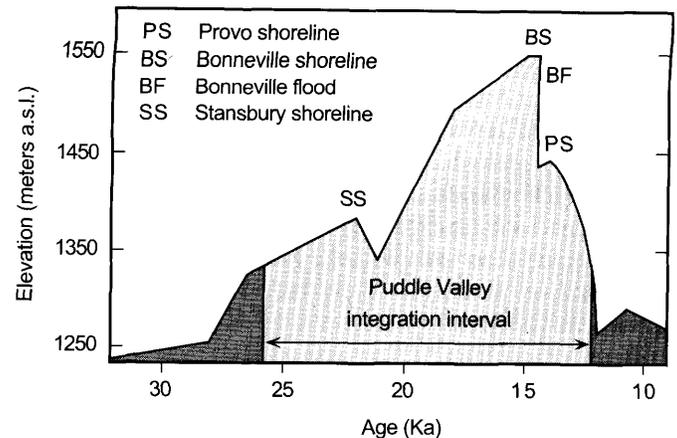


FIGURE 6.—Estimated interval of Puddle Valley's integration with Lake Bonneville.

which are found linguoid, flow-transverse bedforms, i.e., three-dimensional subaqueous dunes (Figure 8) (Ashley, 1990). Both the bar and the subaqueous dunes are composed of gravel. The feature ranges in elevation from 1341 m at the distal (southern) base of the bar to 1357 m at the crest of the highest bedform. The bar, which is about 1.5 km long and up to 1.2 km wide, consists of a stoss-side pan bordered by a continuous lateral and lee-side rim. Along the lee side the rim has a maximum lakeward slope of 15°. The bar complex is mantled with Lake Bonneville marl, clastic lacustrine fine-grained sediments, and postlacustrine eolian sandy silt. The maximum measured thickness of this post-inflow sequence is 1.9 m. Over the ridges of the linguoid bedforms, where the post-inflow sequence is thinner, the surface is gravelly. Postlacustrine eolian fines thicken dramatically toward the northeastern portion of the feature; yellowish gray eolian sandy silt found along the northern end of the left lateral rim is at least 1.0 m thick.

A measured cross section (Figure 9) shows that the three-dimensional dunes are moderately asymmetrical and com-

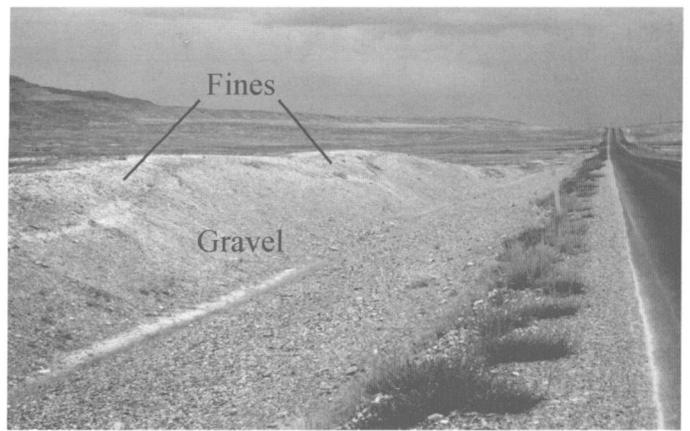


FIGURE 8.—Large-scale subaqueous gravel dunes overlain by light-colored lacustrine and eolian fines exposed in a road cut along the measured section in Puddle Valley.

pound, with medium-scale dunes superposed on large-scale dunes, which, in turn, are superposed on very large dunes (Ashley, 1990). Measured lengths ( $L$ ) range from 6.1 to 143.3 m, heights ( $H$ ) from 0.2 to 3.2 m, and the vertical-form index ( $L/H$ ) from 17.8 to 62.2. The equation that expresses the height versus length relationship of the Puddle Valley subaqueous dunes,

$$H = 0.0445L^{0.90}, \quad (\text{Equation 2})$$

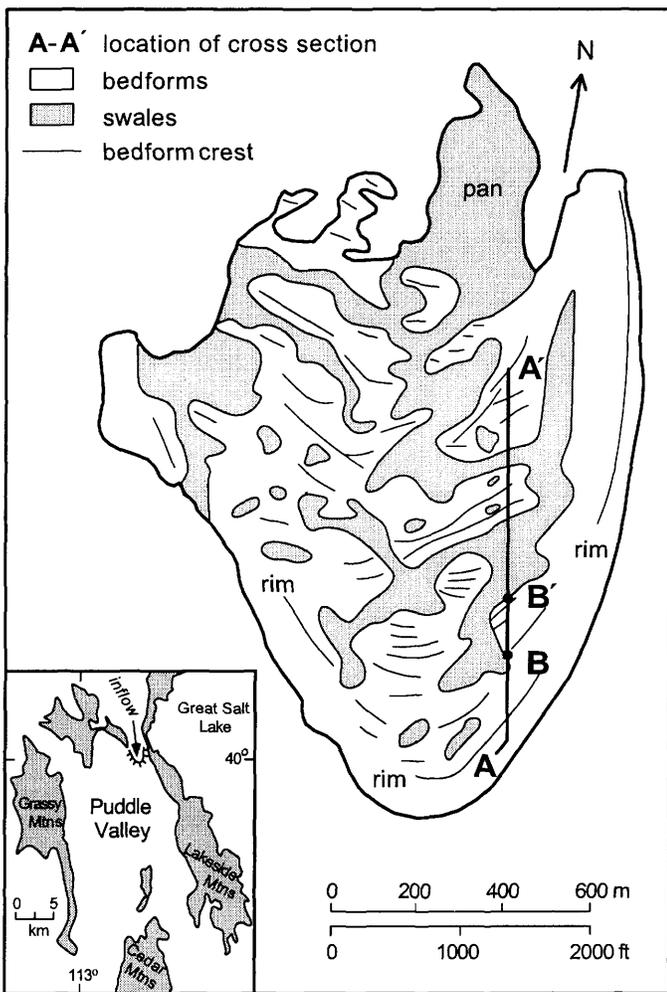


FIGURE 7.—Map-view diagram of the Puddle Valley inflow bar, showing line of measured section, A-A'.

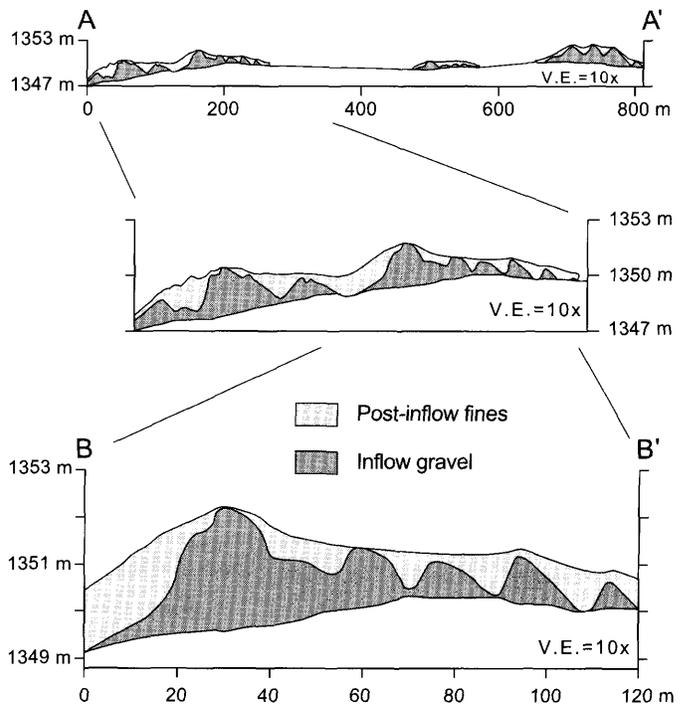


FIGURE 9.—Measured cross section through gravel dunes on the Puddle Valley inflow bar. Location of measured section is shown on Figure 7. (V.E. = vertical exaggeration.)

TABLE 3.—Metric height (H) vs. length (L) relationships for subaqueous dunes.

Equation	Source
$H = 0.074L^{0.77}$	Allen (1968)
$H = 0.0052L^{1.5}$	Baker (1973)
$H = 0.0677L^{0.898}$	Ashley (1990)
$H = 0.0445L^{0.90}$	Puddle Valley (this paper)
$H = 0.0409L^{1.13}$	Tule Valley (this paper)

is similar to those derived from “giant current ripples” by Allen (1968) and Baker (1973:50) and is close to the equation determined from almost 1500 bedforms, reported in Ashley (1990) (Table 3).

The subaqueous dunes on the Puddle Valley inflow bar consist of cross beds that, at the measured section, dip 9° to 24° to the east-southeast. Orientation data collected from the 10 largest clasts at 14 different sediment-sample sites along A–A' also show a current direction to the east-southeast (Figure 10). This direction of dip for beds and clasts reflects the position of the line of section to the east of the main axis of flow (Figure 7). East-southeast is perpendicular to the crestral trend of the subaqueous dunes along A–A'.

Sampled clasts were predominantly rounded or subrounded, and the 10 largest had an average longest axis (A-axis) of 19 cm. The overall 10 largest clasts observed anywhere along the length of the cross section had a mean A-axis of 35 cm. In addition to the local Paleozoic limestones, dolomites, cherts, and sandstones, gravel-size clasts of tufa-cemented conglomeratic beachrock, tufa, and laminated marl were noted in the sample pits and elsewhere along the cross section. A gravel-size rip-up clast of marl that was collected from one of the sediment-sample pits contained an ostracode assemblage that appears to be of pre-Bonneville age (R.M. Forester, pers. comm., 1992).



FIGURE 10.—Representative sediment-sample pit dug in the Puddle Valley gravel dunes. Note size of clasts and dip of beds. Shovel handle is approximately 0.5 m long.

INFLOW DISCHARGE.—In order to reconstruct the paleodischarge during inflow from Lake Bonneville to Puddle Valley several variables have to be determined. Depth of the inflow current can be estimated from the following regression equation derived for particle diameters between 5 and 330 cm (Knox, 1987):

$$d = 0.0001D^{1.21}S^{-0.57}, \quad (\text{Equation 3})$$

where  $d$  is the competent flow depth (in meters),  $D$  is the intermediate axis (B-axis) of the coarsest particles moved (in mm), and  $S$  is the dimensionless energy slope. For the Puddle Valley data,  $D = 133.0$  mm, which is the mean of the B-axes of the 10 largest clasts sampled from the A–A' cross section.  $S$ , the hydraulic slope, is estimated with 0.0000747, the value derived from field measurement of the topographic slope just upflow from the gravel dunes. When substituted into Equation 3 these values yield a flow depth,  $d$ , of 8.36 m. From flow depth and from the representative particle diameter, a roughness value,  $n$ , is calculated with Limerinos' (1970) equation,

$$n = \frac{0.113d^{1/6}}{1.16 + 2.0\log(d/D)}, \quad (\text{Equation 4})$$

with  $D$  now expressed in meters. For relatively wide and shallow channels it is generally considered acceptable to substitute flow depth for hydraulic radius in the Manning equation (Leopold et al., 1964),

$$v = \frac{d^{2/3}S^{1/2}}{n}, \quad (\text{Equation 5})$$

where  $v$  is flow velocity. Using the depth and slope values from above and using  $n = 0.034$ , as calculated from Equation 4, velocity of flow during dune formation would have been 1.05 m/s. Paleodischarge,  $Q$ , is calculated as

$$Q = vwd, \quad (\text{Equation 6})$$

where  $w$  is the channel width. Setting approximate channel width to 1200 m, which is the width of the bar at its proximal end, and using the values of  $d$  and  $v$  calculated above, discharge becomes 10,500 m<sup>3</sup>/s ( $\approx 370,000$  ft<sup>3</sup>/s). If the maximum height of the subaqueous dunes, 3.2 m, is substituted for depth in Equations 4 through 6, a discharge of 2000 m<sup>3</sup>/s ( $\approx 73,000$  ft<sup>3</sup>/s) results. This latter value is considered a minimum estimate of discharge during inflow.

TIMING AND NATURE OF THE INFLOW EVENT.—The white marl is a prominent Lake Bonneville marker bed that was deposited during the deeper levels of Lake Bonneville (Gilbert, 1890; Oviatt, 1987). Its location on top of the inflow bar indicates the bar was not created during the regressive phase of Lake Bonneville, as was previously implied by Currey (1980). There is no evidence of subaerial alteration of the dunes, and the contact between the inflow gravel and marl appears conformable (Figure 9); therefore, it is concluded that the inflow bar was created when the transgressing Lake Bonneville spilled

into Puddle Valley about 25.8 Ka, rather than during a previous lake cycle.

The dimensions of the bedforms, the size of constituent clasts, and the presence of rip-up fragments of marl, tufa, and beachrock, together with the discharge estimate, indicate that spillover was a powerful event. It seems likely that most of the material transported in the inflowing current was eroded from the threshold area. From the rounded to subrounded shape of the gravels and the present lack of bedrock outcrop at the threshold it is inferred that just prior to inflow the pass consisted mostly of unconsolidated or semiconsolidated deposits rather than coherent bedrock. This unconsolidated material may have had alluvial and colluvial as well as lacustrine components.

No geomorphic or stratigraphic evidence has yet been found to indicate the presence of an isolated water body in Puddle Valley just before inflow from Lake Bonneville. If there was one it must have been quite small, occupying only the lowest part of the subbasin. In the absence of pre-integration Lake Puddle shorelines near the inflow landform, there is no reason to conclude that the landform was created by anything other than the strictly fluvial processes of the inflow current per se, shortly before being submerged under the rising Puddle Valley arm of Lake Bonneville. If inflow discharge was indeed within the 2000 to 10,500 m<sup>3</sup>/s estimated range, the volume of Puddle Valley below the sill ( $\approx 4$  km<sup>3</sup>) would have filled in roughly four to 23 days.

#### TULE VALLEY

**GENERAL SETTING.**—Tule Valley lies between the House and Confusion Ranges in the southwestern part of the Bonneville Basin, approximately 210 km southwest of Salt Lake City (Figures 3, 11). Like Puddle Valley, it is currently an independent desert basin of interior drainage with only ephemeral streamflow. Several springs, however, are found on the Tule Valley floor and along its piedmont junction. Tule Valley has greater relief (1340–2950 m) and a larger area (1425 km<sup>2</sup>) than Puddle Valley. Climatic conditions are essentially the same on the two subbasin floors, but because of elevation differences, somewhat cooler and wetter conditions exist in the ranges adjacent to Tule Valley compared with those bordering Puddle Valley (Stevens and Brough, 1987; Sack, 1990).

The lowest point on the drainage divide between Tule Valley and the main body of Lake Bonneville is located at Sand Pass in northeastern Tule Valley (Figures 11, 12). Sand Pass has an elevation of 1446 m, which is approximately 21 m below the local elevation of the Provo shoreline. A channel-like depression slopes about 1.2° from the threshold to the Tule Valley inflow bar. The Sand Pass threshold area consists of a complicated assemblage of primarily coastal sediments deposited near the elevation of the Provo shoreline. In addition to Provo shoreline deposits, white marl, coastal gravel from the transgression of Lake Bonneville, and indurated remnants of a par-

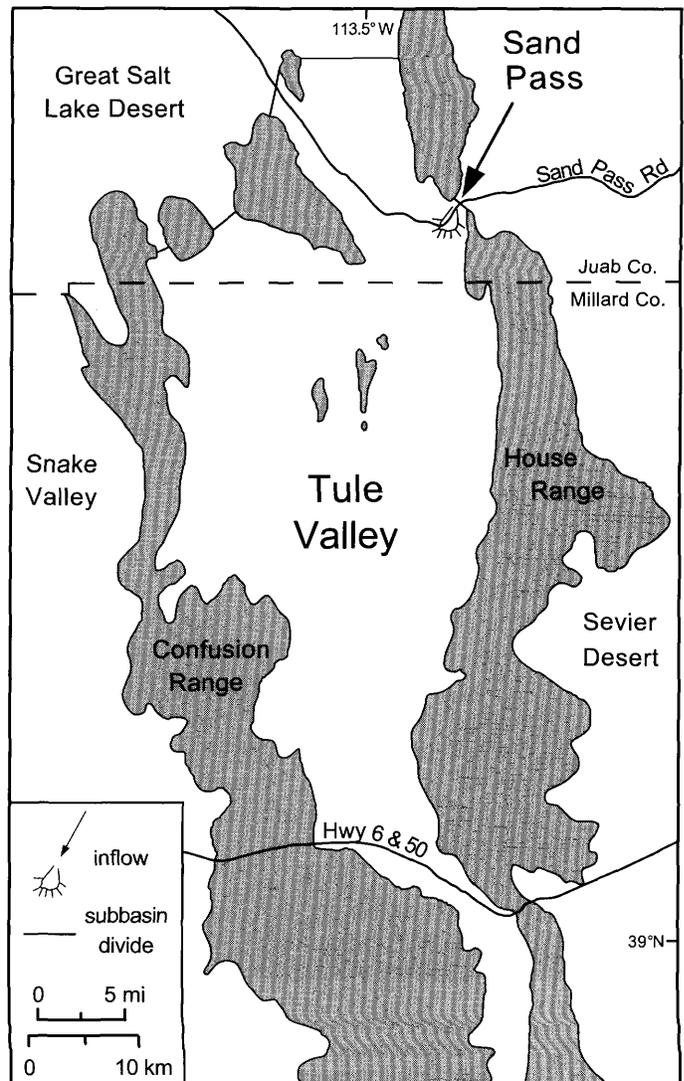


FIGURE 11.—Regional map of Tule Valley.

tially eroded sand and gravel coastal landform, interpreted as an oxygen isotope stage (OIS) 6 barrier complex, are found in the threshold area. Remnants of the barrier complex consist of in-place as well as large, partially collapsed blocks of cemented, cross-bedded sandstone and conglomerate beachrock exposed on both the east and west sides of the channel-like depression. The central portion of the barrier, representing most of its original length, has been completely eroded away. Lacustrine tufa deposited after the barrier was breached fills tension cracks between semicollapsed blocks of the cross-bedded sandstone and conglomerate (Figure 13). Interpretation of the barrier complex as an OIS 6 feature is supported by amino-acid analyses (conducted by the Amino Acid Geochronology Laboratory (AGL), University of Massachusetts) of gastropod shells (AGL2083, AGL2084, AGL2085) collected from indurated coastal deposits inferred to be topsets of the barrier. In addition, along the west side of the channel the beachrock lies beneath

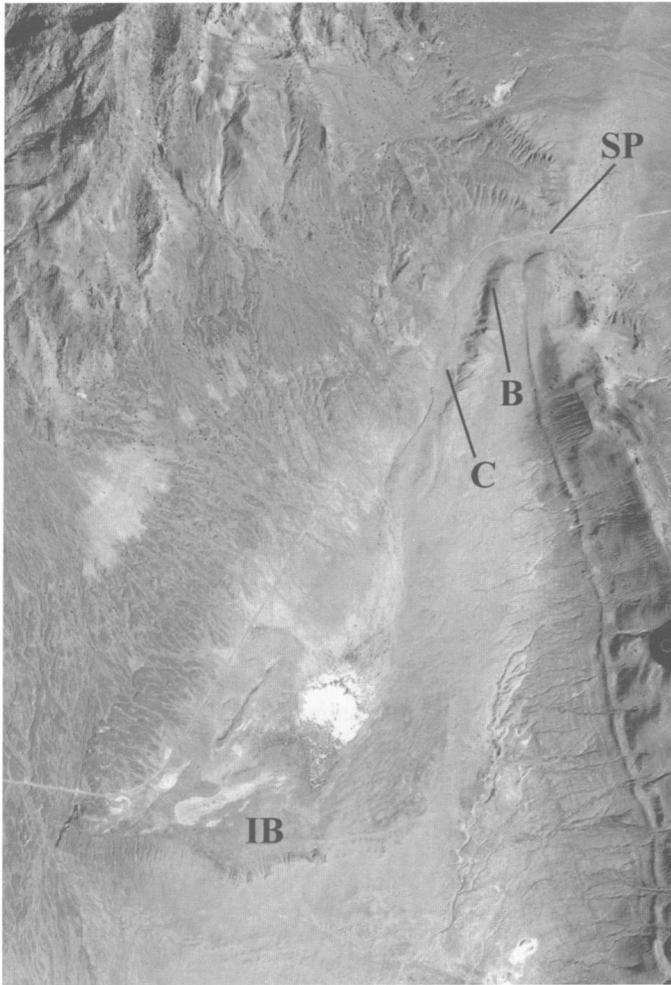


FIGURE 12.—Aerial photograph of the Sand Pass area showing Sand Pass (SP), the channel-like depression extending from the pass (C), remnants of cemented, cross-bedded sandstone and conglomerate beachrock interpreted as pre-Bonneville coastal deposits (B), and the Tule Valley inflow bar (IB). Cross-bedded sandstone and conglomerate beachrock also crop out along the west side of the channel-like depression.

the transgressive Lake Bonneville sequence of coastal gravel and white marl.

**INTEGRATION INTERVAL.**—As with Puddle Valley, the interval of Tule Valley’s integration with Lake Bonneville can be estimated by plotting the rebound-corrected elevation of the threshold on the Lake Bonneville hydrograph. Using the modern elevation of Sand Pass, 1446 m, as an approximation of the pre-integration threshold elevation ( $Z_r$ ) and 1583 m for the local elevation of the Bonneville shoreline ( $Z_b$ ), Equation 1 yields a rebound-corrected elevation ( $Z_a$ ) of 1426 m. According to the hydrograph of Oviatt et al. (1992), the Bonneville Basin landscape at 1426 m was submerged by Lake Bonneville from about 19.4 to 13.5 Ka (Figure 14). These estimates are consistent with stratigraphic observations and numeric ages obtained in association with Tule Valley lake sediments. A radiocarbon age of  $17,710 \pm 320$  yr before present (B.P.) (Beta-

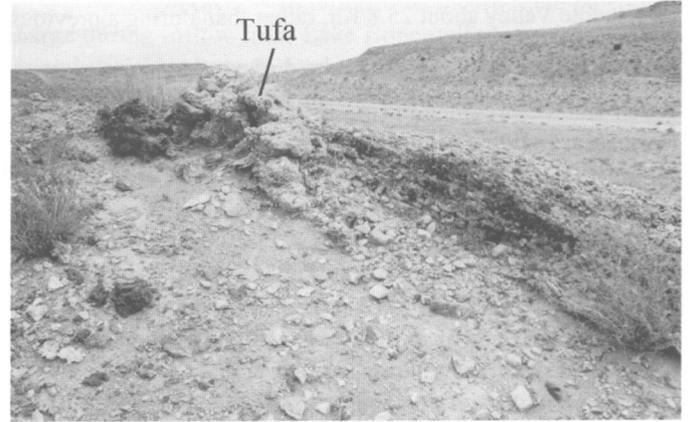


FIGURE 13.—Lacustrine tufa deposited in a tension crack separating a collapsed block of the cross-bedded conglomeratic beachrock from an intact portion of the beachrock.

26795,  $^{13}\text{C}$  adjusted;  $17,300 \pm 320$  yr B.P., unadjusted), determined on gastropod shells collected from the top of a Lake Bonneville gravel spit located 45 km south-southwest of Sand Pass, shows that Tule Valley was integrated with Lake Bonneville at least by 17.7 Ka (Sack, 1990). The 13.5 Ka estimated age of reisololation of Tule Valley from Lake Bonneville is supported by a radiocarbon age of  $13,430 \pm 130$  yr B.P. (Beta-47754,  $^{13}\text{C}$  adjusted;  $13,020 \pm 130$  yr B.P., unadjusted) determined from gastropod shells found in fine-grained calcareous sediments overlying the Tule Valley inflow bar. The approximately 10 cm thick fine-grained unit containing those gastropod shells and the overlying 60 cm thick gravel are interpreted as sediments of independent Lake Tule deposited after Tule Valley’s reisololation from Lake Bonneville.

**GEOMORPHOLOGY AND SEDIMENTOLOGY OF THE INFLOW BAR.**—Like the Puddle Valley example, the inflow landform in Tule Valley consists of a large-scale linguoid bar that displays large transverse bedforms, a stoss-side pan, and a lateral and lee-side rim (Figures 12, 15). The Tule Valley inflow bar is ap-

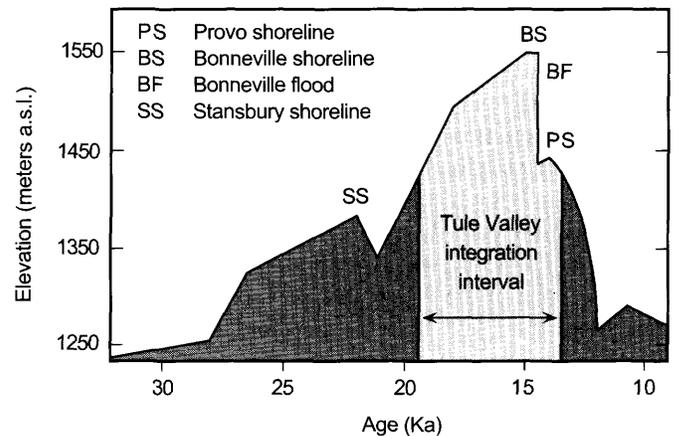


FIGURE 14.—Estimated interval of Tule Valley’s integration with Lake Bonneville (a.s.l. = above sea level).

proximately 2 km long and 1.5 km wide, with elevations ranging from 1391 m at the foot of the distal edge to at least 1426 m on the right lateral rim. The lakeward slope off the lee-side rim is about 4.5°. In contrast to the arcuate distal end of the Puddle Valley feature (Figure 7), the Tule Valley inflow bar displays in planimetric view a much straighter lee-side rim. The Tule Valley bar is overlain by Bonneville white marl, by coastal sediments of the post-Bonneville independent Lake Tule (Säck, 1990), and in some places by significant accumulations of post-lacustrine subaerial deposits. Compared with the Puddle Valley bar, morphologic details of the Tule Valley bar are more obscured by postlacustrine fluvial, eolian, and mass-wasting processes. Nevertheless, the gravel dunes in Tule Valley also appear to be three-dimensional.

A cross section was measured along the right lateral margin of the bar where a gravel pit south of Sand Pass Road and a stream cut north of the road provided good exposures (Figures 15, 16). The representative portion of the measured cross section presented in Figure 16 shows subaqueous dunes overlain by marl and capped by coastal deposits of regressive Lake Tule. The lower portion of the marl sequence is Lake Bonneville white marl, but the upper part of the unit is interpreted as Bonneville marl reworked by Lake Tule after Tule Valley's re-isolation from Lake Bonneville.

Dunes from the entire measured section are large (Ashley, 1990), ranging in length ( $L$ ) from 15.9 to 61.6 m, in height ( $H$ ) from 0.9 to 4.8 m, and in vertical-form index ( $L/H$ ) from 10.0 to 30.2. The relationship between length and height is described by the equation

$$H = 0.0409L^{1.13} \quad \text{(Equation 7)}$$

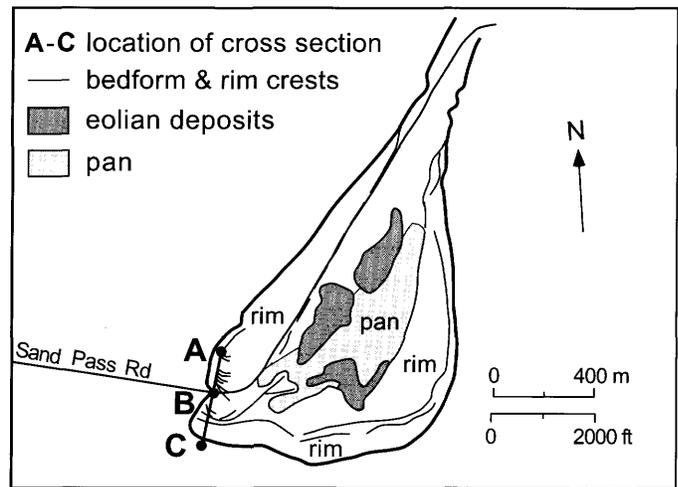


FIGURE 15.—Map-view diagram of the Tule Valley inflow bar, including the location of the measured cross section (A-C).

Although the exponent in this equation is somewhat larger than that reported by Ashley (1990) for a very large data set, it is smaller than the exponent that Baker (1973:50) found for “giant current ripples” created by the Lake Missoula Flood (Table 3).

The subaqueous gravel dunes studied in detail along the right margin of the inflow bar (Figure 15) consist of cross beds that dip 12° to 31° to the southwest. An exposure at the southeast corner of the bar, however, exhibits gravel bedform cross beds that dip 15° to 20° to the southeast.

The 10 largest clasts were investigated from eight sediment-sample sites along the entire right-lateral exposure. Measured clasts had an average A-axis of 18 cm and showed dips to the

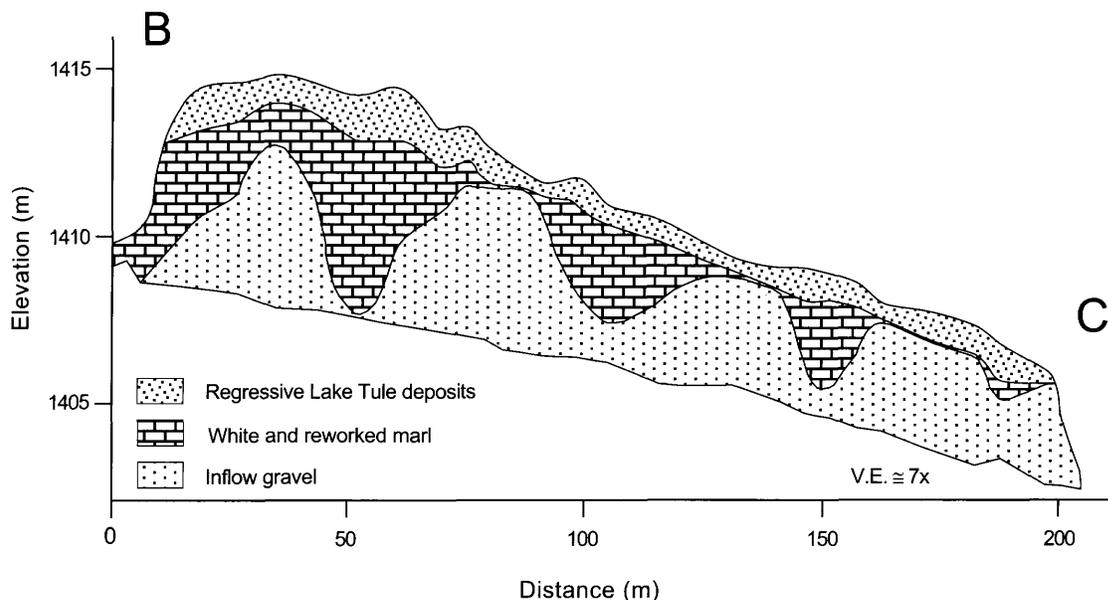


FIGURE 16.—Cross-sectional diagram of large-scale subaqueous dunes exposed along the southwest edge of the Tule Valley inflow bar. See Figure 15 for location of B-C. (V.E. = vertical exaggeration.)

southwest or west. Most of the sampled gravels were subrounded or subangular. Numerous boulders were noted in dune gravel along the distal edge of the bar (Figure 17). A-axis measurements of the 10 largest clasts observed along the entire length of the lee-side rim ranged from 100 to 200 cm, with a mean length of 120 cm. Dune and bar gravels consist primarily of limestones, dolomites, and quartzites derived from the adjacent mountain ranges, but clasts of conglomerate and sandstone beachrock identical to the indurated remnants of the breached barrier found adjacent to Sand Pass are common. The 10 largest clasts of sandstone and conglomerate beachrock found in the inflow bar, up to 2.5 km downflow from the breached barrier, had an average A-axis of 100 cm.

**INFLOW DISCHARGE.**—The large subaqueous dunes and large size of constituent gravel reveal that inflow from Lake Bonneville was a high-velocity event. Paleodischarge can be reconstructed using the same technique as was employed with the Puddle Valley data (Equations 3–6). With a representative clast diameter,  $D$ , of 115 mm, which is the average B-axis of the 10 largest sampled clasts from the Tule Valley gravel dune sediment pits, and an approximate slope near the pan of

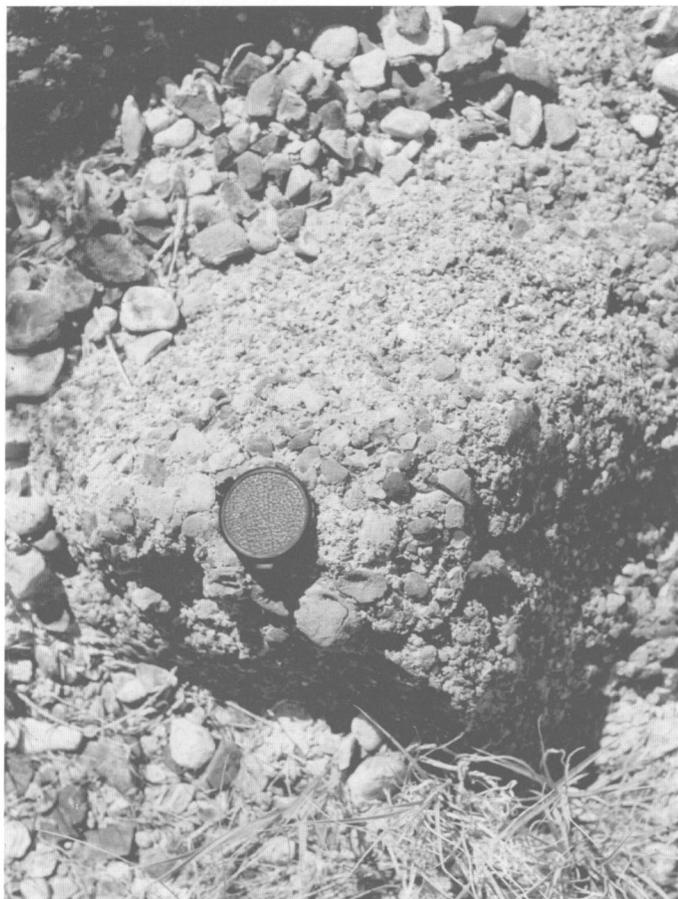


FIGURE 17.—Boulder-size clast of conglomerate beachrock like that found in outcrop near Sand Pass (Figure 12) but located at the distal edge of the Tule Valley inflow bar. Lens cap has a 50 mm diameter.

0.0036, depth is estimated to be 0.77 m. These values yield a roughness coefficient of 0.038 and a velocity of 1.33 m/s. Using the 1450 m maximum width of the bar for channel width results in an estimated discharge of 1500 m<sup>3</sup>/s ( $\approx$  52,000 ft<sup>3</sup>/s). The depth of 0.77 m calculated from Knox's (1987) empirical equation, however, is much smaller than the maximum bedform height, 4.8 m. Substituting 4.8 m for flow depth yields a velocity estimate of 5.17 m/s and a discharge estimate of 36,000 m<sup>3</sup>/s ( $\approx$  1,271,000 ft<sup>3</sup>/s).

**TIMING AND NATURE OF THE INFLOW EVENT.**—The conformable sequence of white marl overlying preserved subaqueous dunes verifies that the Tule Valley inflow bar is of transgressive Lake Bonneville age and not from a previous lake cycle. According to the above estimates of the Tule Valley interval of integration into Lake Bonneville, the inflow bar was deposited before 17.7 Ka and probably about 19.4 Ka.

The common occurrence within the subaqueous dunes of conglomerate and sandstone beachrock clasts derived from the breached barrier located near the divide helps support the notion that the barrier was created during a pre-Bonneville lake cycle and eroded during the spillover of Lake Bonneville into Tule Valley. Apparently, the relict pre-Bonneville barrier that crossed the Sand Pass threshold area failed suddenly either when the hydraulic load from Lake Bonneville exceeded the barrier's strength, thereby initiating inflow, or shortly after the lake began to spill over the barrier into Tule Valley.

Tule Valley definitely contained an independent, transgressive lake, called Lake Tule, when Lake Bonneville spilled over Sand Pass (Sack, 1990). Shorelines created by Lake Tule are well exposed around the valley. Their pre-integration relative age is determined from the conformable relationship between the shoreline gravel and the Bonneville white marl. The highest Lake Tule shoreline lies at an approximate elevation of 1416 m. Above that level, shoreline evidence is lacking in a vertical null zone stretching to about 1446 m, the elevation of the Sand Pass threshold. A continuous series of Lake Bonneville shorelines extends from about 1446 m to the Bonneville shoreline at approximately 1583 m. When Lake Bonneville stood at the brink of spilling into Tule Valley, it occupied the highest elevation it had yet achieved in the lake cycle. At that same time, Lake Tule was probably also at its highest level; therefore, the 1416 m Lake Tule shoreline should mark the position of the independent water body when Lake Bonneville began flowing over Sand Pass (Sack, 1990). Exposures of this highest Lake Tule shoreline are found adjacent to the lee-side rim on both the east and west sides of the Tule Valley inflow bar. The distal end of the Tule Valley inflow bar was apparently deposited at the margin of the water body in Tule Valley. At the estimated inflow discharge of 1500 to 36,000 m<sup>3</sup>/s, the water level in Tule Valley would have risen the 30 m from the Tule Valley shoreline to Sand Pass ( $<22.5$  km<sup>3</sup>) in roughly seven to 174 days.

## Discussion

The linguoid bars created by inflow of Lake Bonneville into Puddle and Tule Valleys appear very similar to the bars that Rundle (1985a, 1985b) observed in the first stage of fluvial braid-bar formation (Figure 18). According to Rundle, that initial tongue-shaped braided stream deposit, referred to in this paper as the "Rundle tongue," is an ephemeral, constructional form deposited downstream from a comparatively deep, confined channel reach. It is created under conditions of radiating flow where water discharging from the confinement mixes with calmer water beyond the orifice. Turbulent mixing along the contact between the stream and quiet water "saps the momentum of the stream and reduces its velocity progressively toward the core" (Rundle, 1985a:9–10). Flow is retarded along the edges of the spreading jet relative to its axis, causing the flow to turn and spread away from the axis. As flow velocity decreases, the load is deposited downstream from the orifice of the confined channel. The resulting deposit, a kind of expansion bar, is linguoid, consists of an upstream pan and a lateral and downstream rim, and displays a steep lee-side slope. In addition, Rundle (1985b) observed that some bars have multiple concentric rims, formed by successive sheets of gravel being transported over the pre-existing pan surface. The complete Rundle tongue is a transient feature in braided streams because it is soon dissected by chutes at falling- and low-water stages. This dissection of the tongue is, according to Rundle, the mechanism of braiding. Remnants of the Rundle tongue preserved between the chutes constitute longitudinal braid bars.

In many respects the Puddle Valley and Tule Valley inflow bars are analogous to the initial stage of the braid bar. Like the Rundle tongue, the inflow bars extend downcurrent from the orifice of a confined channel, which is the sloping, trough-like depression leading from each of the thresholds. The Rundle

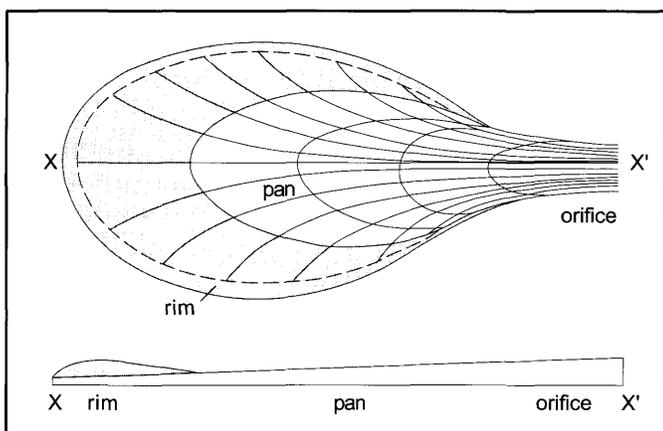


FIGURE 18.—Plan and profile views of the ideal tongue-shaped bar that forms where water flowing as a fast jet leaves an orifice and spreads out into a region of quieter water (after Rundle, 1985b). The Puddle Valley and Tule Valley inflow bars closely resemble this model.

tongue and the inflow bars consist of a pan and a well-developed rim. The subaqueous dunes of the inflow bars are similar to Rundle's (1985b) multiple concentric rims, and both show that bedload was being transported across the top of the linguoid bars. A major chute, like those that dissect the initial braided-stream tongue structure, has breached the Puddle Valley inflow bar on its western side (Figure 7).

Although the Lake Bonneville inflow bars and the Rundle tongue are similar, they do have some differences. The pan on the Puddle Valley example appears smaller than that on the ideal Rundle tongue because of the presence of numerous subaqueous dunes on the bar (Figures 7, 18). Unlike the Rundle tongue, which forms where a jet spreads out into quieter water, Lake Bonneville's inflow bars are deposits of the rapid and expanding inflow current alone. Deposition of the Lake Bonneville inflow bars occurred where the inflow current spread out on the piedmont and was not caused by the presence of lake water in the receiving basins. Deposition of the Tule Valley inflow bar, in fact, ended bluntly where the inflowing current struck the rising Tule Valley water body. The water level in Tule Valley rose so rapidly that inflow current expansion ceased virtually at the moment of contact.

The presence of a large receiving lake in Tule Valley and the absence of one in Puddle Valley is regarded as responsible for the difference in planimetric shape of the distal end of the bars (Figures 7, 15). The flattened distal end of the Tule Valley bar reflects a sudden decrease in velocity that occurred where the inflowing jet hit Lake Tule. In Puddle Valley there is no evidence to indicate that the inflow current interacted with a pre-existing water body. The Puddle Valley inflow bar was deposited by the jet of water spreading out onto the piedmont of an initially dry subbasin, or, perhaps more likely, onto the slope well above a very small Puddle Valley lake or marsh. By not meeting rising lake waters until after the bar was completely formed, the Puddle Valley current expanded symmetrically outward from the axis of flow, giving the resulting deposit a more arcuate shape at its distal end. As a result, compared with the Tule Valley example, the Puddle Valley bar is regarded as having the more ideal inflow-bar shape.

In contrast to the Rundle tongue of braided fluvial environments, which is dissected after its formation by falling water levels (Rundle, 1985a, 1985b), both Lake Bonneville inflow bars are mostly preserved because their formation was followed by rising instead of falling water levels. As the expanding water bodies in the subbasins rose rapidly to equilibrate with the main body of Lake Bonneville, no major reworking of the features occurred; however, for 13.6 and 5.9 Ky after their respective formation, the Puddle Valley and Tule Valley inflow bars existed at the bottom of a water column that was as much as 275 m and 183 m deep, respectively. During the sublacustrine period the inflow bars were blanketed with pelagic white marl.

### Conclusions

The Rundle tongue reported from a braided stream system (Rundle, 1985a, 1985b) provides a good analogue for the general form of the studied Lake Bonneville inflow bars; however, details of the geomorphology and sedimentology of the Lake Bonneville inflow bars reflect the site-specific physical conditions under which they formed. The large size of transported clasts, the presence of three-dimensional subaqueous dunes, and the paleohydraulic reconstructions support the notion that in both studied subbasins Lake Bonneville spillover was a high-discharge event, probably resulting from an outburst through material at the threshold. Field evidence in Tule Valley indicates that Lake Bonneville inflow burst through a relict OIS 6 barrier complex at Sand Pass. Because such relict "divide barriers" (including tomolos) created during the Bonneville lake cycle are common in the landscape today in passes throughout the lake basin, and considering the nature of the dune gravel, it is probable that before integration the unnamed pass separating Puddle Valley from the main body of Lake Bonneville was also crossed by some kind of divide barrier. Both of the studied inflow bars date from the transgressive phase of Lake Bonneville and are relatively well preserved because the subbasin water level rose rapidly over them on the transgression and fell relatively quickly past them during the regressive phase of the lake cycle. Their original surface form was subdued under a mantle of lacustrine fine-grained sediments, regressive coastal deposits, and later subaerial sediments.

The geomorphic and hydrologic circumstances within Puddle Valley and Tule Valley at the time of Lake Bonneville spillover were such that the integrating fluvial current was a very short-lived but continuous flow, although some initial minor spillover may have occurred. Water flowed through a fairly confined region adjacent to the threshold as a fast jet. Very coarse sediment provided by threshold failure and spillway erosion was transported by that current. Where the jet emerged from the orifice of the confined zone, it spread out. Flow divergence just outside of the orifice formed the pan. Beyond the pan, bedload was transported in the form of large-scale subaqueous dunes. The spreading current caused a comparative decrease in flow velocity especially near the margins of the flow, resulting in deposition of a fluvial bar. The tongue shape of the bar reflects this velocity decrease along the edges of the spreading jet relative to its axis, which effected a rotational motion in the flow (Bates, 1953).

Considering the fluvial processes by which they formed, the inflow landforms in Puddle and Tule Valleys are most appropri-

ately referred to as bars. The ideal, linguoid bar form was more effectively developed in Puddle Valley than in Tule Valley because in the latter subbasin expansion of the fluvial current ceased abruptly where it struck the Tule Valley lake waters. Rather than being responsible for formation of the inflow landform, interaction of the inflow current with the Tule Valley lake actually terminated the process of bar formation. For this reason, and because no evidence has been found to indicate the existence of a transgressive-phase Lake Puddle anywhere near the Puddle Valley inflow landform at the time of its deposition, the term delta, although originally applied to these landforms (Currey, 1980; Currey and Oviatt, 1985; Sack, 1990), is no longer considered the most appropriate term.

Studying Lake Bonneville as a complex system of component subbasins focuses attention on aspects of its geomorphology, sedimentology, and chronology that have been generally overlooked by studying the lake as one simple, coherent unit. This subsystem approach may be, and to some extent already has been (e.g., Benson, 1978), profitably applied to other large paleolake basins, which typically consist of several subbasins. Because lakes and lacustrine deposits are sensitive indicators of climate change, paleolake investigations can make important contributions to reconstructing paleoclimates. The accurate modelling of paleoclimates, moreover, is essential for the refinement of general climate models. Lake-level changes, however, are influenced by tectonism, drainage-basin changes, and subbasin integration as well as by climate change. Because lacustrine inflow bars are evidence of subbasin integration, recognizing them will help paleoenvironmental researchers to accurately reconstruct the hydrographic history of a paleolake, thereby contributing to an improved understanding of the true paleoclimatic signal.

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# Environment and Paleolimnology of Owens Lake, California: A Record of Climate and Hydrology for the Last 50,000 Years

*J. Platt Bradbury and R.M. Forester*

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## ABSTRACT

Diatoms and ostracodes from lake-sediment cores beneath Owens Lake playa in southeastern California document an almost continuous paleolimnological record of limnological, hydrological, and climatological changes for the last 50 thousand years (Ky), based upon an extrapolated radiocarbon chronology. Close-interval sampling enabled chronological resolution at a century-scale or less. Modern ecologic studies of diatoms and ostracodes, as well as climatic and hydrologic processes affecting the Owens Lake basin, were used to track environmental changes. The middle Wisconsin to Holocene record indicates that climates wetter than those of modern times existed 80 percent of the time, but that changes between wet and dry climates occurred rapidly—within 300 years to a century or less in some instances. The ostracode record indicates that polar air masses permanently resided at the latitude of Owens Lake during parts of the full-glacial period, whereas the diatom record and heavy-mineral analyses imply that extensive alpine glaciers (on the scale of the full-glacial period) did not exist in the Owens Lake drainage before 22 thousand years ago (Ka) and that the effects of glaciation on sedimentation in this area ended by 13 Ka.

During oxygen-isotope stage 3 (~50–25 Ka) at Owens Lake, summer-season freshwater planktonic diatoms correlate with geochemical evidence related to increased winter precipitation in marine cores at similar latitudes on the California margin. These data document southward shifts and increased strength of the Aleutian low-pressure system (Aleutian Low) in the northeast Pacific Ocean and its role in determining the hydrologic balance of

western North America as well as its effect on the California Current. Such correlations indicate that the Owens Lake paleolimnological record responded to the major dynamics of climate variation in the northern hemisphere.

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## Introduction

Thick, fossiliferous lacustrine deposits underlying Owens Lake (Smith and Pratt, 1957) in southeastern California have been cored and analyzed to extract millennium-scale paleolimnologic and paleoclimatic information for the Owens Lake basin and surrounding region spanning the last 800 thousand years (Ky) (Bradbury, 1997a; Smith and Bischoff, 1997). In this paper, we interpret climate-controlled paleolimnological changes, documented in diatom and ostracode records at relatively high chronological resolution, between the middle Wisconsin (~50 thousand years ago (Ka)) and the late Holocene (0.27 Ka). Sample resolution averages about 250 years for diatoms and about 75 years for ostracodes. In addition, we synthesize ecological, hydrological, limnological, and climatological data for the lake and its drainage to provide a background for interpreting the fossil record. We compare the Owens Lake paleolimnological history to local packrat midden records of past vegetation and to the glacial records in the Sierra Nevada. Our data provide an independent chronology for the timing and magnitude of Sierra Nevada glaciation that augments conclusions of Bischoff et al. (1997b). Finally, we evaluate the middle Wisconsin paleolimnology of Owens Lake in terms of paleoceanographic and paleoclimatic changes registered in marine cores off the California coast spanning the same time interval as at Owens Lake. This detailed, multiproxy record of past climate and hydrology from Owens Lake provides important insights to the timing, magnitude, and character of expected future climate changes at Yucca Mountain, a proposed nuclear waste repository site 140 km east of Owens Lake.

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## Modern Owens Lake Basin

### SETTING

Owens Lake (playa floor elevation, 1080 m; area, 182 km<sup>2</sup>) occupies a graben immediately east of the highest part of the Sierra Nevada (Mt. Whitney, 4418 m), near the intersection of coordinates 36.5°N and 118.0°W (Figure 1). Drainage from the eastern flank of the Sierra Nevada contributes the major volume of water to the Owens River. Although streams from the White and Inyo Mountains east of Owens Lake also recharge groundwater to the basin, the streams rarely reach the Owens River (Hollett et al., 1991). Today, most of the water in the Owens River is diverted to Los Angeles, and the lake basin is almost dry.

The Owens Lake playa is surrounded by desert saltbush (*Atriplex*) and shadscale (*Sarcobatus*) plant communities. Salt

grass (*Distichlis*) grows on alkaline soils near the playa, whereas grasses (Poaceae), sedges (*Scirpus*), and reeds (*Phragmites*), along with riparian communities of cottonwoods (*Populus*) and willows (*Salix*), characterize the valley floor vegetation close to the Owens River (Höllermann, 1973). Shrub communities of creosote bush (*Larrea*) grow south of the playa lake, whereas sagebrush (*Artemisia*) and blackbrush (*Coleogyne*) dominate upstream and to the north of the basin. Scattered stands of Utah juniper (*Juniperus osteosperma*) and single-leaf pinyon (*Pinus monophylla*), as well as sagebrush, occupy surrounding mountain slopes as low as 1600 m elevation (Litwin et al., 1997). Along the Owens Valley, these conifers can form open pygmy conifer forests above 2100 m elevation (Koehler and Anderson, 1994). Montane and subalpine forests of pine (*Pinus*) and fir (*Abies*) occupy elevations between 2500 m and the tree line at 3600 m (Höllermann, 1973).

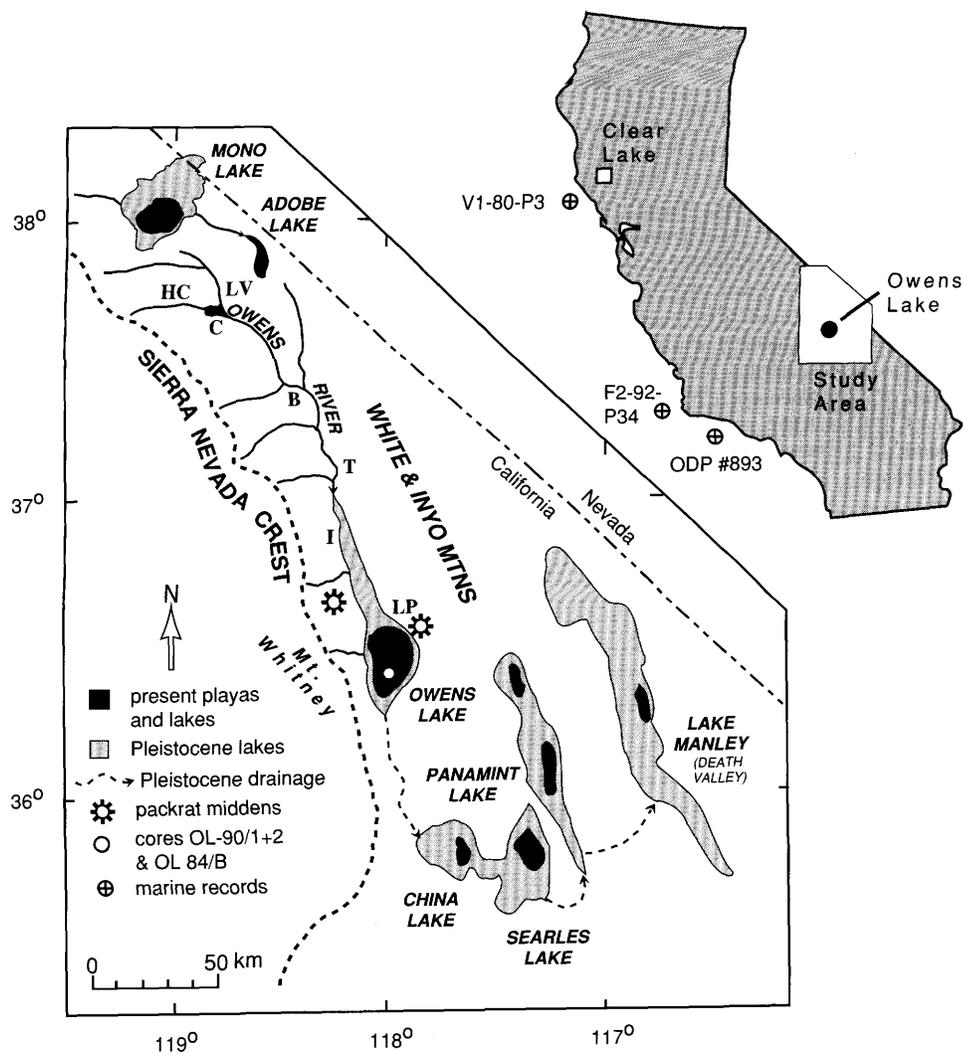


FIGURE 1.—Index map showing Owens Lake and Owens River drainage system in southeastern California and locations of marine cores along the California margin. B = Bishop, C = Crowley Reservoir, HC = Hot Creek, I = Independence, LP = Lone Pine, LV = Long Valley, T = Tinemaha.

CLIMATE

Owens Lake has a wet-winter climate regime. Moisture is delivered to the west coast of California by the southward migration of the Polar Front (and the associated Aleutian Low) as Arctic high-pressure systems expand and coalesce in the winter. As the Subtropical (Hawaiian) High weakens and moves southwestward, westerly air flow drives storms toward the Sierra Nevada where heavy snowfall accumulates; however, because Owens Lake lies to the east of the Sierra Nevada, a pronounced rain shadow affects the basin. Mean annual precipitation is only about 14 cm; about 80 percent of which falls in the winter (Smith and Bischoff, 1997). Annual temperatures average 15.6° C. Lake evaporation rates are high (1.5 m/yr), and arid conditions prevail, especially during the summer when temperatures are high (Figure 2). West of Owens Lake, up to the crest of the Sierra Nevada, precipitation, mostly as snow, accumulates rapidly to local annual amounts greater than 150 cm. Today, annual precipitation increases at a rate of about 23 cm per 1000 m elevation in this area (Smith and Bischoff, 1997).

Eighty percent of the variation in California precipitation relates to the direction and speed of the Polar Front jet stream over the California coast (Bell and Basist, 1994). Interannual variation of precipitation near Owens Lake occurs as irregular, circa-decadal cycles (Figure 3). These cycles may reflect unstable air-sea interactions in the North Pacific that ultimately govern the speed and direction of the jet stream (Latif and Barnett, 1994). Heavy precipitation years may or may not coincide with the El Niño–Southern Oscillation pattern. Substantial summer precipitation at Owens Lake occurs mostly when tropical cyclones bring moisture from the Gulf of California

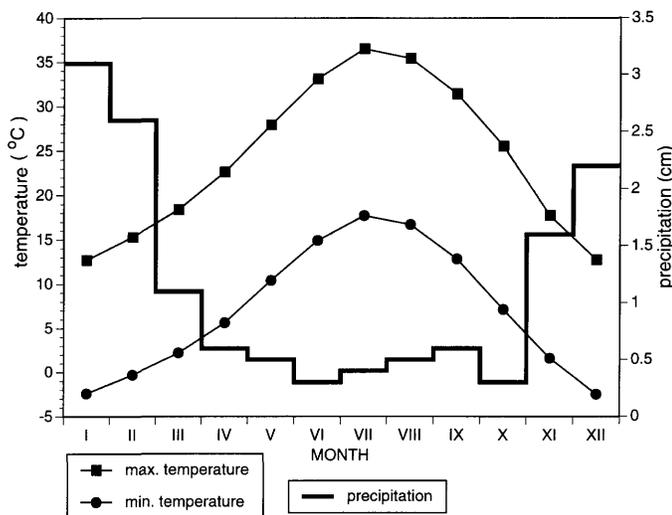


FIGURE 2.—Thirty-year (1961–1990), monthly normals (mean values) of precipitation, and maximum and minimum temperatures at Independence, California. Data are from the National Weather Service as contained on the World Weather Disk, 1994 edition, version 1.4.

and the adjacent Pacific Ocean. Such storms often characterize those years when the previous winter precipitation in the area was low.

HYDROLOGY

**SURFACE WATER.**—In today’s climate, precipitation at Owens Lake is limited and has minor relevance to hydrology

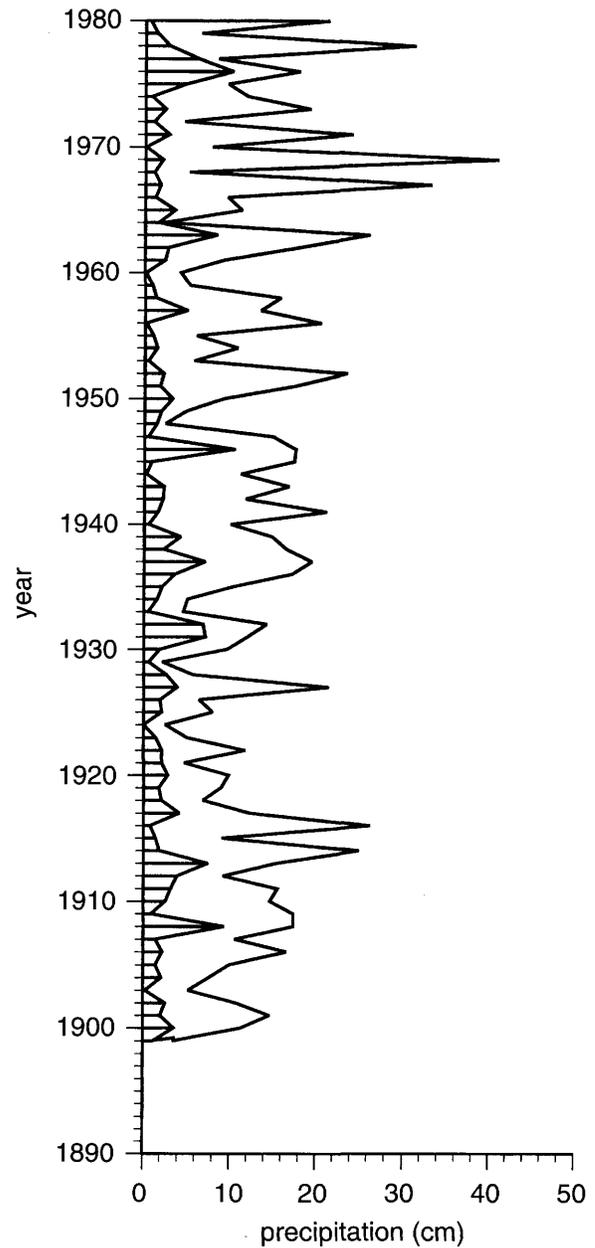


FIGURE 3.—Variation of annual precipitation at Independence, California (water years 1899–1980). A water year begins on 1 October and ends on 30 September of the following year. Silhouette with horizontal lines represents summer (May to October) precipitation. Data are from the State of California, Department of Water Resources.

and limnology. Nevertheless, wet winters in the Owens Valley are positively correlated with heavy snowfall in the Sierra Nevada (Figure 4), and snowmelt runoff dominates flow in the Owens River. Consequently, there is a positive relationship between winter precipitation and upper Owens River discharge

(Figure 5). Before diversion of water from the Owens River to Los Angeles, the level of Owens Lake was related to Sierra Nevada winter precipitation and the resulting discharge of snowmelt down the Owens River. For example, the abundant local precipitation and snowfall during the winter of 1968–1969 (Figures 3–5) so greatly exceeded the capacity of the Los Angeles Aqueduct that the excess runoff was delivered to Owens Lake, raising the level of the almost dry playa to a depth of 2.4 m (Friedman et al., 1976). Two years later, Owens Lake had almost desiccated again, and dissolved salts reprecipitated over the playa floor.

The unusually abundant precipitation that occurred during the winter of 1968–1969 provided a perspective for evaluating the capability of surface water to fill and maintain Owens Lake by indicating how sensitive this basin is to increases in effective moisture. Runoff from snowmelt and precipitation at the town of Lone Pine (19 km upstream from Owens Lake) reached 26.8 cm (more than twice the normal) that season and added 390 hm<sup>3</sup> to Owens Lake (Friedman et al., 1976). At that time, the water diverted to Los Angeles equaled 350 hm<sup>3</sup>; if this water had not been diverted, it would have provided a potential total discharge to Owens Lake of 740 hm<sup>3</sup> (Smith and Street-Perrot, 1983). This potential total discharge was 87 percent of that required to maintain a full and overflowing Owens Lake at present temperatures and evaporation rates. Smith and Street-Perrot (1983) also calculated that the annual discharge of Owens River would have to be 210 percent of historic values (410 hm<sup>3</sup>) to fill the basin to overflowing. The relative discharge of the Owens River and its tributaries during water year 1969 (October 1968 through September 1969) was 180 percent of the historic discharge. After the wet winter (January and February) and spring of 1969, evaporative loss exceeded surface-water input, and Owens Lake desiccated by 1971. Never-

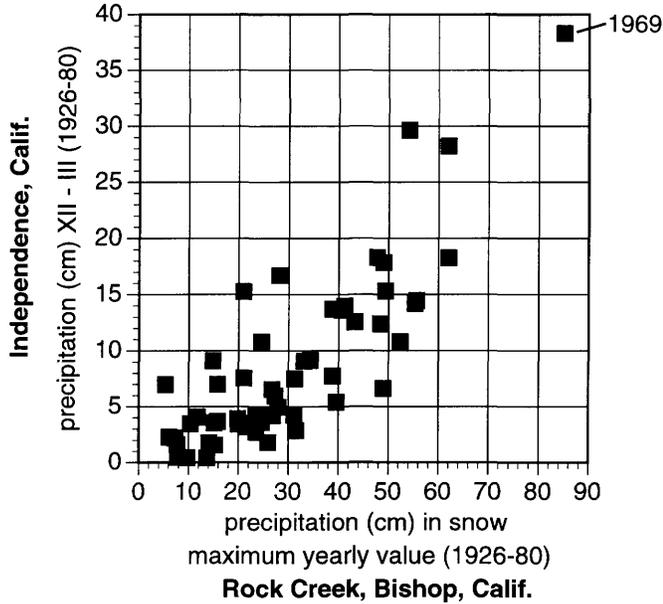


FIGURE 4.—Relationship between annual maximum water content of snow averaged for three Rock Creek snow course stations (elevations of 3049 m, 2759 m, and 2652 m) 30 km WNW of Bishop, California (37°27.0'N, 118°44.5'W), and winter precipitation [December (XII) to March (III)] at Independence, California (elevation 1195 m). Snow data are from the State of California Department of Water Resources, California Cooperative Snow Surveys. Precipitation data sets span 1926–1980. The 1969 data point identifies data for that year.

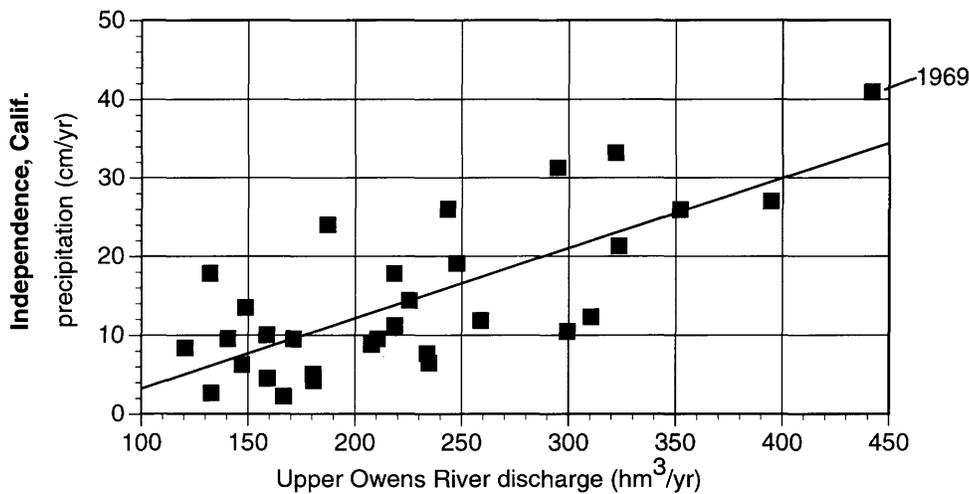


FIGURE 5.—Relationship between annual precipitation at Independence, California, and full natural flow discharge on the upper Owens River (Long Valley to Tinemaha) (see Figure 1). Data span 1962–1992. Discharge data are from the State of California Department of Water Resources, Division of Flood Management. The 1969 data point identifies all data for that year.

theless, the magnitude of the anomalous precipitation during the winter of 1968–1969 was almost the amount needed to fill the lake, especially if mean annual temperatures had been several degrees lower (Smith and Street-Perrot, 1983, tbl. 10.2).

The major dissolved ions in high-elevation water from the Sierra Nevada and White Mountains along the Owens River drainage are Ca and  $\text{HCO}_3$  (Table 1). The ratio of total alkalinity (mostly  $\text{HCO}_3$ , in meq/L) to Ca is usually  $<2$  (see Table 1). Sodium (Na), Mg, and Cl are present in low concentrations compared with the other major ions, except in White Mountain drainages that have somewhat higher Mg concentrations derived from dolomite dissolution. Concentration of total dissolved solids (TDS) in high-elevation water is low, mostly less than 200 mg/L. As high-elevation surface water flows down the Owens Valley, it becomes enriched in Na and total alkalinity ( $\text{HCO}_3$ ) that the river gains from groundwater input, which is modified by interaction with volcanic rock. Locally, water from highly alkaline, thermal springs (Table 1) enters tributaries to the Owens River, making water in the river more alkaline.

**GROUNDWATER.**—The input of groundwater via springs and seeps to the immediate Owens Lake groundwater basin (39 km in length) was estimated to be  $28.6 \text{ hm}^3$  (Lopes, 1987). Hollett et al. (1991) estimated spring and seep discharge along the Owens Valley aquifer north of Owens Lake (108 km in length) to be  $40.7 \text{ hm}^3$ . If these figures are approximately correct, they indicate that proportionally more spring discharge occurs in the immediate Owens Lake groundwater basin than along the Owens Valley. The combined discharge, about  $69 \text{ hm}^3$ , is about 20 percent of the average natural discharge of the Owens River ( $370 \text{ hm}^3$ ) at Lone Pine (Gale, 1914). Accordingly, groundwater input could have an important effect in determining the volume of Owens Lake were it not for withdrawal of water to the Los Angeles Aqueduct.

Springwater and groundwater chemistries along the Owens Valley have two distinct categories: low-salinity water dominated by Ca and  $\text{HCO}_3$  and alkalinity-enriched water of modest to high salinity (Hollett et al., 1991). Groundwater from relatively shallow, permeable, hydrogeologic units that is chiefly recharged through alluvial fans by Sierra Nevada runoff characterizes the low-salinity water. This type of groundwater is typical of the west side of Owens Lake and of the aquifer associated with the Owens River delta at Owens Lake. Deep and presumably old groundwater associated with active volcanic processes or with ancient deposits from Owens Lake is saline and high in Na,  $\text{HCO}_3$ , and Cl. This alkalinity-enriched groundwater characterizes the east side of Owens Lake where it rises along permeable fracture zones and mixes to variable degrees with fresher, shallow groundwater sources associated with alluvial fans (Font, 1995).

Large, active springs, such as Casa Diablo Hot Springs and others along Hot Creek, discharge into the Owens River system in the Long Valley caldera area (Figure 1) and can supply large amounts of dissolved solids to surface water that ultimately

flows to Owens Lake (Smith, 1976a; Menking et al., 1997). Crowley Reservoir, on the Owens River, receives a mixture of alkaline-enriched springwater and relatively low-salinity, calcium bicarbonate water from high-elevation Sierra Nevada sources. We estimate that about 10 percent of Crowley Reservoir water input comes from springs and seeps in the Long Valley caldera region. This estimate was based upon the percent of Cl in the Hot Creek thermal springs (Smith, 1976b) and in the high-elevation Sierra Nevada water sources (Table 1).

The input of alkaline-enriched groundwater via springs and seeps is important in the hydrochemistry of Owens Lake, especially during times of low surface-water discharge. Low-elevation water derived from spring discharge is dominated by Na,  $\text{HCO}_3$ , and Cl. Sulfate is variable, and Ca and Mg are at low concentrations. The alkalinity to Ca ratio (alk/Ca) is large, generally  $\gg 2$ , and the TDS are high, often greater than 500 mg/L (Table 1). During evaporation, the low-elevation, alkaline-enriched springwater and seep water becomes increasingly more concentrated with solutions of Na and  $\text{HCO}_3$ . This hydrochemistry characterized Owens Lake in the late nineteenth century (Gale, 1914), because surface-water input was low and alkaline-enriched springwater input was proportionally high during arid climate conditions. Owens Lake hydrochemistry is predisposed toward Na,  $\text{HCO}_3$ , and Cl enrichment from the chemical character of its groundwater input, and dissolved solids in the lake water can undergo considerable concentration before saline minerals begin to precipitate and change the basic hydrochemistry. In such a system, Ca entering the lake via the Owens River would soon precipitate as  $\text{CaCO}_3$ .

#### LIMNOLOGY

The earliest limnological observations concerning Owens Lake are from the 1861 Nevada–California border survey (Woodward, 1961). The cited description (on 27 March 1861) indicated an approximately oval or pear-shaped lake about 26 km long and 15 km wide, with an extensive, shallow littoral area. A white alkali efflorescence bordered the lake margin; this was replaced farther upslope by a belt of salt grass (*Distichlis?*) and rushes (probably *Scirpus*). High winds made the water turbulent and turbid. In the middle to late nineteenth century, Owens Lake was a closed basin about 15 m deep and alkaline. Between 1872 and 1905, the lake received only about 25 percent of its natural input because of water divergence for irrigation in the Owens Valley (Gale, 1914). Nevertheless, the inflow was sufficient to maintain a perennial, if saline, lake about 6 m deep. The construction of the Los Angeles Aqueduct in 1913 removed the principal source of water to the lake, and by 1923 it desiccated (Smith, 1976b; Tyler et al., 1997). If filled to its spill point today (1145 m), Owens Lake would be about 65 m deep with an area of  $622 \text{ km}^2$  and a volume of  $22,100 \text{ hm}^3$  (Bischoff et al., 1997a).

In its low-stage, Holocene phase, Owens Lake would have had a seasonal (early summer) input of freshwater that would

TABLE 1.—Water chemistry of selected sites in the Owens Lake and eastern Sierra Nevada drainages. Sample sites marked MLD, TRD, WRD, and WM are in the Mono Lake, Truckee River, Walker River, and White Mountain drainages, respectively. Upper Klamath Lake in Oregon is included for comparison. Unless otherwise noted, data are from the U.S. Geological Survey. The HCO<sub>3</sub> column represents HCO<sub>3</sub> + CO<sub>3</sub>. Total dissolved solids (TDS) is by summation of major components expressed as milligrams per liter (mg/L). The ratio of alkalinity to Ca (alk/Ca) is based on milliequivalents (meq) of alkalinity (the total acid-neutralizing capacity of the sample presented in terms of HCO<sub>3</sub> + CO<sub>3</sub> (data not shown)) divided by the milliequivalents of Ca per liter. Data not available are indicated by "nd."

Locality	Latitude (°N)	Longitude (°W)	Elevation (m)	Lab. cond. (µS/cm)	Field pH	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	K (mg/L)	HCO <sub>3</sub> (mg/L)	SO <sub>4</sub> (mg/L)	Cl (mg/L)	TDS (mg/L)	SiO <sub>2</sub> (mg/L)	Alk/Ca (meq)	B (µg/L)	Sr (µg/L)	Li (µg/L)	
<b>Streams</b>																			
Mammoth Creek	37.60	119.00	2731	27	6.72	4.0	0.1	0.7	0.3	13.4	1.9	0.1	21	5.4	1.1	9.6	7	0	
Sherwin Creek	37.63	118.94	2324	24	6.59	2.7	0.1	1.2	0.5	11.2	0.8	0.1	17	6.4	1.4	9.6	10	0	
Deadman Creek	37.74	119.00	2305	38	7.04	3.8	1.1	1.4	1.1	20.7	1.7	0.1	30	21.0	1.8	12.8	39	0	
Rush Creek at Bridge MLD	37.77	119.12	2205	135	6.74	19.0	1.9	5.2	1.2	68.3	2.5	6.8	105	11.0	1.2	109	57	18	
Hot Creek below springs <sup>1</sup>	37.66	118.83	2122	nd	7.02	14.8	7.8	113.9	12.1	243.6	30.4	63.5	nd	59.0	5.4	281	nd	nd	
Marble Creek (WM)	37.78	118.41	2012	188	7.89	30.0	3.9	3.4	1.4	94	14	0.7	147	14.0	1.0	22.4	110	0	
Milliner Creek (WM)	37.60	118.34	1768	150	8.14	20.0	3.1	3	2.1	54	24	0.5	107	15.0	0.9	16.6	64	0	
Moss Power Plant (WM)	37.68	118.39	1426	86	7.37	11.0	2.4	2.6	1	42.7	5.6	0.4	66	15.0	1.3	19.2	30	0	
Silver Canyon Creek (WM)	37.40	118.31	1379	370	8.42	49.0	15.0	8.3	1.7	186	43	1.7	305	17.0	1.2	23.7	410	0	
Owens River (slough) <sup>2</sup>	36.57	118.01	1090	793	7.65	56.0	14.0	94	9.5	380	23	55	632	41.0	2.2	1,080	390	100	
Owens River 1908 <sup>3</sup>	37.19	118.23	1213	nd	nd	30.2	11.7	60	7	205.5	52.6	32.2	339	41.9	2.2	nd	nd	nd	
Owens River at Tinemaha <sup>4</sup>	37.06	118.23	1178	295	8.1	21.6	4.0	31.9	3.9	121.7	22.6	13	181	23.4	1.9	330	nd	110	
<b>Lakes and Reservoirs</b>																			
Little Virginia Lake WRD	38.05	119.26	2965	62	7.2	9.7	0.3	0.8	0.5	15.9	14	0.2	41	4.6	0.5	10	28	0	
Rock Creek Lake	37.45	118.74	2955	17	7.55	1.6	0.1	0.8	0.3	8	0.5	0.1	11	4.7	1.6	11.5	6	0	
Pond north of Tioga Lk. MLD	37.93	119.25	2938	18	6.72	2.1	0.2	0.6	0.4	7.1	2.4	0.1	13	4.2	1.1	10	9	0	
Mary Lake	37.60	119.00	2731	29	6.88	4.1	0.2	0.8	0.3	14.6	1.6	0.1	22	5.9	1.2	5.8	12	0	
Lower Twin Lake	37.62	119.01	2605	54	6.83	7.0	1.2	1.9	0.7	30.5	2.1	0.2	44	6.8	1.4	20	23	0	
Lundy Reservoir MLD	38.03	119.23	2378	54	7.71	8.1	0.3	1	0.7	18.3	9	0.2	38	5.8	0.7	10.2	21	0	
Convict Lake	37.59	118.86	2323	145	8.03	28.0	0.4	1.1	0.7	74	11	0.1	115	9.1	0.9	13.4	34	0	
June Lake MLD	37.79	119.07	2323	265	8.24	30.0	3.8	20	4.5	156	4.2	4.5	223	0.4	1.7	66.9	120	9	
Gull Lake MLD	37.78	119.08	2317	146	8.02	20.0	1.4	8.4	2.7	81.8	5.5	2	122	4.2	1.3	30	57	6	
Grant Lake MLD	37.85	119.11	2174	51	7.48	6.4	0.7	1.6	0.7	24.9	2.4	0.9	38	8.0	1.3	21.1	22	0	
Upper Twin Lake WRD	38.15	119.36	2162	44	7.42	5.9	0.6	1.4	0.5	20.5	2.5	0.2	32	6.3	1.1	7	39	0	
Lower Twin Lake WRD	38.16	119.34	2158	56	7.6	7.3	0.8	1.8	0.6	26.4	4	0.3	41	6.3	1.2	12.8	50	0	
Big Alkali Lake south	37.67	118.78	2093	1,460	9.88	6.1	3.1	290	28	625	46	120	1,118.2	86.0	33.7	210	92	1,300	
Crowley Reservoir	37.59	118.73	2067	311	9.49	19.0	4.5	40	4.6	151	10	18	247	19.0	2.6	784	82	160	
Mono Lake MLD	38.00	119.00	1952	77,000	9.7	5.1	37.0	40,000	1200	20,800	13,000	21,000	96,442	nd	2680	nd	nd	nd	
Topaz Reservoir WRD <sup>5</sup>	38.68	119.52	1518	107	8	12.0	23.0	7.4	1.5	64	4.8	2.4	104	10.0	1.8	nd	nd	nd	
Upper Klamath Lake <sup>6</sup>	42.37	122.87	1262	130	8.7	7.8	4.3	11	2.8	71	6.8	3.3	128	30.0	3.2	nd	nd	nd	
Walker Lake WRD <sup>5</sup>	38.70	118.72	1212	15,214	9.2	11.0	136.0	3,120	166	1,790	2,060	2,260	10,650	0.7	87.3	nd	nd	nd	
Tinemaha Reservoir	37.06	118.23	1178	178	9.03	18.0	2.6	12	2.2	77	16	4.9	133	15.0	1.4	185	69	24	
Pyramid Lake TRD <sup>5</sup>	40.05	119.66	1156	8,900	9.4	9.0	114.0	1,720	118	860	280	2,080	5,110	2.0	53.5	nd	nd	nd	
Diaz Lake Aug 1995	36.56	118.05	1119	535	8.15	26.0	9.6	79	9.1	245	36	27	432	24.0	3.1	890	280	140	
Diaz Lake June 1996	36.56	118.05	1119	983	8.37	45.0	19.0	150	15	453	75	52	809	33.0	3.3	1,450	540	240	
Owens Lake 1905 <sup>7</sup>	36.50	118.00	1086	nd	nd	34.0	15.0	81,176	3448	106,325	21,174	52,898	213,197	298.0	1025	82,500	nd	57,000	
Little Lake west pond	35.94	117.91	962	1,170	10.2	7.1	28.0	210	11	386	140	98	880	24.0	17.9	4,390	49	240	
<b>Springs</b>																			
Hot Creek Spring <sup>8</sup>	37.66	118.83	2122	nd	nd	15.6	0.5	358	39.1	604	48	222	1,287	20.0	38.7	10.3	nd	nd	
Hot Creek geyser <sup>8</sup>	37.66	118.83	2122	nd	nd	12.4	5.0	361	32.1	570	87	215	1,283	82.0	15.0	10	nd	nd	

TABLE 1.—Continued.

Locality	Latitude (°N)	Longitude (°W)	Elevation (m)	Lab. cond. (µS/cm)	Field pH	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	K (mg/L)	HCO <sub>3</sub> (mg/L)	SO <sub>4</sub> (mg/L)	Cl (mg/L)	TDS (mg/L)	SiO <sub>2</sub> (mg/L)	Alk/Ca (meq)	B (µg/L)	Sr (µg/L)	Li (µg/L)	
<b>Springs (continued)</b>																			
Bachelor Spring (WM)	37.24	118.19	1828	465	7.3	82.0	14.0	12	0.7	237	56	6.9	409	22.0	0.9	83.1	690	0	
Dirty Socks Spring	36.33	117.95	1094	11,400	9.2	10.0	79.0	2,600	120	4,015	130	2,200	339	111.0	131.9	39,330	1,370	4,240	
Spring near Keeler	36.45	117.85	1069	9,060	9.57	8.0	13.0	2,300	110	4,064	570	920	1,621	4.3	166.9	42,400	1,400	2,700	

<sup>1</sup>Data are from station 4 of Wilcox (1946); values represent a mean of five determinations in 1933 and 1934 as reported in Smith (1976b).

<sup>2</sup>Owens River was not flowing at time of collection; stagnant water.

<sup>3</sup>Data are from Gale (1914).

<sup>4</sup>Data are from Hollett et al. (1991). Boron and lithium values are from the Owens River aqueduct at Los Angeles in 1975 (Smith, 1976a).

<sup>5</sup>Data are from Bradbury (1987).

<sup>6</sup>Data are from Sorensen and Schwarzbach (1991).

<sup>7</sup>Data are from Lee (1906).

<sup>8</sup>Data are from Wilcox (1946).

have soon mixed throughout the water column because of the lake's large fetch and comparatively shallow depth. As a consequence of snowmelt and runoff, levels in Owens Lake would have fluctuated seasonally, as has been documented at Mono Lake (Mason, 1967). The presence of abundant oolites in the predesiccation sediments of Owens Lake implies that conditions of calcite supersaturation and shallow depths sufficient for wind-generated currents to agitate sediment grains prevailed at that time (Smith, 1997).

The salinity of historic Owens Lake varied between 60 and >200 g/L TDS as a result of short-term climate variation and increasing use of water for irrigation. The lake water was a sodium bicarbonate plus carbonate brine that supported abundant brine flies (*Ephydra*), brine shrimp (*Artemia*), and assorted microorganisms (infusoria) (Lee, 1906). Fishes, such as the Owens sucker (*Catostomus fumeiventris* Miller), now living in the Owens River might have survived in the lake during periods of freshwater inflow and stratified lake conditions until high salinities eliminated the populations, as documented by Smith et al. (1987).

The lake could have stratified thermally, at least for short periods of calm, warm weather (Friedman et al., 1976), but at its shallow-depth stages, the water column usually would have mixed completely, as reported in 1861. Most of the time, therefore, bottom-water temperature would have been close to the mean monthly air temperature (Smith et al., 1987). Possibly, short-lived periods of chemical stratification also existed during the runoff season when less dense, freshwater could float on top of dense, saline water. Owens Lake was almost certainly a warm, polymictic system—a lake mixing throughout the year without ice cover (Lewis, 1983). Pyramid and Walker Lakes in Nevada, 250 and 400 km north of Owens Lake, respectively, do not freeze today, although they are fresher and deeper than the historic Owens Lake. At high stages (e.g., 30+ m in depth), Owens Lake probably would have resembled the warm monomictic Pyramid and Walker Lakes, which circulate in the winter and thermally stratify in the summer.

#### DIATOM ECOLOGY

Diatoms certainly lived in Owens Lake in the late nineteenth and early twentieth centuries, even when lake salinity was almost 100 g/L, but apparently no information exists from those times. The modern diatom flora of Mono Lake may be representative of the diatom communities of the historic Owens Lake, at least in part. Historically, Mono and Owens Lakes had similar chemistries and high alk/Ca ratios (Lee, 1906). The present Mono Lake salinity of about 100 g/L (Table 1) is of the same order of magnitude as the salinity for historic Owens Lake before the diversion of water from the Owens River, although considerable variation in salinity characterized both lakes in the early twentieth century (Lee, 1906; Gale, 1914). In littoral samples between 0.15 and 10 m depths, Kociolek and Herbst (1992) listed *Anomooneis sphaerophora* (Ehrenberg)

Pfitzer, *Navicula crucialis* (O. Müller) Frenguelli, *Nitzschia frustulum* (Kützing) Grunow, *Nitzschia latens* Hustedt, and a new species, *Nitzschia monoensis* Kociolek and Herbst, as the numerically important diatoms in Mono Lake. The same, or closely related, species occur in the Holocene sediments of Owens Lake.

Diatoms in the Owens Lake sediments may be grouped into taxa having ecological associations with freshwater (<1 g/L TDS) and saline water (>1 g/L TDS). Many species found in the cores overlap in their salinity tolerances, so these associations need to be used carefully. For example, although most of the taxa considered to live in freshwater have optima well below 1 g/L TDS, they may inhabit waters two to three times more saline. Furthermore, saline taxa, which often tolerate (or even prosper in) a broad range of salinities above 5 g/L TDS, may be present in waters with less than 1 g/L TDS.

Diatoms occupy different physical habitats in the photic zone of lakes: planktonic diatoms remain in open water and are suspended by turbulence; benthic semiattached diatoms are loosely attached to substrates, such as submerged vascular plants; benthic motile diatoms are capable of moving over and through the mud in illuminated areas of the lake bottom; and benthic adnate diatoms are firmly attached by stalks or pads of mucilage to substrates in the shallowest parts of lakes and can withstand strong currents. In modern lakes, these habitats are more or less distributed along a water depth gradient (deeper to shallower) controlled by the photic zone and the effect of currents.

As with salinity, diatoms overlap in habitat, especially seasonally. Semiattached species may become planktonic when there is sufficient turbulence, as do some benthic motile species of *Campylodiscus*, *Nitzschia*, and *Surirella*. Planktonic species often settle to the lake bottom until favorable conditions return to support them in the open-water photic zone. These criteria and habitat options characterize three principal ecological groups that have more or less coherent ecological distributions (Figures 6–8).

1. Saline diatoms (Figure 6). Benthic species: *Amphora coffaeiformis* (Agardh) Kützing, *Anomoeoneis sphaerophora*, *Campylodiscus clypeus* Ehrenberg, *Navicula crucialis*, *Navicula pygmaea* Kützing, *Nitzschia frustulum*, *Nitzschia monoensis*, *Nitzschia pusilla* Grunow, *Rhopalodia acuminata* Krammer, *Surirella hoefleri* Hustedt, *Surirella ovalis* Brébisson, *Surirella striatula* Turpin. Planktonic species: *Chaetoceros muelleri* Lemmermann, *Cyclostephanos* sp., *Cyclotella meneghiniana* Kützing, *Cyclotella quillensis* Bailey.

2. Freshwater benthic diatoms (Figure 7). Attached species: *Achnanthes lanceolata* (Brébisson) Grunow, *Amphora ovalis* (Kützing) Kützing, *Amphora perpusilla* Grunow, *Cocconeis placentula* Ehrenberg, *Cymbella muelleri* Hustedt, *Epithemia adnata* (Kützing) Brébisson, *Epithemia turgida* (Ehrenberg) Kützing, *Fragilaria capucina* Desmazières, *Rhoicosphenia curvata* (Kützing) Grunow, *Rhopalodia gibba* (Ehrenberg) O. Müller. Semiattached species: *Fragilaria vaucheriae* (Kützing) Peterson, *Pseudostaurosira brevistriata* (Grunow) Williams & Round, *Staurosira construens* (Ehren-

berg) Williams & Round, *Staurosirella pinnata* (Ehrenberg) Williams & Round, *Synedra rumpens* Kützing, *Synedra ulna* (Nitzsch) Ehrenberg.

3. Freshwater planktonic diatoms (Figure 8). All species of *Aulacoseira* and *Stephanodiscus*; *Asterionella formosa* Hassall, *Cyclotella bodanica* Grunow, *Cyclotella ocellata* Pantocsek, some *Cyclostephanos* spp., *Fragilaria crotonensis* Kitton, *Tabellaria flocculosa* (Roth) Kützing.

Because of the great variety and abundance of freshwater planktonic diatoms in the Owens Lake cores, the ecological dynamics and limnological relationships of these species are important in the interpretations of past environments in Owens Lake.

*Stephanodiscus* species generally characterize phytoplankton blooms in the spring or fall (Kilham et al., 1986; Bradbury, 1988). In the Owens Lake drainage, *Stephanodiscus oregonicus* (Ehrenberg) Håkansson and the small *Stephanodiscus* species (*S. minutulus* (Kützing) Round and *S. parvus* Stoermer and Håkansson) are indicators of major hydrologic input in the spring, probably associated with melting of the Sierra Nevada snowpack and discharge into the Owens River. In March 1996, *S. oregonicus* was numerically dominant within the phytoplankton communities in Klamath Lake, Oregon (Figure 8). *Stephanodiscus niagarae* Ehrenberg is probably a fall species because it was numerically dominant in the September 1994 bloom at Crowley Reservoir, upstream from Owens Lake (J.P.B., unpublished data).

Except for *Stephanodiscus niagarae*, the *Stephanodiscus* species common in the Owens Lake cores cannot be perfectly related to existing taxa in the Western United States. In general, the fossil Owens Lake species are more robust and more heavily silicified than modern relatives, perhaps as a result of distinctive nutrient conditions that existed in ancient Owens Lake (Theriot and Stoermer, 1981). Descriptions of some Quaternary fossil *Stephanodiscus* taxa, however, fit the morphological characteristics of the fossil Owens Lake diatoms fairly well, although much variation exists in the assemblages. For example, the fossil taxa *Stephanodiscus subtransylvanicus* Gasse and *S. asteroides* Gasse (Gasse, 1980) are morphologically close to *S. oregonicus* (and to each other), but they tend to be larger, heavier, and more coarsely structured than modern representatives of *S. oregonicus* in the western United States. Because *S. asteroides* compares favorably with the Owens Lake fossil *Stephanodiscus* taxa, this epithet is used for this species complex in the core studies. Because of its general similarities to *S. oregonicus*, *S. asteroides* was assumed to occupy a similar ecological niche as *S. oregonicus*, i.e., blooming in the spring shortly after ice breakup when circulation and river inflow provide abundant nutrients.

*Asterionella formosa* blooms in low-conductivity lakes when phosphorus to silicon ratios are low, usually in the early summer or early fall (Kilham and Kilham, 1978). Its presence in Owens Lake would indicate conditions of comparatively dilute freshwater and seasonal nutrient supplies governed by phytoplankton succession and lake stratification. *Asterionella for-*

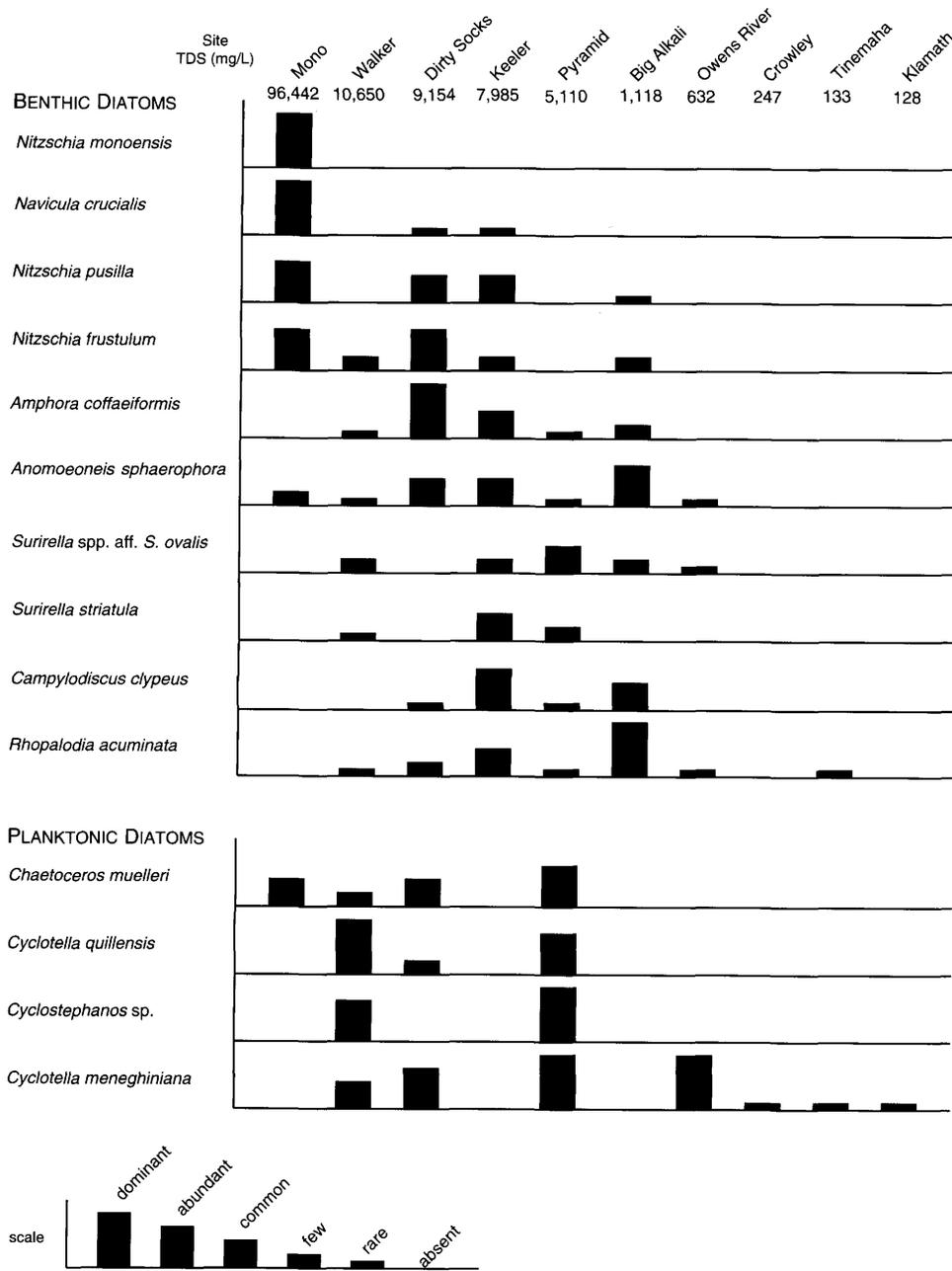


FIGURE 6.—Estimated abundance of saline-habitat diatoms from modern aquatic environments in the western Great Basin. Sites along the abscissa are arranged in order of decreasing salinity (see Table 1).

*mosa* was common in phytoplankton collections taken in June 1996 from Sierra Nevada lakes and reservoirs above an elevation of 2000 m (J.P.B., unpublished data).

Little is known about the ecology and nutrient requirements of the *Cyclostephanos* species, although some prosper in highly eutrophic and often turbid freshwater systems (Håkansson and Kling, 1990). The species found in the sediments of Owens Lake presently lives in Utah Lake (500–1300 mg/L TDS) during the winter (under ice) and early spring (Squires and Rushforth, 1986; they initially identified this diatom as *Stephanodis-*

*cus dubius*). In the Owens Lake system, this taxon also probably represented winter or very early spring diatom production. A similar diatom lives in hypereutrophic Upper Cow Lake in Malheur County, Oregon, and in Diaz Lake, about 4 km northwest of the Owens Lake playa (J.P.B., unpublished data).

*Aulacoseira granulata* (Ehrenberg) Simonsen and *A. ambigua* (Grunow) Simonsen bloom when wind-driven mixing of the water and a deepening of the thermocline supply nutrients, generally phosphorus and silica, from the hypolimnion and when turbulence maintains the diatoms in the photic zone.

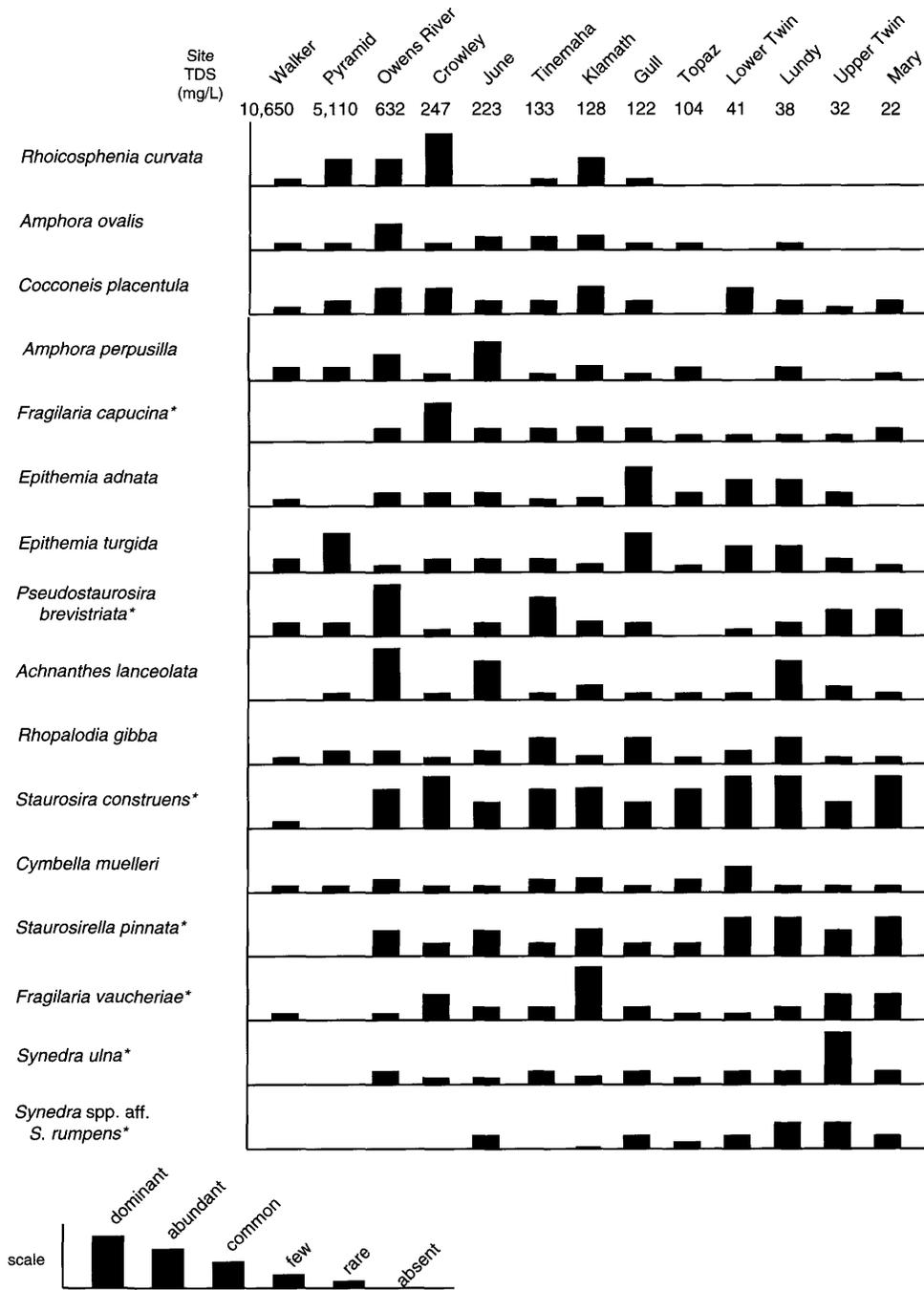


FIGURE 7.—Estimated abundance of benthic diatoms from modern freshwater aquatic environments in the western Great Basin. Sites along the abscissa are arranged in order of decreasing salinity (see Table 1). Taxa with asterisks are semiattached species.

These diatoms are indicators of warm, open-water (or at least high light) conditions and abundant nutrients. *Aulacoseira granulata* often lives in shallow lakes where nutrients are readily available during windy periods (Brugam, 1983). In Owens Lake, these species represented favorable limnological environments in the summer, perhaps because summer precipitation maintained the lake against excessive salinities from

evaporation or, more likely, because substantial discharge from the Owens River persisted through the summer and into the fall. The modern limnology of Crowley Reservoir and Lower Twin Lake may serve as reasonable analogs for *Aulacoseira*-rich intervals of the Owens Lake core. These lakes are 1000 m or more above Owens Lake and are in moister, cooler climatic zones that have abundant hydrologic input from the Owens

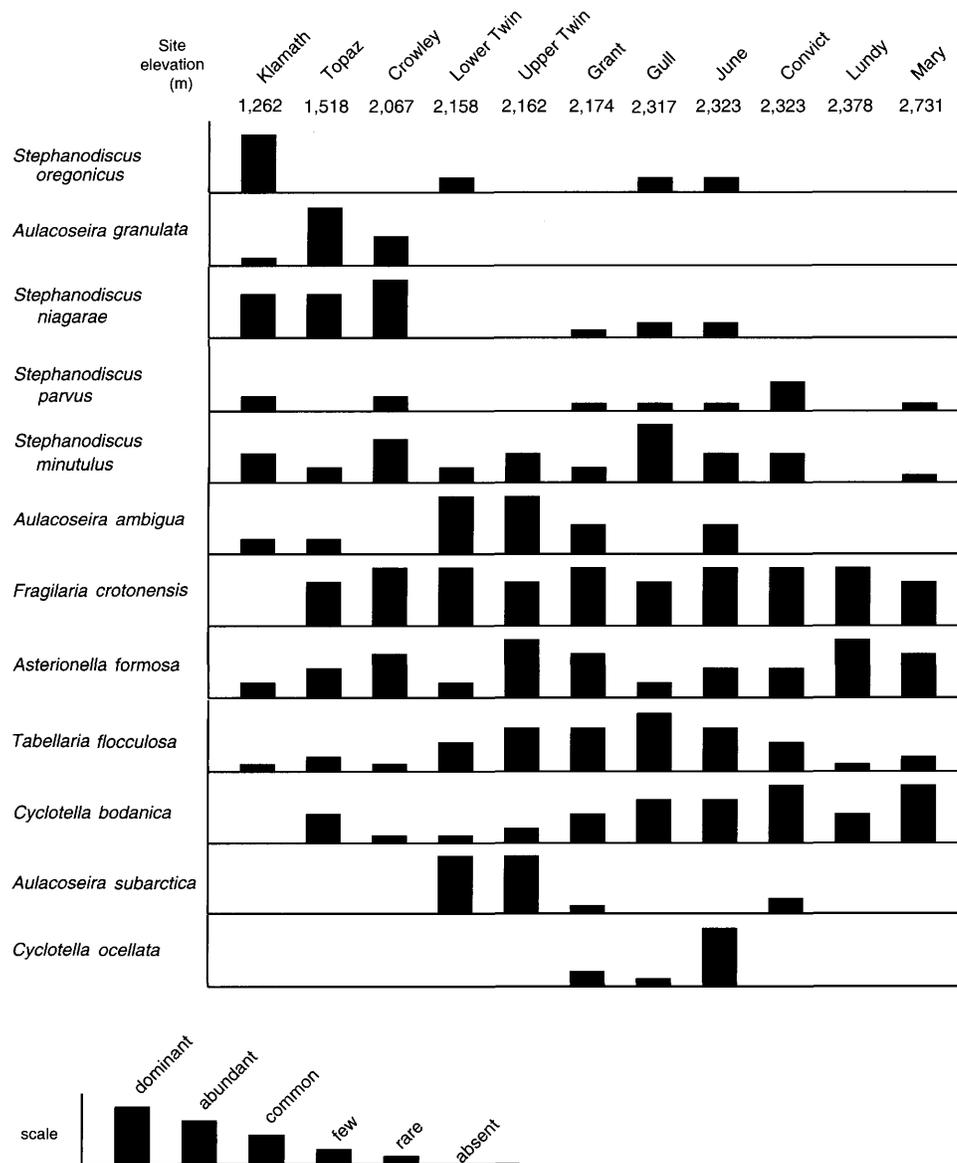


FIGURE 8.—Estimated abundance of planktonic freshwater diatoms from modern aquatic environments in the western Great Basin. Sites along the abscissa are arranged in order of increasing elevation (see Table 1).

River. Both lakes have low summer turbidity that promotes high-light-dependent diatoms.

Freshwater diatoms disperse to and proliferate in new habitats rapidly and easily. In addition to water transport, diatoms may be carried by birds and wind because many species have resistant resting spores or accumulate oils to retard desiccation. The ability of diatom communities to rapidly respond to habitat changes makes them excellent paleolimnologic indicators.

OSTRACODE ECOLOGY

Our interpretation of the fossil ostracode data is based on the chemical preferences and biogeographic distribution of these

species, which we derived from mostly unpublished United States Geological Survey (USGS) ostracode habitat and chemical data sets. The data were collected by USGS staff, Donald F. Palmer and Alison J. Smith (Kent State University), and by B. Brandon Curry (Illinois State Geological Survey) from springs, wetlands, lakes, and a few streams, totaling about 800 localities throughout the United States. Additional information on ostracode distribution and ecology came from more than 3500 Canadian sites (Delorme, 1989).

*Candona caudata* Kaufmann, *Cytherissa lacustris* Sars, *Limnocythere ceriotuberosa* Delorme, and *L. sappaensis* Staplin, the most common ostracodes in the Owens Lake cores, now live in lakes that have varied chemical, thermal, and hydrocli-

matic characteristics (Forester, 1986, 1987, 1991; Delorme, 1989; Forester et al., 1994; Smith and Forester, 1994; R.M.F., unpublished data). *Candona caudata* also commonly inhabits streams, whereas *L. sappaensis* lives in some spring pools and wetlands. *Limnocythere ceriotuberosa* and *L. sappaensis* commonly live in slightly to very saline water, respectively, that has high alk/Ca ratios, whereas *Cytherissa lacustris* and *Candona caudata* more typically live in freshwater habitats (Forester, 1983, 1986; Bradbury et al., 1989; Forester et al., 1994).

In the Owens Lake drainage, *Candona caudata* lives in the Owens River and also in a number of lakes at higher elevation (>2000 m) in the Sierra Nevada. *Limnocythere sappaensis* lives in saline springs around Owens Lake, such as Dirty Socks Spring and the Keeler springs on the eastern margin of Owens Lake, and in wetlands and shallow lakes having high alk/Ca ratios (>7) along the Owens River (e.g., Big Alkali Lake and Little Lake). *Limnocythere ceriotuberosa* lives in Diaz Lake, which varies seasonally in water volume and amount of TDS (as a result of controlled input from the Los Angeles Aqueduct) and has a moderately elevated alk/Ca ratio of just more than 3. This species has not been collected elsewhere in the Owens River drainage.

*Cytherissa lacustris* does not live in the Owens River drainage nor in any lake south of Canada that was sampled during this study, except for rare populations in the Great Lakes and in Yellowstone Lake. In Canada and Alaska, *C. lacustris* lives in dilute, oligotrophic, cold-water lakes of the boreal forest. Delorme (1989) reported the upper TDS tolerance of *C. lacustris* at 300 mg/L. The level of TDS alone, however, does not account for the distribution of *C. lacustris*. This species also requires lakes that have interseasonal chemical stability and low, or at least predictable, thermal variation.

The biogeographic distribution, temperature, and chemical preferences of these four ostracode species provide a means of understanding the probable climate and limnological history of Owens Lake. The presence of *Cytherissa lacustris* in core sediments implies there once was an almost continuous residence of polar air in the Owens Lake region. Today, this air mass remains in the boreal regions of Canada and southern Alaska. The presence of polar air in the Owens Lake drainage during past climates reflects the continental glaciation that existed in northern North America, which maintained polar air south of the ice-sheet margin. The subsequent disappearance of *C. lacustris* from the fossil record implies the retreat of polar air northward and the start of deglaciation. From a limnological standpoint, the presence of *C. lacustris* implies, by analogy, that a dimictic lake with a long ice-cover season existed in the Owens Lake basin.

*Candona caudata* may be present with *Cytherissa lacustris*, but *Candona caudata* has a wider distribution in lakes and streams well south of Canada and Alaska. The southernmost modern record of *Candona caudata* is in southern Nevada, and its upper TDS limit is about 3 g/L (Bradbury et al., 1989). At Owens Lake, the presence in the fossil record of *Candona cau-*

*data* without *Cytherissa lacustris* implies the generally freshwater conditions and temperature regimes that are characteristic of the Great Basin today also occurred in the past. To maintain freshwater habitats in the shallow lake basin, flow in the Owens River needed to have been sufficient on a seasonal basis to offset potentially high valley-bottom evaporation rates; therefore, the presence of *Candona caudata* in the fossil record indicates a positive hydrological balance that, at least, partly reflects greater precipitation at that time.

*Limnocythere ceriotuberosa* usually lives in lakes that have strong seasonality in volume and associated chemistry. It has been collected alive in lakes that have a TDS level as low as 400 mg/L and as high as 12 g/L. Lakes such as Pyramid and Walker Lakes, which seasonally freshen and increase in size from surface flow but then shrink and become more saline once surface flow decreases, are common settings for this ostracode. Often these limnological changes in such lakes represent a seasonal riverine hydrological shift from surface flow derived from snowmelt to base flow derived from shallow aquifers. Generally, such lakes and rivers are in semiarid, temperate settings. Increased abundance of *L. ceriotuberosa* in Owens Lake deposits suggests surface-water discharge into the Owens River and then to Owens Lake varied seasonally. *Limnocythere ceriotuberosa* often appeared in the Owens Lake fossil record during transitions between glacial and interglacial climates.

*Limnocythere sappaensis* commonly lives in wetlands and lakes that are saline or that maintain a saline, alkaline-enriched solute composition during the year (Forester, 1983, 1986). The species lives in wetlands and lakes that have salinities as low as 650 mg/L and as high as 110 g/L. The solute and salinity characteristics of its habitat indicate that *L. sappaensis* would have lived in Owens Lake during arid interglacial periods when alkaline base flow predominated in the Owens River, which resulted in a generally low-volume lake with alkaline, saline hydrochemistry. Present-day Owens River water, if combined with alkaline spring discharge and allowed to enter Owens Lake, could support *L. sappaensis*.

Like diatoms, ostracodes disperse rapidly and easily, and they proliferate quickly. Because of their larger size, most adult and juvenile ostracode transport is by birds. Ostracode eggs, some of which are sticky and require desiccation to hatch, may be transported by fish, birds, insects, and other terrestrial animals, or perhaps by wind. Ostracode eggs apparently survive transport through the digestive tracts of most transport animals.

## Fossil Record from Owens Lake Basin

### METHODS

The paleolimnological history of Owens Lake is based upon three continuous sediment cores. Core OL-84-B was raised in 1984 from near the center of the Owens Lake playa (Figure 1) (36°23.91'N, 117°56.142'W) using a modified Livingstone piston corer (Lund et al., 1996; Benson et al., 1997). It bottomed at a depth of 11.6 m. Cores OL-90-1 and OL-90-2 were

obtained about 3 km southwest of core OL-84-B using a truck-mounted, hydraulic, split-spoon sampler (Benson et al., 1996). Cores OL-90-1 and OL-90-2 bottomed at depths of 32.8 and 28.2 m, respectively. For diatom and ostracode analyses, a 34 m composite section (OL-90-1+2) containing the upper 28.16 m of core OL-90-2 and the basal 5.91 m of core OL-90-1 was constructed from a magnetic susceptibility correlation at 3 cm intervals (Benson et al., 1996).

One-half cubic centimeter splits of magnetic susceptibility samples from core OL-84-B and from the upper 16 m of core OL-90-2 provided material for diatom studies. The remaining samples from cores OL-90-2 and OL-90-1 were excised with a spatula and placed in labeled, air-tight plastic bags. Approximately 0.5 cm<sup>3</sup> subsamples were processed for diatoms by using concentrated HNO<sub>3</sub> in a water bath at 100° C. After the residue was washed free of acid and dissolved solids, it was settled onto coverslips and mounted in naphrax (Bradbury, 1997a). Diatom data were presented as relative abundance. In samples that had diatom valve counts less than 100, an artificial count of 100 was used to calculate percentages, thereby underweighting relative diatom abundances in samples of low diatom concentration. Silt-sized heavy-mineral grains of magnetite, zircon, and monazite were tallied from the diatom microslides on the basis of color, transparency, and crystal form. Heavy-mineral grain concentration is presented as the number of grains per millimeter of microscope transect at ×1000 magnification. Heavy-mineral grain identifications were verified by petrography.

Estimated abundance of diatoms in modern samples are denoted as follows: dominant = more than 10 specimens of a taxon in every field of view examined; abundant = taxon occurred in every field of view; common = taxon present in every fourth field of view; few = taxon present in one of 10 fields of view; rare = taxon present in one of 20 fields of view; and absent = not seen.

Sections of about 3 cm thickness were cut from core OL-84-B between 1.63 m and 9.11 m to obtain ostracode samples. Sections of about 2 cm thickness were cut from cores OL-90-1+2. The sediment was weighed, disaggregated, and washed through sieves to concentrate the ostracodes, which were reported as number of adult valves per gram of sediment.

#### CHRONOLOGY

Polynomial-age models were based upon 40 radiocarbon dates from the total organic fraction using accelerator mass spectroscopy (AMS) (Benson et al., 1996; Benson et al., 1997). These provided the chronologies for cores OL-84-B and OL-90-1+2. The radiocarbon dates indicate hiatuses or periods of very slow deposition at 2.25 m and 9.13 m in core OL-84-B. A hiatus at 9.13 m in core OL-84-B correlates with one at 6.0 m in core OL-90-2. In both cores, this hiatus separates lithostratigraphic units C and D of Lund et al. (1996) and represents about 2000 years of missing time (and sediment?) between about 15.5 and 13.5 <sup>14</sup>C Ka in core OL-90-2 (Benson et al.,

1996). In core OL-84-B, the C–D transition occurs 30 cm above a radiocarbon date of 15.02 ± 0.1 Ka, indicating that, in this core, the hiatus may span only from 14.7 to ~13.5 Ka. Uncalibrated radiocarbon dates used in this paper are reported as thousands of years ago (Ka). According to these chronologies, samples from cores OL-90-1+2 date from 52.5 to 12.7 Ka. Samples from core OL-84-B date between 17.3 and 0.27 Ka.

#### CORES OL-90-1+2

**DIATOMS.**—Freshwater planktonic diatoms numerically dominate most of the OL-90-1+2 record. Saline diatoms only appear near the base of the core at an extrapolated age of about 52.5 Ka (Figure 9). The saline diatom assemblage is an indicator of environmental conditions, including low lake levels, important hydrologic contributions from alkaline, mildly saline springs along the Owens River, and seasonal but reduced input of surface water from the Owens River and tributaries marginal to Owens Lake.

*Cyclostephanos* spp., *Stephanodiscus asteroides*, *S. niagarae*, and *Aulacoseira ambigua* rapidly replaced the saline diatom assemblage by 52.0 Ka and continued to characterize Owens Lake until about 41 Ka when *Stephanodiscus* sp. cf. *S. carconensis* Grunow became the predominant diatom in the lake. Benthic freshwater diatoms (Figure 10) also formed an important part of the assemblage. *Pseudostaurosira*, *Staurosira*, and *Staurosirella* species, hereafter referred to as “*Fragilaria*” species because they once resided in that genus, fluctuated but increased in abundance from 52 Ka until 41 Ka. This trend indicates a progressively greater representation of shallow-water habitats through time and may imply either a gradual shallowing of the lake caused by sedimentation or the establishment of marsh and shallow, freshwater habitats around Owens Lake and upstream along the Owens River. Other benthic diatom ecological groups had less regular fluctuations. These fluctuations in benthic freshwater diatoms, as well as the fluctuations of the planktonic freshwater diatoms, partly reflect percentage control when one or another species, usually a planktonic diatom, became especially abundant, causing the other taxa to decrease to proportionally lower percentages. Nevertheless, high percentages of both groups document limnological changes, which were possibly climate mediated, at comparatively short intervals. *Aulacoseira* spp. and *Stephanodiscus niagarae* assemblages alternated with minor, but approximately regular, increases in *S. asteroides* (Figure 9), perhaps indicating alternations of greater and lesser Sierra Nevada precipitation, respectively. In particular, the five regular pulses of *S. asteroides* between 50 and 43 Ka (Figure 9) indicate a cyclicity of 1.4 Ky, a millennial-scale rhythm (within the limits of chronological control) that has also been observed in marine cores that reflect discharge of cold, ice-bearing water into the North Atlantic Ocean (Bond et al., 1997).

*Aulacoseira ambigua*, *A. granulata*, and *Stephanodiscus niagarae* bloom today in the summer or early fall in intermediate-

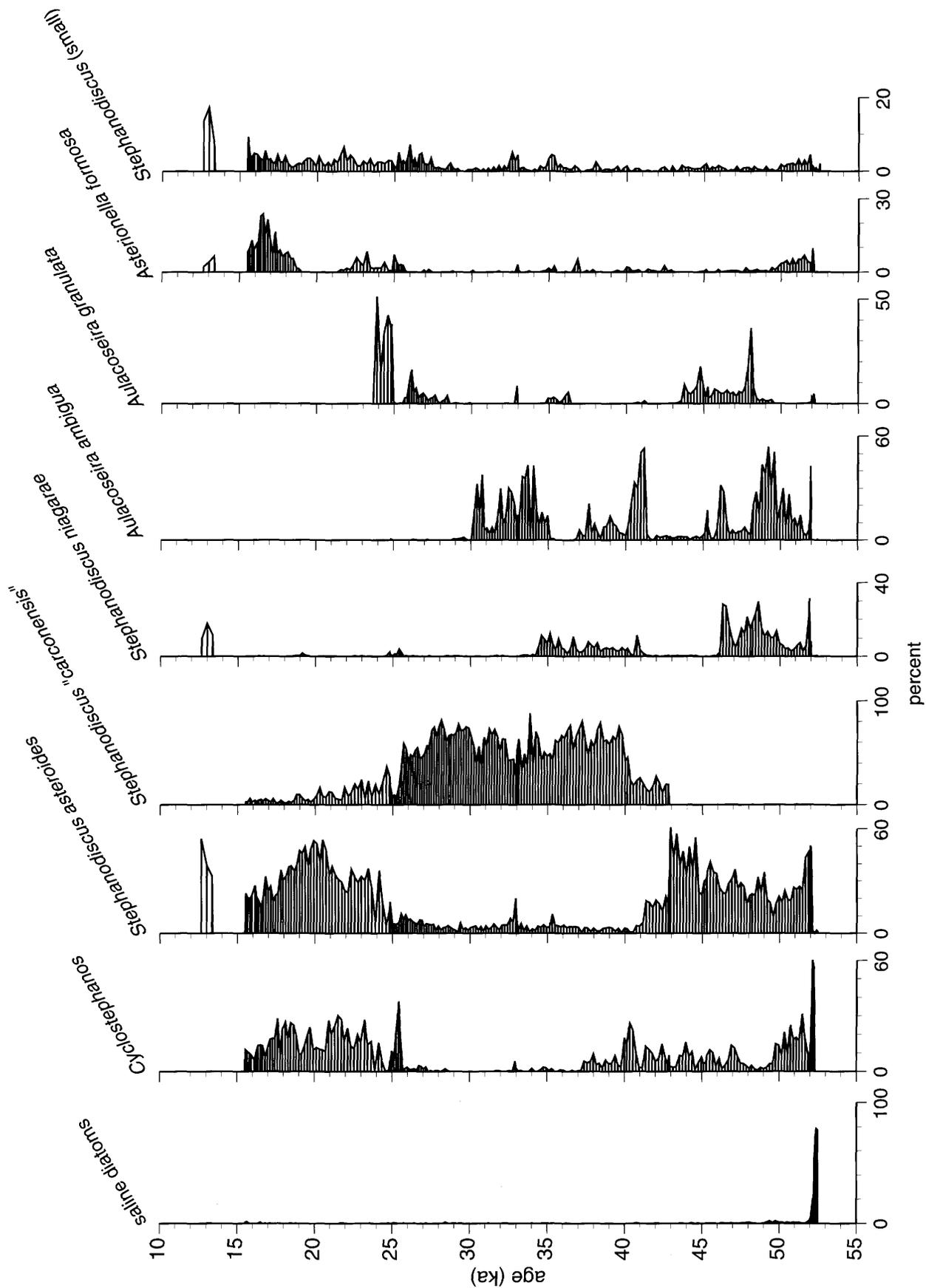


FIGURE 9.—Percentage of all saline diatoms, major centric planktonic diatoms, and *Asterionella formosa* versus age in cores OL-90-1 and OL-90-2 from Owens Lake. *Stephanodiscus* (small) represent taxa allied to *S. minutulus*, *S. hantzschii*, and *S. parvus*.

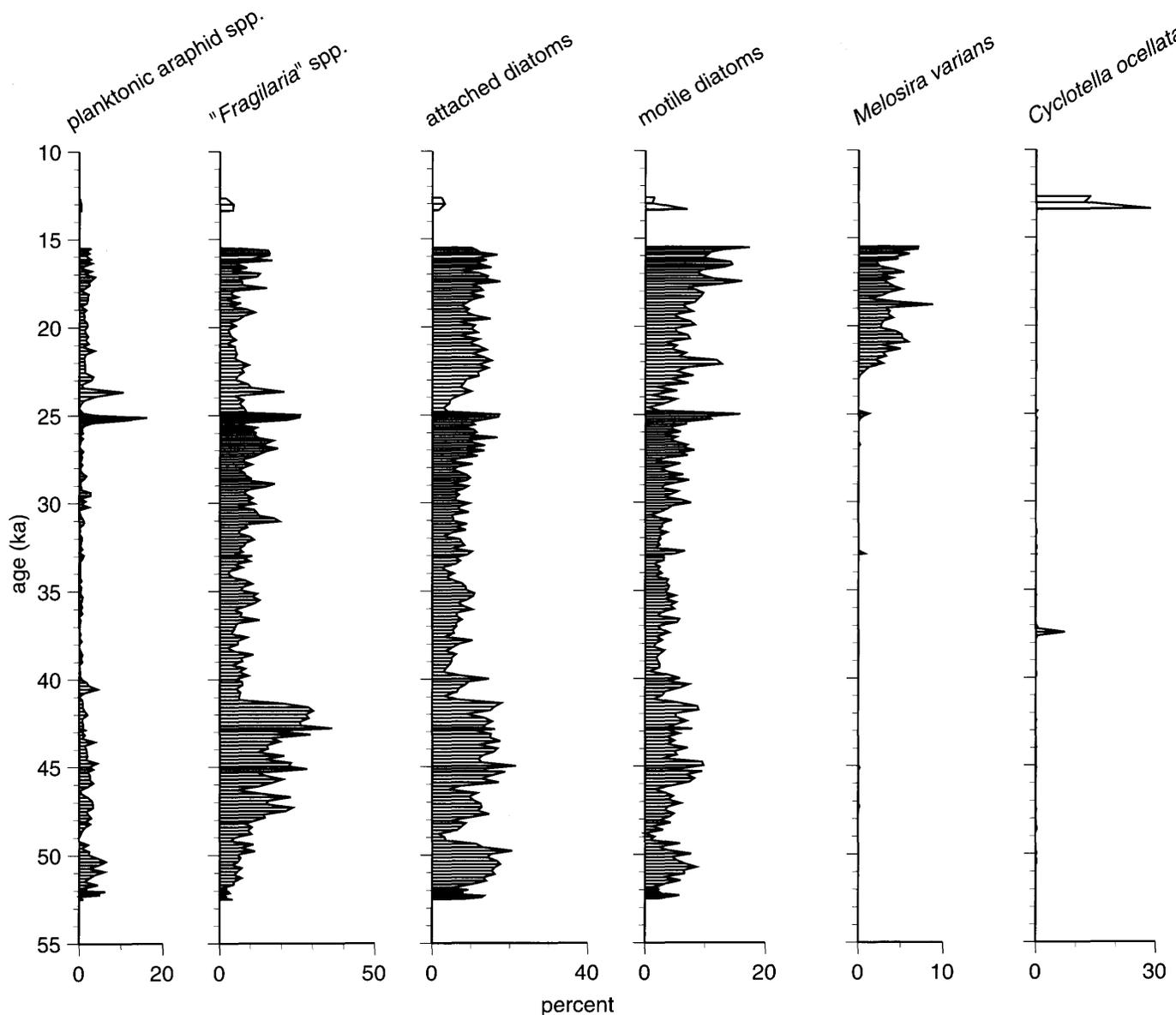


FIGURE 10.—Percentage of minor planktonic and benthic freshwater diatoms versus age in cores OL-90-1 and OL-90-2 from Owens Lake. Planktonic araphid spp. represent *Fragilaria crotonensis*, *F. vaucheriae*, *F. capucina*, *Synedra acus*, and *S. rumpens*. "Fragilaria" spp. include members of *Staurosira*, *Pseudostaurosira*, and *Staurosirella*. Attached diatoms mostly represent *Cymbella*, *Epithemia*, *Cocconeis*, *Achnanthes*, *Gomphonema*, and *Rhoicosphenia*. Motile diatoms mostly represent *Navicula* and *Nitzschia*.

elevation lakes (1000 to 1300 m above Owens Lake) in the Sierra Nevada (Figure 8). These diatoms require freshwater conditions (generally <1000 mg TDS/L) during the summer; thus, their presence implies the existence of temperate to warm-temperate environments and water bodies that have sufficient hydrologic input to offset evaporative losses. Consequently, these analogs indicate periods of temperate, but moist, climate at Owens Lake between 52 and 24 Ka (Figure 9). Although the episodes characterized by *Aulacoseira* spp. do not form a particularly coherent signal, their waxing and waning indicates

multi-millennial scales of climate variability that also has been documented in the North Atlantic Ocean (Heinrich, 1988).

After 40 Ka, *Stephanodiscus* sp. cf. *S. carconensis* Grunow, hereafter referred to as *S. "carconensis"*, dominates the diatom record of Owens Lake. Its coherent stratigraphy defies an obvious interpretation; however, the persistence of associated minor diatom taxa before, throughout, and after the *S. "carconensis"* zone indicates there was no major change in lake ecology. As with other large species of *Stephanodiscus*, the morphology of *S. "carconensis"* indicates a planktonic habitat,

but it provides no evidence about seasonal dynamics. This taxon is now apparently extinct; rare records of *S. carconensis* Grunow from modern diatom collections probably represent contamination or misidentification (Bradbury, 1991).

Other paleolimnological and paleoecological data provide insights into the limnology of Owens Lake when *S. "carconensis"* predominated (43–25 Ka). High organic-carbon values (2%–4%) in this interval (Benson et al., 1996) as well as the great abundance of diatoms in the sediment (Bradbury, 1997a) indicate lake productivity had been moderate to high and may have resulted in periodic bottom-water anoxia. The absence of ostracodes in samples from the *S. "carconensis"* zone also could reflect seasonal anoxia in Owens Lake at that time. Lowenstein et al. (1997) reported halite crystallization air temperatures at 34–25 Ka (obtained from core samples from Death

Valley) that were 8°–15° C below modern air temperatures in Death Valley. These lower crystallization air temperatures likely reflect the cool temperatures during springs and summers when halite generally crystallizes from this system. The modest heavy-mineral content between 43 and 27 Ka in cores OL-90-1+2 (Figure 11) indicates decreased alpine glacial activity compared with later in the record. Consequently, the volume of Owens River discharge may have been low during this period. Pollen evidence (Woolfenden, 1996) also indicates cool, but relatively dry, summer climates prevailed, whereas the presence of *Yucca brevifolia* Engelman (Joshua tree) in association with *Juniperus osteosperma* (Torrey) Little in the Alabama Hills packrat midden at 31 and 26 Ka (Koehler and Anderson, 1994) indicates warmer winters than today, at least at those times. Together, these data indicate that from 43 to 25

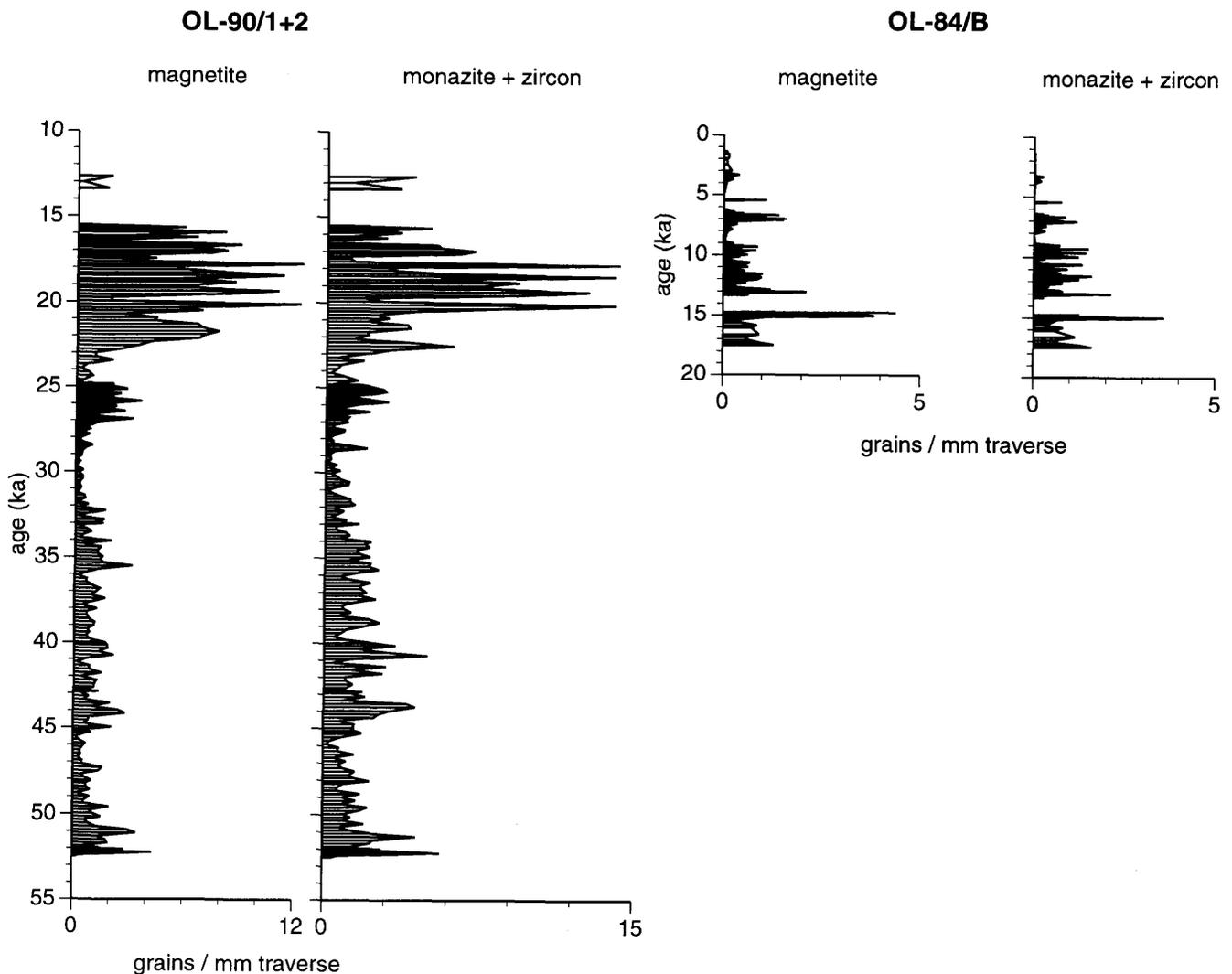


FIGURE 11.—Concentration of heavy-mineral grains versus age in cores OL-90-1+2 and OL-84-B.

Ka Owens Lake probably stratified during the summer after productive fall and spring seasons when lake circulation would have provided abundant nutrients to support large diatom blooms. Perhaps *S. "carconensis"* predominated during the fall circulation phase in monomictic Owens Lake just as the similar-sized *S. niagarae* does in Crowley Reservoir today.

By 24 Ka, *Stephanodiscus asteroides* and *Cyclostephanos* sp. returned to predominance, whereas *S. "carconensis"* decreased to low numbers and *Aulacoseira* species disappeared (Figure 9). *Melosira varians*? Agardh became common throughout the remainder of the record (Figure 10). The peak in abundance of *Stephanodiscus asteroides* and the presence of large numbers of heavy-mineral grains in the sediments at about 20 Ka mark the existence of full-glacial conditions (Figure 11). At that time, Owens Lake probably had sufficient winter ice cover to behave as a dimictic lake, with the water circulating after ice breakup and again before freezing, as do many temperate lakes today. The diatom assemblages in Owens Lake during the full-glacial period are typical of species that have late winter (during and after ice breakup) and spring production. Presumably, glacier meltwater entering the basin during the summer and fall rendered the lake too turbid to support diatom photosynthesis during those seasons (Bradbury et al., 1994). The diatom identified as *Melosira* sp. cf. *M. varians* may represent a thick-walled form, perhaps a resting spore, of extant *M. varians*. This form apparently has not been found in modern aquatic systems, although a similar diatom has been found in late Pleistocene deposits at Kenai, Alaska (McLaughlin and Stone, 1986, pl. 7: fig. 114). *Melosira* sp. cf. *M. varians* probably occupied the same habitat as *M. varians*, which today lives in shallow, littoral regions of lakes and low-gradient reaches of streams and rivers. The variant's presence in the Owens Lake stratigraphy during the full- and late-glacial periods probably relates to increased input from shallow-water riverine and lake-margin water sources.

Late-glacial limnologic changes at Owens Lake (18–15.5 Ka) were marked by an increase in *Asterionella formosa*. This increase in abundance implies a favorable open-water environment (less turbid) existed during the summer and early fall, according to the distribution of this species in Sierra Nevada lakes today. For example, *A. formosa* numerically dominated plankton net hauls in Mary, Lundy, and Grant Lakes during June 1996, whereas it was numerically subdominant (38%) in the September 1994 collection in Upper Twin Lake (J.P.B., unpublished data).

A hiatus interrupts the OL-90-1+2 sediment record at 15.5 Ka. Sedimentation resumed shortly before 13 Ka with abundant *Cyclotella ocellata* and *Stephanodiscus niagarae* (Figures 9, 10), indicating a correlation to the post-hiatus interval of core OL-84-B.

OSTRACODES.—The OL-90-1+2 ostracode record begins at about 52.5 Ka with large numbers of *Limnocythere ceriotuberosa* and *L. sappaensis* (Figure 12). These species are indicators of alkaline, saline, shallow water, and their presence sug-

gests that the climate of Owens Lake and its immediate drainage was arid to semiarid at that time. Under such climates, strong, basin-floor evaporation rates, and decreased snowpack in the Sierra Nevada, the Owens River would have been unable to maintain a deep and overflowing lake system. Like today, alkaline-rich springs along the Owens River and around the lake would have contributed substantially to the hydrochemistry of the lacustrine environment. Closed-basin conditions at this time also were documented by geochemical data in another Owens Lake core (Bischoff et al., 1997a).

*Limnocythere bradburyi* Forester, a warm-climate, hydrochemical and ecological equivalent of *L. ceriotuberosa*, became common during one short interval after the predominance of *L. sappaensis*. Its abundance documents a brief period (~300 yrs) when the lake became deeper as a result of increased discharge from the Owens River. Because this ostracode is cold sensitive (Forester, 1985; Smith and Forester, 1994), it indicates that increased discharge began when climates were still warm (winter temperatures above 0° C).

At 52 Ka, *Limnocythere ceriotuberosa* and *Candona caudata* characterize the ostracode record. Their abundance documents an abrupt increase in Owens River discharge into the basin (Figure 12). As lake levels rose and salinity decreased, the variable lacustrine environments preferred by *L. ceriotuberosa* disappeared, and *C. caudata* and small numbers of *Limnocythere* sp. aff. *L. itasca* Cole remained. The change in abundance from *L. ceriotuberosa* to *C. caudata* identifies a change from highly seasonal discharge to a more continual discharge. The more consistent discharge probably, in part, reflected low summer air temperatures, which caused slower snow melt and decreased evaporative loss, and resulted in a spilling lake that had a stable volume. *Candona caudata* and *Limnocythere* sp. aff. *L. itasca* make pulse-like reappearances in the record for the next 10 Ky, approximately matching the minor fluctuations of *Stephanodiscus asteroides* described above. Although not perfectly cyclic, the average recurrence times for these pulses is 1.4 Ky, matching the millennial-scale climate oscillations recorded in high-resolution marine cores from the North Atlantic Ocean (Bond et al., 1997). In this case, the pulses of *C. caudata* and, to a lesser extent, of *Limnocythere* sp. aff. *L. itasca* apparently mark brief episodes of cooler temperatures and increased river input to Owens Lake.

Between 40 and 24 Ka, the Owens Lake record lacks ostracodes (Figure 12), perhaps because unfavorable (anoxic) lake-bottom conditions precluded ostracodes or dissolved their calcareous carapaces in the sediments. At 24 Ka, however, *Candona caudata* reappears in the core with large numbers of *Cytherissa lacustris*. This assemblage persisted until about 21 Ka and reappeared briefly in small numbers at about 19 Ka. These ostracodes, particularly *C. lacustris*, indicate the limnologic conditions were very cold but reasonably stable. According to the modern distribution of *C. lacustris*, its presence in Owens Lake during the full-glacial period implies that polar air masses were present year-round at the latitude of Owens

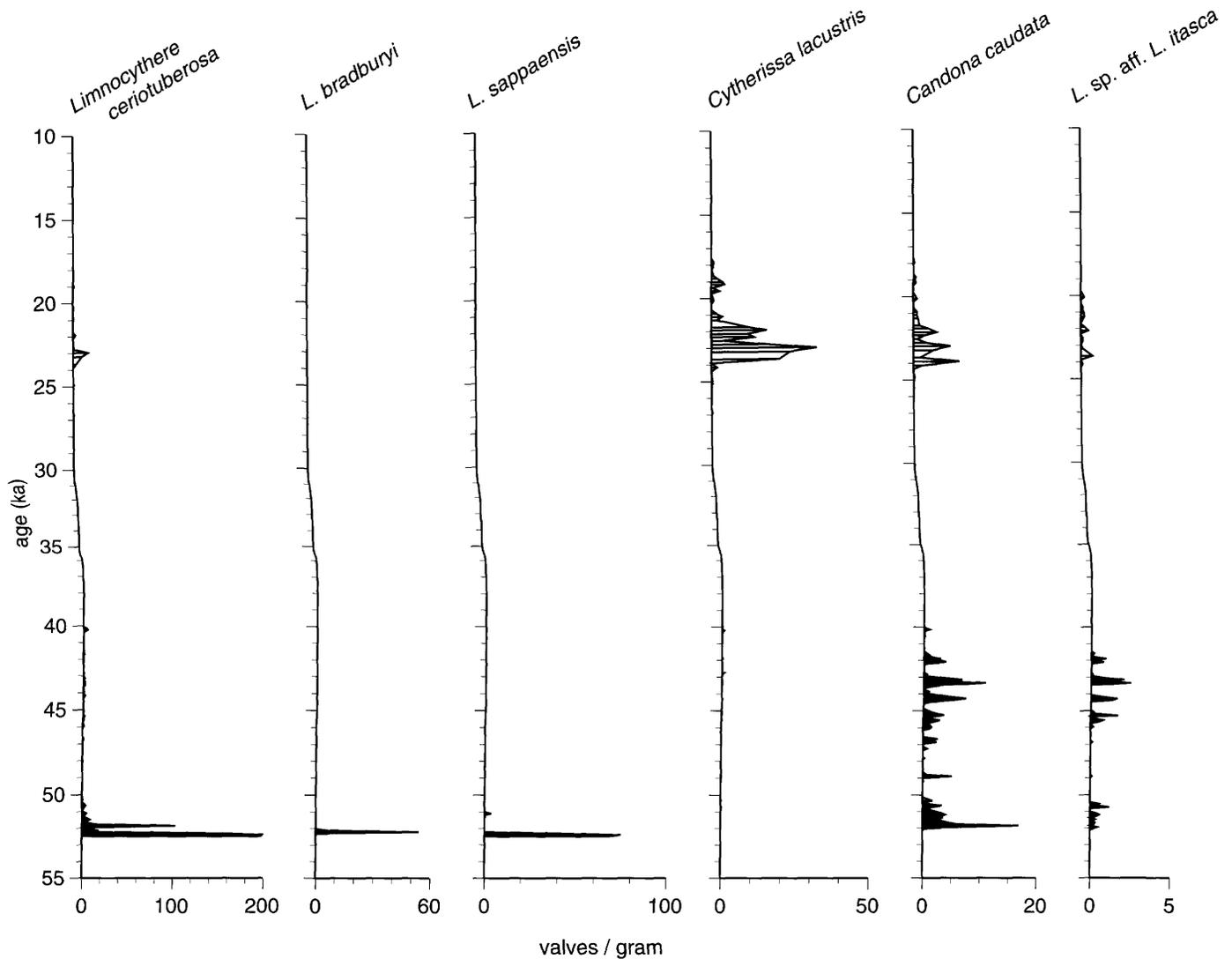


FIGURE 12.—Concentration of ostracode valves versus age in cores OL-90-1+2 from Owens Lake.

Lake. The residence of such cold air masses would have maintained seasonally stable climatic and limnologic environments.

#### CORE OL-84-B

**DIATOMS.**—Freshwater planktonic diatoms are predominant in core OL-84-B from the base of the core (extrapolated age of 17.3 Ka) until the break in sedimentation at 14.7 Ka (Figures 13–15). *Stephanodiscus asteroides*, *Asterionella formosa*, and *Cyclostephanos* sp. characterize this assemblage (Figure 13) and indicate that fresh, open-water limnological conditions prevailed in the spring (*S. asteroides*), summer (*A. formosa*), and winter to early spring (*Cyclostephanos*). The large *Stephanodiscus* species, *S. "carconensis,"* also is present in this late-glacial assemblage, but it may have been reworked from sediments surrounding Owens Lake that predated the full-glacial period (Figure 9).

Freshwater benthic diatoms also are conspicuous in the late-glacial part of core OL-84-B and imply there was substantial water input from littoral, marginal areas of the ancient lake (Figure 13). Collectively, benthic diatoms make up 46 percent of the late-glacial assemblage. The relationship between lake depth and benthic diatom percentages among lakes in the eastern Sierra Nevada has considerable scatter (Figure 16) because of the variable efficiency of the lakes' currents to redeposit benthic diatoms. Nevertheless, shallow lakes generally contain greater numbers of benthic diatoms because illuminated, shallow-water habitats characterize these systems. The high percentages of benthic diatoms in the post-glacial period of core OL-84-B imply lake depths generally were shallower than 30 m; these freshwater benthic diatoms also indicate that Owens Lake must have spilled at this time. The shallow lake depths probably resulted from high, full-glacial sedimentation

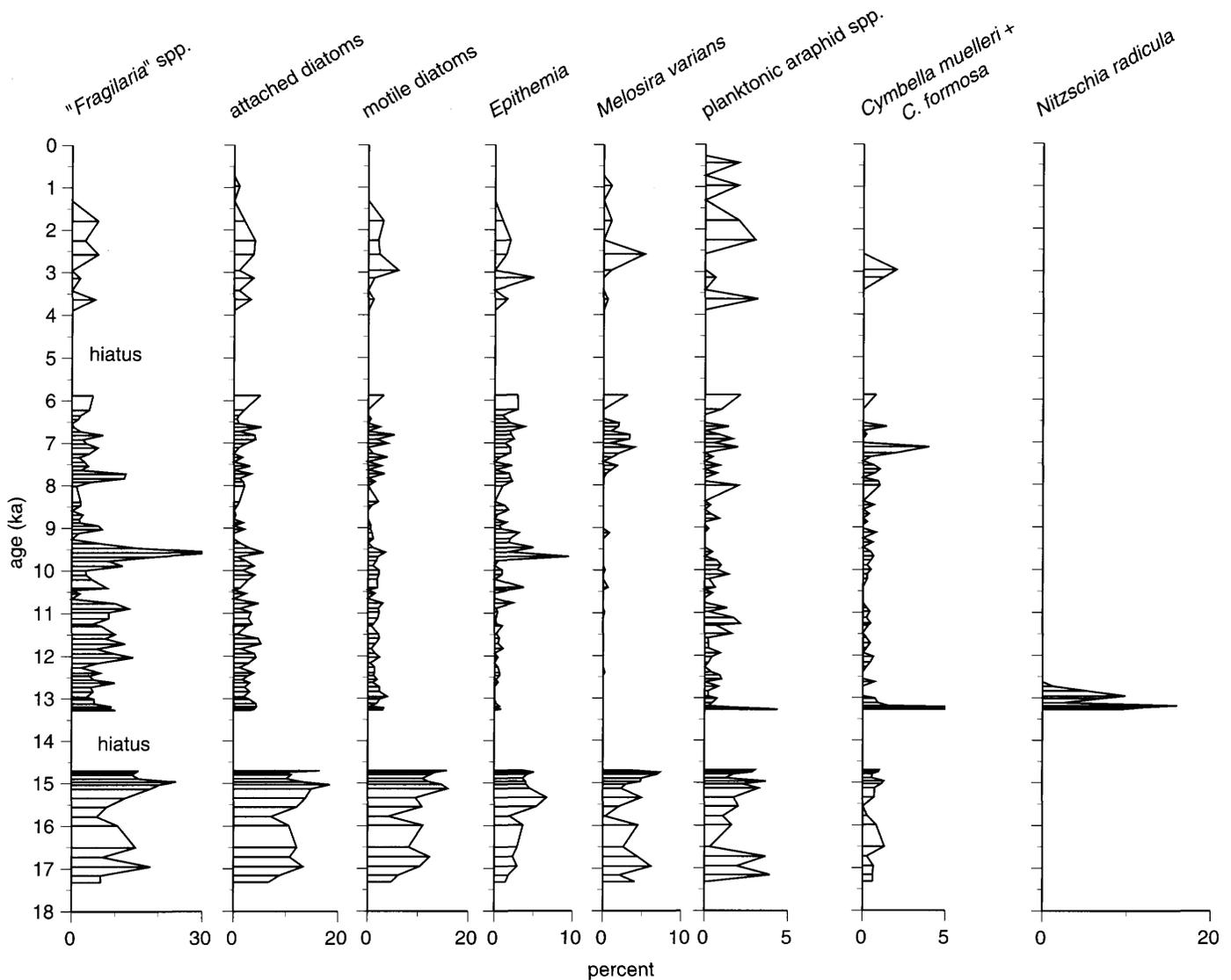


FIGURE 13.—Percentages of diatom ecologic groups and selected benthic diatoms versus age in core OL-84-B. See Figure 10 for explanation of silhouette headers.

rates, which decreased the basin's water capacity after the Tioga glaciation. An erosional hiatus between 14.7 and 13.5 Ka, as reflected in the sediments from cores from this part of the Owens Lake basin, may have resulted from increased resuspension of sediments from the bottom of the shallow lake. Benson et al. (1996) suggested lake desiccation and subsequent deflation as the cause of this erosional hiatus. Although diatom stratigraphy indicates modest lake depths, it does not document the increased salinity that would have preceded desiccation; however, deflation may have removed all traces of that episode. Alternatively, a flood of fresh, sediment-laden water could have scoured previously deposited sediments from the Owens Lake basin (J.P. Smoot, pers. comm. to J.P.B., 1997). A sediment unit called the Parting Mud in Searles Lake, which is down-river from Owens Lake, documents the continuous depo-

sition of dolomite, aragonite, and calcite laminae between 17.1 and 10.5 Ka (Smith, 1979; Benson et al., 1990), which would have required at least some overflow from Owens Lake. The origin and importance of the hiatus needs further study. The widespread hiatus in Owens Lake records may reflect a combination of morphometric, climatic, hydrologic, and possibly tectonic events.

After the erosional hiatus (13.4 Ka), the Owens Lake basin received silty sediment containing the same freshwater planktonic diatom species present before the hiatus. Oscillating peaks of *Stephanodiscus asteroides* characterize this assemblage. *Stephanodiscus niagarae* initially became abundant, and *Cyclotella ocellata* increased shortly thereafter (Figure 14). These diatoms currently bloom in the summer or early fall in Sierra Nevada lakes (Figure 8) and indicate that Owens Lake was less

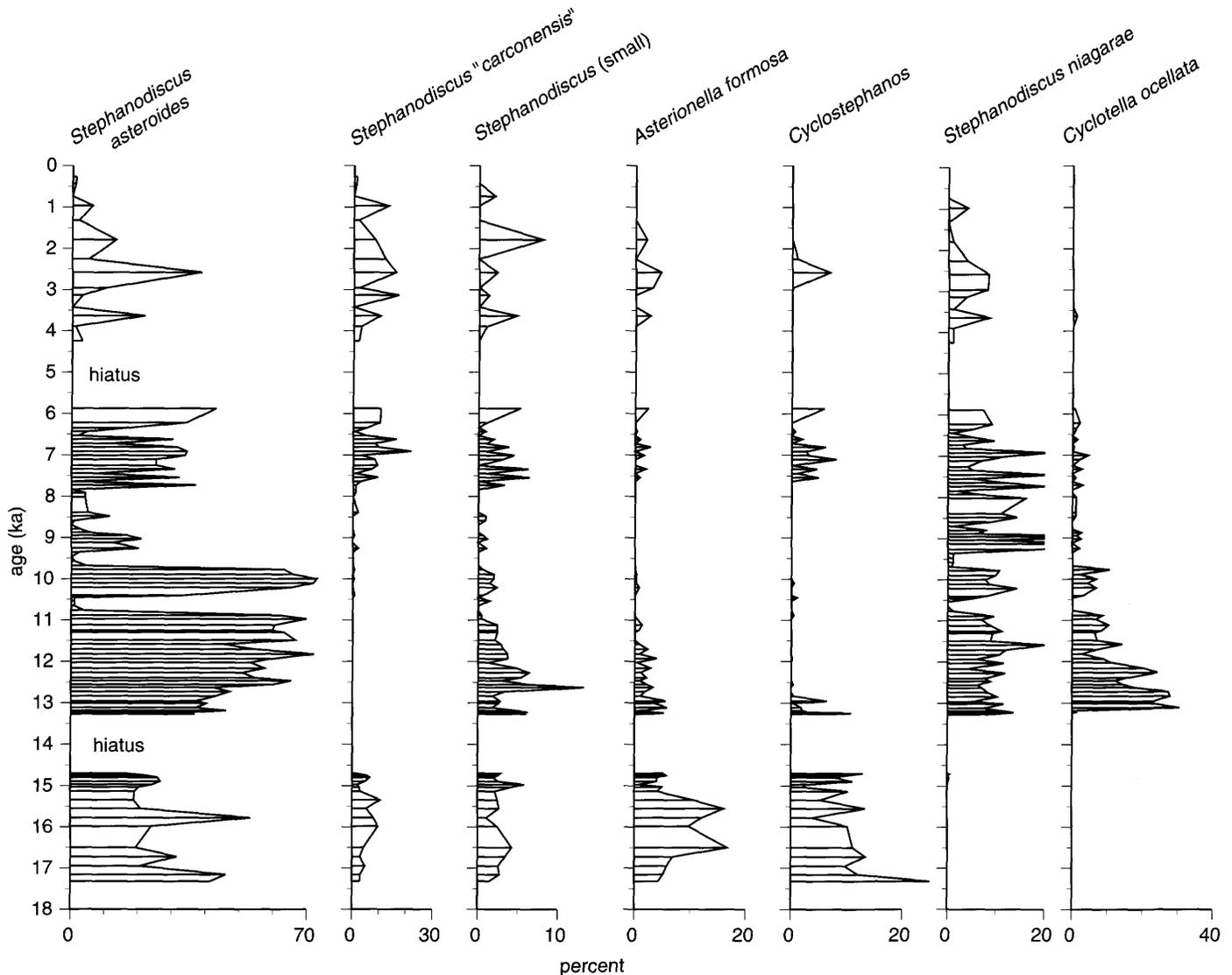


FIGURE 14.—Percentages of selected planktonic freshwater diatoms versus age in core OL-84-B. See Figure 10 for explanation of silhouette headers.

turbid and received more continuous Owens River discharge during the summer and fall than it did before 13.4 Ka. Melting alpine glaciers during the summer may have contributed substantially to the Owens River discharge. This lacustrine phase lasted until shortly after 11.0 Ka and may document the final disappearance of large alpine glaciers in the Sierra Nevada.

Two benthic freshwater diatoms, *Nitzschia radicularis* Hustedt and *Cymbella formosa* Hustedt, characterize the sediments initially deposited in Owens Lake after 13.4 Ka (Figure 13). *Cymbella formosa* is morphologically and ecologically similar to *Cymbella muelleri*, which is widely distributed in shallow-water habitats of lakes and in streams east of the Sierra Nevada (Figure 7). This species usually lives firmly attached to the submerged stems of aquatic vegetation or to other suitable substrates (wood, stones) in mucous mats or coatings as an adapta-

tion to resist dislodgment by currents (Peterson, 1996). *Nitzschia radicularis* lives among submerged plant stems on the bottom of shallow, macrophyte-rich ponds, marshes, and small lakes (Cumming et al., 1995).

The presence of these benthic diatom taxa in core OL-84-B after 13.4 Ka implies there was substantial hydrologic input to Owens Lake from the Owens River and marginal habitats (possibly marsh environments at the head of Owens Lake or upstream in the Owens Valley), because these diatom species would not have lived in large numbers in the deep, open-water habitats of the lake itself. Perhaps these redeposited riverine and marsh diatoms recorded the diminishing effects of a flood that eroded the bottom of Owens Lake and initiated the hiatus.

After 12.5 Ka, planktonic freshwater diatom assemblages predominated until 10.9 Ka when saline, shallow-water diatom

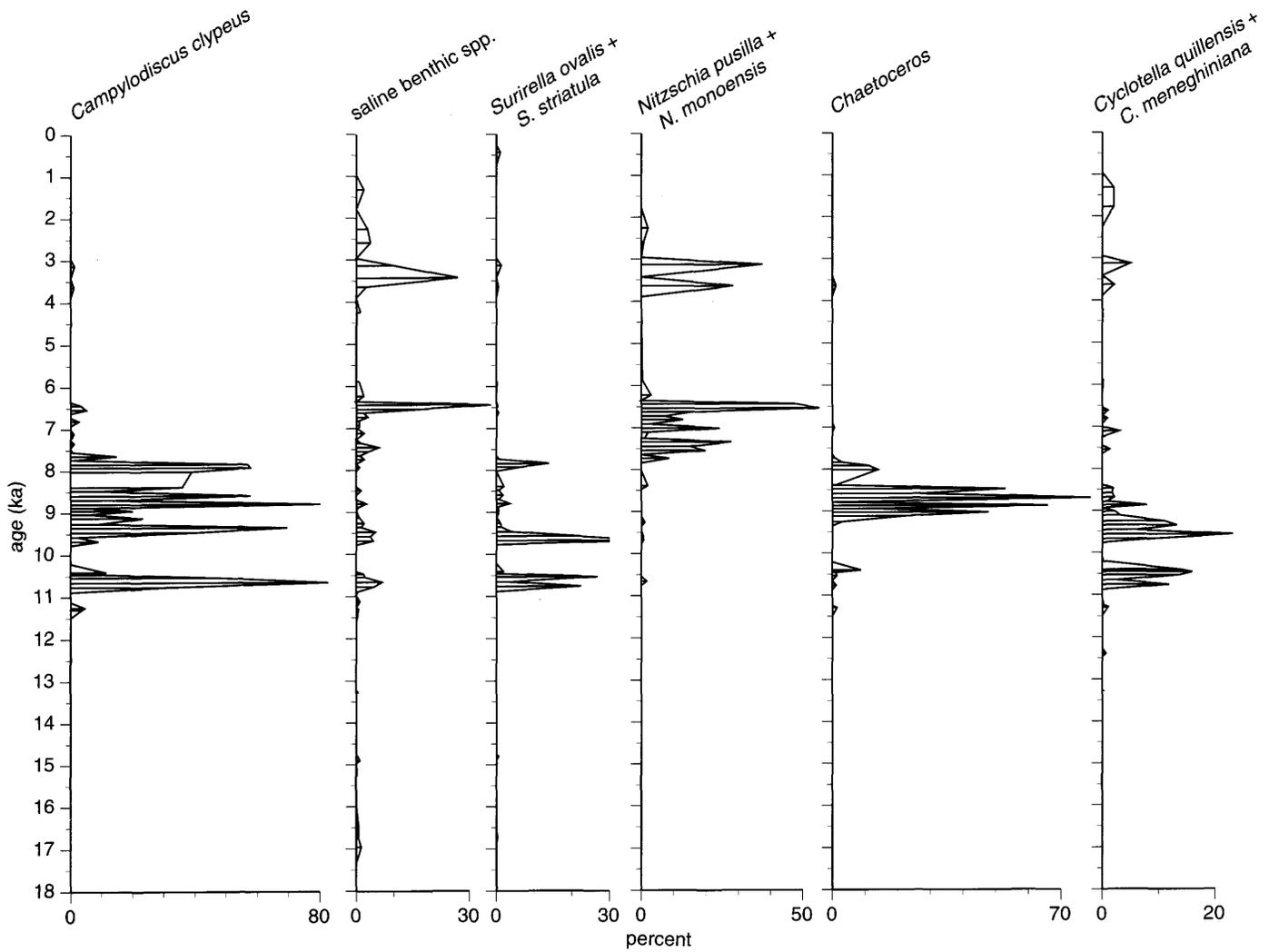


FIGURE 15.—Percentages of selected saline diatoms versus age in core OL-84-B. Saline benthic species include *Amphora coffaeiformis*, *Anomoeoneis sphaerophora*, *Navicula crucialis*, *N. halophila* (Grunow) Cleve, *Nitzschia frustulum*, *Rhopalodia gibberula* (Ehrenberg) O. Müller, *R. acuminata*, and *Surirella hoefleri*.

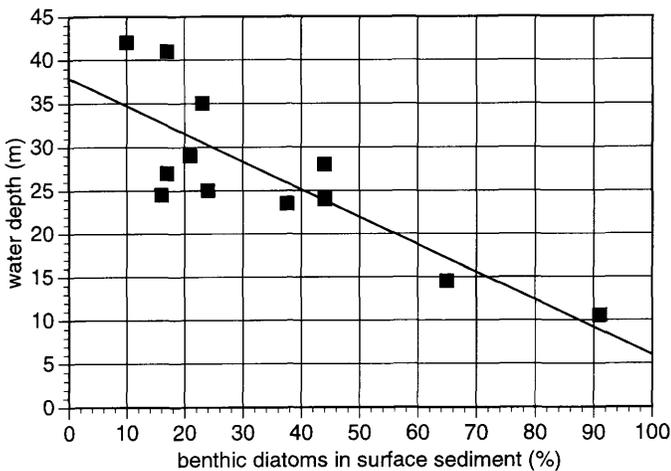


FIGURE 16.—Percentage of benthic diatoms in surface sediment versus water depth in selected Sierra Nevada freshwater lakes.

assemblages suddenly appeared (Figure 15). *Campylodiscus clypeus*, a benthic species of alkaline and moderately saline habitats, predominated; the assemblage also included small percentages of benthic *Surirella ovalis* and *S. striatula* and planktonic *Cyclotella meneghiniana* and *C. quillensis*. Collectively, this assemblage indicates lake salinities were 3–10 g/L and alk/Ca ratios were >4. This short-term (500 year) saline event ended by 10.4 Ka when freshwater planktonic diatoms returned to predominance for about 800 years (Figures 14, 15). This freshwater phase in Owens Lake may correlate with sedimentological evidence for an early Holocene lake at Silver Lake playa, about 200 km southeast of Owens Lake, that existed just before 9.3 Ka (Enzel et al., 1989).

After 9.6 Ka, the record of saline diatoms in Owens Lake becomes more continuous (Figure 15). A short interval (9.4–8.5 Ka) of mixed freshwater and saline diatom assemblages, including large numbers of *Chaetoceros* sp., documents a transition to

higher lake salinity and indicates arid climate. Today, *Chaetoceros* is an open-water planktonic diatom that is common in Pyramid and Walker Lakes (Figure 6). Its wide salinity tolerance (Fritz et al., 1993) may indicate that Owens Lake remained fairly deep during this short interval. The freshwater planktonic diatom (*Stephanodiscus* spp.) component of this assemblage (Figure 14) could have prospered in the lake seasonally when spring runoff sufficiently diluted salinities or during short periods when the lake spilled and became fresh.

After 8.5 Ka, benthic saline species, such as *Campylodiscus clypeus*, persisted in the extensive shallow-water habitats created by low lake levels. By 8 Ka, saline *Nitzschia* species (*Nitzschia latens*, *N. pusilla*, *N. monoensis*), which presently inhabit very saline, shallow-water habitats in Mono Lake and similar environments (Kocielek and Herbst, 1992; Blinn, 1993), became prominent in response to a substantial decrease in Owens River flow, a proportional increase in alkaline spring discharge, and high evaporation rates. Owens Lake remained saline and shallow until about 6.5 Ka when, according to the radiocarbon chronology, the lake desiccated and clastic sedimentation ended (Benson et al., 1997). Sedimentation of oolitic sand resumed after 4.3 Ka, and freshwater and saline diatoms are sparsely represented in core OL-84-B by fragments of corroded valves (Figures 13–15). The presence of freshwater planktonic and benthic diatoms in samples from after about 8 Ka may have resulted from the reworking of diatomaceous highstand deposits left behind as Owens Lake shrank. These reworked diatoms do, however, indicate episodic fluxes of water into the basin that may reflect flooding during very wet years (Smith et al., 1987). Saline benthic diatoms, including the *Nitzschia* species of very saline habitats, returned between 4 and 3 Ka.

In-situ diatom productivity certainly occurred throughout the late Holocene in Owens Lake, but, generally, high lake alkalinities and salinities combined with episodic desiccation likely destroyed sedimented diatoms by dissolution and breakage.

**OSTRACODES.**—Except for isolated, presumably reworked valves of *Cytherissa lacustris* from highstand, full-glacial deposits (Figure 17), core OL-84-B has no substantial late-glacial (15–12.5 Ka) ostracode record. Decreased inflow from the Owens River and a climate regime of increased summer insolation would have promoted lake stratification, and seasonal anoxia may have eliminated ostracode habitats in the central regions of the Owens Lake basin. The presence of ostracodes, however, would have indicated that shallow and saline lake conditions existed between 15.5 and 13.5 Ka, but those deposits could have been removed by erosion.

At 11.5 Ka, *Limnocythere ceriotuberosa* appeared (Figure 17); its presence indicates this was a time of variable lacustrine conditions associated with seasonal filling and freshening of Owens Lake that was followed by lake evaporation, concentration, and shrinkage. Larger pulses of *L. ceriotuberosa*, accompanied by *Candona caudata*, occurred from 11.0 to 10.5 Ka and from 9.9 to 9.5 Ka. These ostracode pulses approximately coincided with the shallow-water, moderately saline lake envi-

ronments evidenced by the diatoms, particularly "*Fragilaria*," *Campylodiscus clypeus*, *Surirella* spp., and *Cyclotella* spp. (Figures 13–15). The maximum salinity tolerance of *Candona caudata* (3 g/L) and the low (or absent) representation of *Limnocythere sappaensis* also indicate Owens Lake had only modest salinity at those times, although the diatoms and *L. ceriotuberosa* can tolerate considerably higher salinities. These pulses in the fossil record probably record episodes when the Owens River flooded the basin to produce short-lived, reasonably fresh, shallow lake systems. Near the mouth of the Owens River, at an elevation of 1097 m, coarse deltaic sands that have a freshwater molluscan fauna, including the river clam *Anodonta californiensis* Lea (dated at 11.4 Ka), also indicate riverine environments occurred at the north end of Owens Lake (Koehler, 1995).

The large number of *Limnocythere sappaensis* by 9.4 Ka indicates increased salinity and a high alk/Ca ratio. The lake may have become shallower, although this ostracode can live in deep lakes as well. The absence or low abundance of ostracodes between 9.4 and 8.8 Ka in the section of core having abundant *Chaetoceros* may indicate a deeper lake was present at that time, perhaps with seasonally anoxic bottom water.

Progressively larger pulses of *Limnocythere ceriotuberosa* characterized the millennium between 8.8 and 7.8 Ka (Figure 17), documenting a return to lacustrine environments that had variable depths and salinities. Large quantities of *Heterocypris* appeared near the end of this episode. Today, this species resides in springs and seep-fed marsh environments. Its presence between 8.8 and 7.8 Ka implies that Owens Lake had shrunk considerably and was surrounded, at least near the mouth of the Owens River, by marsh communities. The marshes probably were dominated by *Scirpus*, which presently grows abundantly along the Owens River, within the valley, and along the margins of playa springs (Höllermann, 1973).

*Limnocythere sappaensis* dominated the ostracode assemblage from 7.7 to 6.5 Ka. Occasional *Cytherissa lacustris* in this interval resulted from the reworking of highstand lake sediments deposited during the last glacial maximum (Carter, 1997). During this time, saline, alkaline springwater issuing along the Owens River and around Owens Lake probably had a major effect on the hydrochemistry of the lake, although surface water from Sierra Nevada snowmelt continued seasonally to enter the basin. *Nitzschia pusilla* and *N. monoensis* (Figure 15), which tolerate highly saline environments, such as at Mono Lake today, coexisted with *L. sappaensis*.

*Limnocythere sappaensis* remained prominent after the hiatus in sedimentation (6.1–4.3 Ka) (Figure 17), as did benthic saline diatoms and *Nitzschia* spp. (Figure 15). These saline lake assemblages persisted until about 3 Ka, when diatoms occurred only as rare, reworked fragments and ostracodes disappeared from the Owens Lake record; however, in core OL-92-3, oolitic sediment, radiocarbon dated between 5.3 and 5.0 Ka (Bischoff et al., 1997c), had abundant *L. sappaensis*, which indicates

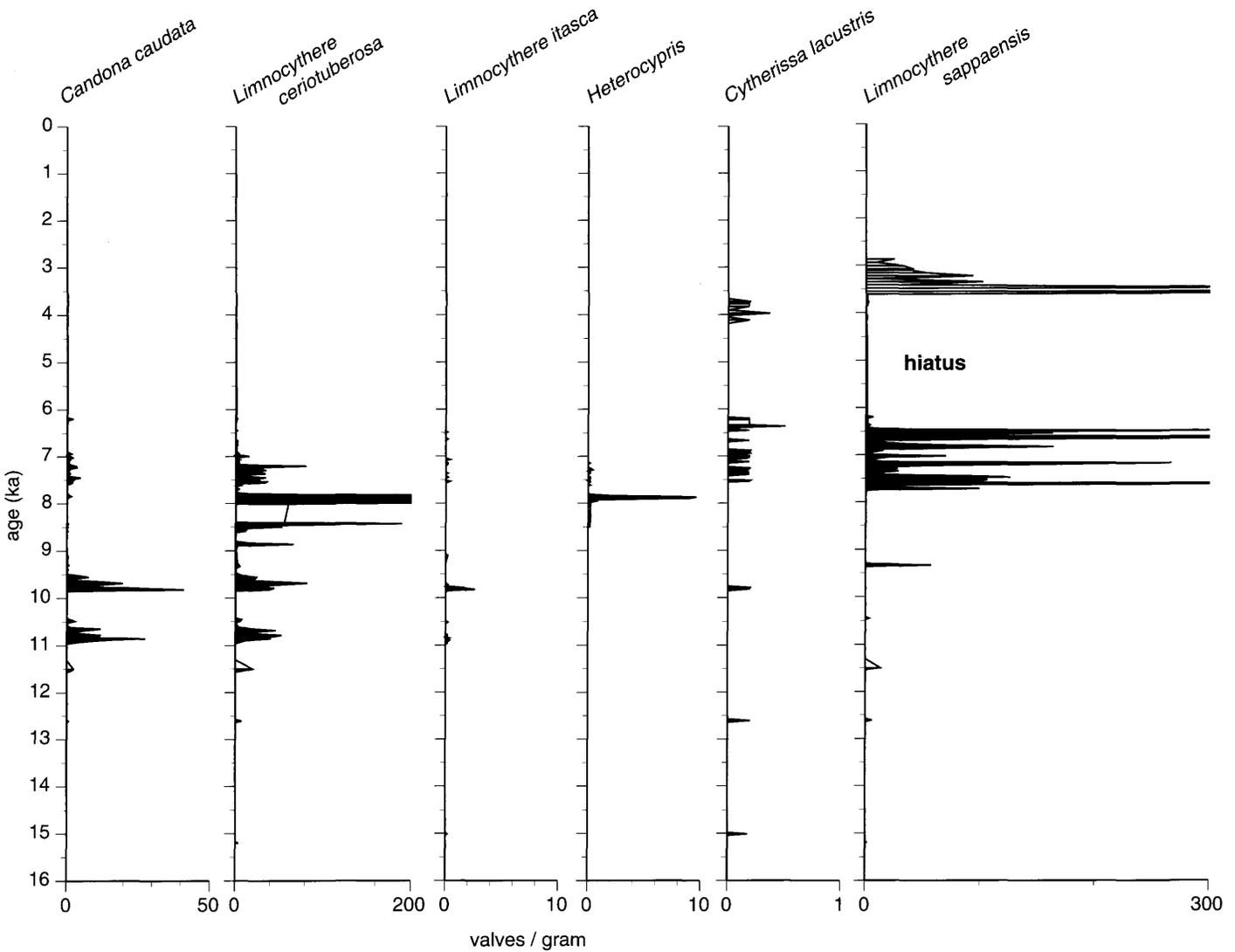


FIGURE 17.—Concentration of ostracode valves versus age in core OL-84-B.

some sedimentation occurred in Owens Lake during the middle Holocene drawdown, at least at the site of core OL-92-3.

**Discussion**

The diatom and ostracode records from the middle Wisconsin to the late Holocene at Owens Lake provide the most continuous paleontological evidence for changing limnological and climatic environments in the southern Great Basin. Because this important record relates to the glacial and vegetational history in this region, it can provide a chronological framework for local glaciation and for isolated vegetation assemblages found in packrat middens. Conversely, the nonlacustrine evidence of climate change from packrat middens and glacial records can refine climate interpretations from lacustrine microfossils.

RECORD OF GLACIATION.—Owens Lake cores OL-90-1+2 and OL-84-B record the timing and intensity of Sierra Nevada alpine glaciation in the Owens River basin. The substantial quantity of heavy-mineral fragments (magnetite and zircon + monazite) in diatom slides (Figure 11) indicates that glacial erosion of the Sierra Nevada granitic plutons occurred. These minerals were incorporated into the base load of the Owens River. The middle Wisconsin period (~54 to ~25 Ka), or oxygen isotope stage (OIS) 3, for the most part, had small, isolated heavy-mineral peaks that may represent minor high-elevation glaciation at 52–51, 44, 40, 35, and 26 Ka. The absence of the boreal ostracode *Cytherissa lacustris* during these periods, however, indicates that severe glacial climates did not affect Owens Lake. In fact, the presence of the warm-season diatoms *Aulacoseira* spp. during most of these periods seems inconsistent with extensive glaciation. These minor peaks in heavy-

mineral concentration may simply have recorded years or decades of exceptional runoff down the Sierra Nevada drainages. Nevertheless, geochemical evidence of glacial-rock flour from Owens Lake core OL-92-1 (Bischoff et al., 1997b), taken in the same area of the basin, approximately correlates with most of the heavy-mineral peaks shown in Figure 11 and supports the interpretation that these peaks represent minor Sierra Nevada glaciations.

The heavy-mineral peaks (Figure 11) approximately correlate with the magnetic-susceptibility and organic-carbon evidence of glaciation recorded by Benson et al. (1996). The magnetic-susceptibility and organic-carbon records, however, contained more peaks, which were interpreted by Benson et al. (1996) as glacial advances, than are present in the heavy-mineral record. Uncertain equivalencies between radiocarbon and calendar years make correlations to  $^{36}\text{Cl}$ -dated moraines (Phillips et al., 1996) problematic; however, the potential glacial advance at about 51 Ka, which perhaps correlates to the younger Tahoe moraines, also may correlate with the double peak in heavy minerals between 52 and 51 Ka (Figure 11). The Tioga 1 stage moraines, which were dated to 32–30 calendar Ka (Phillips et al., 1996), may correspond to heavy-mineral peaks at 27–25 Ka in core OL-90-1+2, assuming an approximate 4 Ky correction to equate the radiocarbon and calendar chronologies. The episodes defined by high concentrations of heavy minerals generally correspond to perennial lake stages in Searles Lake. The mineralogical evidence of a 5° C cooling in Searles Lake at 26–25 Ka (Smith, 1979:89) might corroborate the occurrence of a glacial period at that time.

According to the heavy-mineral record from cores OL-90-1+2 (Figure 11), glaciation during OIS 2 (the last major glacial period) began by 23 Ka. The heavy minerals continued to increase, but with sharp fluctuations, until about 18 Ka when their values decreased, again with strong fluctuations between greater and lesser quantities. In contrast to the Tioga 1 moraines, the Tioga 2 and 3 (glacial maximum) moraine dates (Phillips et al., 1996) correspond closely to the heavy-mineral record of glaciation. The large and persistent peak in magnetite grains centered on 22 Ka probably corresponds to the extensive Tioga 2 moraines identified and dated by Phillips et al. (1996). The several sharp fluctuations in heavy-mineral concentrations afterward may provide much more detail than the Tioga 3 moraine sequences, but transportation of heavy minerals may have occurred during episodes of glacial advance and retreat. The sharp fluctuations in heavy-mineral concentrations correlative to the Tioga 3 glacial deposits generally resemble and partly correlate with the sharp fluctuations in the magnetic-susceptibility record reported by Benson et al. (1996). The Tioga 4 glacial advance at about 15 Ka does not stand out as an especially distinctive peak of large concentrations of heavy minerals in cores OL-90-1+2, although such a peak exists at this time in core OL-84-B (Figure 11).

CLIMATE AND LIMNOLOGICAL EVIDENCE FROM PACKRAT MIDDENS.—Radiocarbon-dated packrat middens near Owens

Lake document paleoclimate records from fossil vegetation assemblages. The closest midden to Owens Lake is from the northeast side of the lake (Figure 1), about 10 m above the highstand elevation (1145 m). *Juniperus osteosperma* dominates the full-glacial levels of this midden (23.0–14.5 Ka), but *J. scopulorum* (Rocky Mountain juniper) and *Pinus monophylla* Torrey and Frémont form large components of the assemblage at midden levels corresponding to 17 Ka (Koehler and Anderson, 1994).

*Juniperus scopulorum* Sargent now lives 2100–2900 m above Owens Lake (Koehler and Anderson, 1994), but it lived at least 900 m lower during the full-glacial period. The presence of *P. monophylla* and *J. osteosperma* at lower elevations indicates that 17 Ka precipitation was greater by a factor of two to three and temperature was about 7° C lower than today, according to modern lapse rates (Smith and Bischoff, 1997). Today in the Great Basin, pinyon–juniper woodland vegetation does not characterize regions where mean January temperatures fall below –1° C (Thompson, 1990). Modern mean January temperature at Independence, California, 100 m above Owens Lake, is about 5° C (Figure 2), so a 7° C decrease would be somewhat below the tolerance of pinyon–juniper woodland. A full and overflowing Lake Owens, however, could have served as a local thermal buffer against very low (and high) temperatures and thereby may have created suitable conditions for the establishment and growth of *P. monophylla* and *J. osteosperma* during the full-glacial period.

Packrat midden sites in the Alabama Hills, at elevations of 1264–1460 m and about 17 km northwest of Owens Lake (Figure 1), extend the fossil vegetation record of the Owens Valley to 31.4 Ka (Koehler and Anderson, 1995). Full-glacial middens in the Alabama Hills do not contain *P. monophylla*, perhaps because of the elevation of this locality. Nevertheless, the presence of *Yucca brevifolia* (Joshua tree) and abundant *J. osteosperma* at 31.4, 25.7, and 21.1–17.8 Ka indicates winter temperatures generally were above freezing. This association now grows on the east side of Walker Pass, about 90 km southwest of Owens Lake, at an elevation of about 1500 m. As suggested above, perhaps the large body of water in the Owens Lake basin during this episode helped mitigate severe winter temperatures in the Alabama Hills. The cold temperature episode from 24 to 21 Ka, implied by the presence of the boreal ostracode *Cytherissa lacustris* (Figure 12), fell between episodes of mild winter temperatures, as evidenced by *Y. brevifolia* in the Alabama Hills packrat middens.

The principal climate change documented by macrofossils from packrat middens in the Alabama Hills occurred at 13.3 Ka when most elements of the modern *Sarcobatus* scrub plant community appeared (Koehler and Anderson, 1995). *Juniperus osteosperma*, however, persisted in the midden sequence, indicating cooler and wetter conditions, compared with modern environments, prevailed until 9.5 Ka. Diatoms and ostracodes in the late-glacial and early Holocene Owens Lake indicate that freshwater and presumed overflowing lake conditions existed

until 11 Ka. Afterward, lake levels and salinity fluctuated, reflecting variable, but decreasing, input from the Owens River. The first major appearance of *Limnocythere sappaensis*, an indicator of shallow and saline aquatic habitats, coincided with the disappearance of *J. osteosperma* and with the complete dominance of desert shrubs and herbs in the middens in Alabama Hills at 9.5 Ka.

**MIDDLE WISCONSIN LINKAGES TO MARINE RECORDS ON THE CALIFORNIA MARGIN.**—Isotopic, magnetic, and geochemical records from Owens Lake have been tentatively correlated with climate changes recorded in North Atlantic Ocean marine sediments (Benson et al., 1996) and Greenland ice cores (Benson et al., 1997). These correlations could imply that hemispheric-scale climate changes affected far-separated regions, but the interactive climatic and oceanographic mechanisms that might link changes in Owens Lake to changes in the North Atlantic Ocean and in Greenland were unspecified.

Gardner et al. (1988) proposed a marine-terrestrial paleoclimate linkage for the past 20 Ky between the lacustrine record at Clear Lake in California (latitude 39°N) and an adjacent marine record (core V1-80-P3) on the continental slope off northern California (latitude 38.43°N) (Figure 1). Benthic coastal and reworked freshwater diatoms in the marine core from the full-glacial period document lower sea levels and greatly decreased deep-water upwelling than today. These marine conditions correlate with cooler climates in coastal California where *Pinus* was the dominant vegetation. An episodic, fluctuating transition to marine planktonic diatoms indicates that upwelling off the California coast characterized the establishment of Holocene conditions. On land, warming temperatures favored abundant growth of *Quercus* (oak) and the local presence of *Sequoia* (redwood). Coastal fogs produced by upwelling may have been responsible for providing suitable conditions for *Sequoia*.

Upwelling of nutrient-rich marine water on the California margin relates to the strength and persistence of the Hawaiian or Subtropical High, whereas increased winter and spring precipitation that causes runoff to California coastal regions reflects the predominance of the Aleutian Low. These two pressure systems affect present-day terrestrial climates and ocean dynamics, although their effects vary from north to south (Gardner et al., 1997). Their important role in glacial, Holocene, and modern marine and terrestrial climate records in western North America implies that similar variations in the strength of the Aleutian Low and the Hawaiian High may also account for earlier paleoceanographical and paleolimnological changes.

The middle Wisconsin, or OIS 3, is represented by the marine core ODP-893 (latitude 34.29°N) from the Santa Barbara Basin (Kennett and Venz, 1995) and by core F2-92-P34 (latitude 35.03°N) from the California margin off Point Conception (Gardner et al., 1997) (Figure 1). Both cores have sufficient chronological control for comparison to the Owens Lake paleolimnological record between 55 and 20 Ka. Perhaps the most distinctive paleolimnological evidence for climate change dur-

ing this interval in the Owens Lake core is the distribution of the summer-season planktonic diatoms *Aulacoseira granulata* and *A. ambigua*. The most logical explanation for the presence of these species relates to past episodes of exceptional snowfall in the Sierra Nevada. During these episodes, high-volume runoff down the Owens River would have persisted into late summer or fall; this would have provided suitable freshwater limnetic conditions for *Aulacoseira* blooms. Intervals in which these diatoms were uncommon or absent represent, by this reasoning, episodes in which precipitation was less but still sufficient to maintain freshwater in Owens Lake, at least during spring and early summer.

Using extrapolations from uncorrected radiocarbon chronologies for marine core F2-92-P34 (Gardner et al., 1997) and for Owens Lake, a correlation between small fluctuations in the percent of aluminum present and the abundance of summer *Aulacoseira* species is evident (Figure 18). Increased concentrations of aluminum and other geochemical evidence of detrital input within the coastal marine cores indicate greater runoff from the Coast Ranges and the Sierra Nevada (Dean et al., 1997), and the same process may explain the approximately coeval proliferation of *Aulacoseira* in Owens Lake.

Gardner et al. (1997) suggested that increased fluxes of detrital material to the coastal sediments during the full-glacial period were caused by the same moisture source that supplied the glaciers in the Sierra Nevada and the lakes in the Great Basin. An intensification and southerly displacement of the Aleutian Low and the storms associated with the Polar Front jet stream, probably forced by a southward expansion of polar air masses, are the most probable reasons for this moisture source. The same climatic mechanisms can be used to explain similar, but less intense, variations during OIS 3.

In core F2-92-P34, intervals that are not characterized by increased percentages of aluminum instead contain evidence of increased anoxia, such as high values of molybdenum and organic matter (Dean et al., 1997). In other presumably correlative marine cores, anoxic conditions excluded burrowing marine organisms, and zones of laminated sediments resulted. Increased productivity (upwelling) of the California Current apparently provided sufficient marine productivity and organic material that, once deposited, promoted the formation and maintenance of anoxic environments.

The history of upwelling intensity of the California Current also can be deduced by the fluctuating presence of the planktonic foraminifera *Globigerina bulloides* D'Orbigny in a core from ODP-893 in the Santa Barbara Basin (Kennett and Venz, 1995). According to the oxygen-isotope chronology developed from this core, fluctuations of *G. bulloides* (Figure 18) were antithetical to the aforementioned evidence of increased precipitation (*Aulacoseira* and Al), suggesting that the same climatic conditions that increased upwelling also decreased winter precipitation along the California coast. In this case, the strength and persistence of the Hawaiian High was the likely candidate because clockwise winds generated around this high-

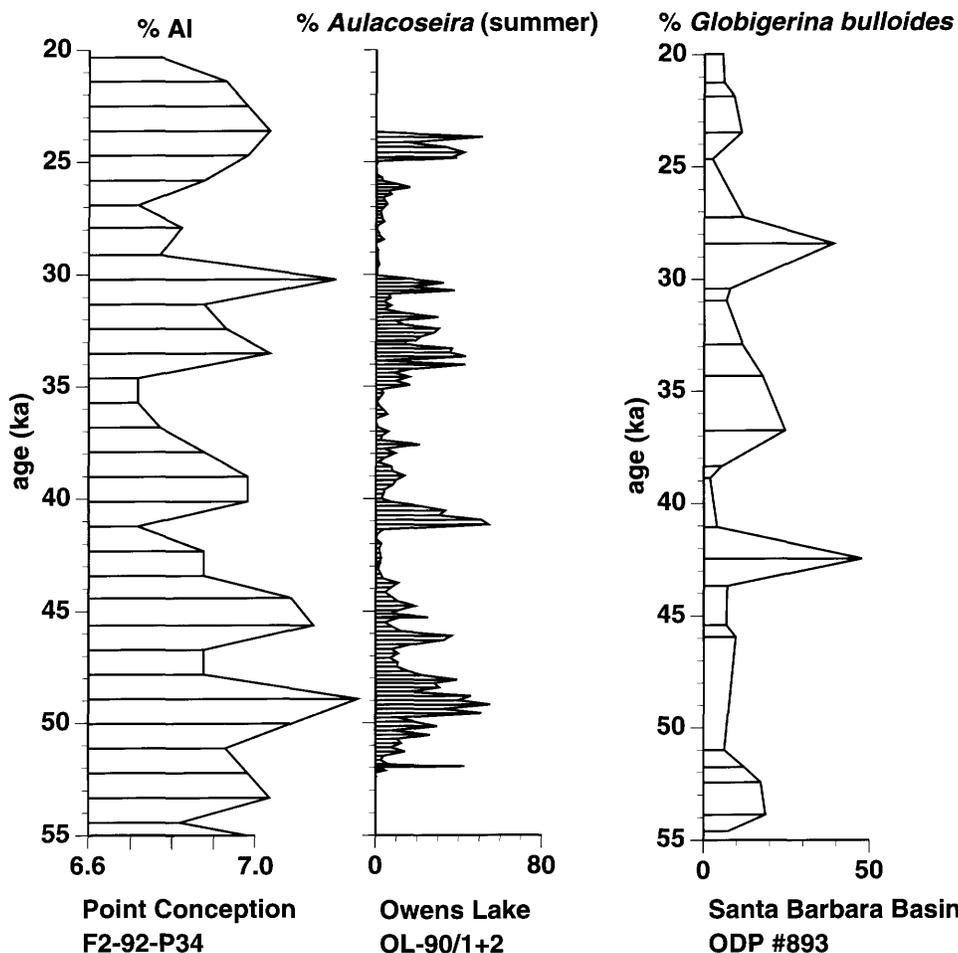


FIGURE 18.—Chronological comparison of middle Wisconsin episodes of abundant *Aulacoseira* species from Owens Lake cores OL-90-1+2, percentage fluctuations of Al from core F2-92-P34 on the California margin west of Point Conception, and percentage of *Globigerina bulloides* from ODP site #893 in the Santa Barbara basin (Figure 1). Aluminum data are from W.E. Dean (USGS). Foraminifera data are from Kennett and Venz (1995).

pressure center would have driven the California Current to the south, which is what happens today. Because this atmospheric circulation pattern would have blocked moisture from the tropical Pacific Ocean, it also would have reduced the annual precipitation reaching the Sierra Nevada and, consequently, Owens Lake.

Admittedly, correlations of the paleoceanographic and lacustrine evidence for past climate change in cores from coastal California and from Owens Lake are not perfect, and they rely on chronologies of uncertain accuracy. Nevertheless, this interpretation is based upon operationally consistent climatic, terrestrial, and oceanographic systems and processes that logically force large changes between glacial and interglacial environments.

### Conclusions

High-resolution diatom and ostracode records from cores from Owens Lake have revealed a sensitive and comparatively

simple record of Sierra Nevada precipitation for the last 55 Ky. At one extreme, high precipitation, combined with cold temperatures associated with the southward expansion of polar air masses, produced glaciation in the Sierra Nevada (Hostetler and Clark, 1997). The Owens Lake basin filled with detrital sediment containing the remains of freshwater diatoms and boreal ostracodes. At the other extreme, scant winter precipitation failed to offset high evaporation rates, and the Owens Lake basin desiccated to playa or near playa conditions. Intermediate limnological and climatic conditions existed at other times. These conditions included episodes of saline lakes of shallow to moderate depths and regimes of greater than modern precipitation under temperatures warm enough to preclude extensive glaciation. During the last 50 Ky, the predominant paleoclimatic scenario at Owens Lake included greater precipitation than at present and probably cooler than modern temperatures. During this time, overflow conditions existed for about 40 Ky (50–10 Ka), and only during the last 10 Ky of the Holocene did Owens Lake remain below its spill level for long periods of

time. The paleolimnological record of the last 50 Ky is consistent with the longer record of Owens Lake reported by Bradbury (1997a, 1997b), which documents overflow conditions for about 80 percent of the last 800 Ky.

The high-resolution study of limnological and climatic variations at Owens Lake also indicates rapid changes between positive and negative hydrologic balance. For example, the change from closed- to open-basin conditions about 52 Ka occurred in less than 300 years. Changes in diatom and ostracode assemblages document the step-like progression of this shift. Holocene changes from fresh to saline diatom floras about 10 Ka indicate that a shift in the hydrologic balance occurred within a century or less. Assuming a reasonable chronological accuracy, this rate of change in salinity was faster than what Bischoff et al. (1997a, fig. 5) predicted for simple evaporative concentration of Owens River water during current climates; thus, saline springwater discharge entering Owens Lake must have had an important hydrochemical effect during arid climate periods. The apparent correlation of the Owens Lake record with the paleoceanographic records indicates that climatic conditions at Owens Lake were not just local, but were part of

a global system that involved major reorganizations of atmospheric and oceanic circulation. The Owens Lake fossil record supports the contention that climate change can be rapid and that future climate in the Owens Lake area could be wetter rather than drier.

### Acknowledgments

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# Biogeography and Timing of Evolutionary Events among Great Basin Fishes

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## ABSTRACT

Hubbs and Miller's Great Basin works are model studies of the evolution of isolated endemic aquatic organisms and of hydrographic history. They investigated spatial and temporal barriers that permitted evolutionary divergence of fishes. They also used fish evidence to identify the locations and possible timings of past aquatic connections among basins. Hubbs and Miller focused on morphological differences among fish populations in related basins and hypothesized that their evolutionary divergence occurred over only hundreds to thousands of years. Their conclusions depended upon the assumption that divergence began after the most recent time of homogeneous ancestral populations, which was assumed to be the time of closure of the most recent hydrographic connection. This approach and its key assumptions are standard in studies of evolutionary rates, but they require reexamination.

Our data suggest that rates of morphological change in oligogenic and ecophenotypic traits of Great Basin fishes may be rapid in the short term (thousands of years), but Miocene to Pleistocene fossils of western North American fishes indicate slow changes over millions of years. Tests of hypotheses about evolutionary rates require independent estimates of both time and degree of divergence. Our evolutionary-rate estimates are based upon regression of percent sequence divergence (of mitochondrial DNA) between pairs of lineages against millions of years of diver-

gence of sister clades, estimated from dates of first appearances in the fossil record. The results indicate rates of molecular evolution in the range of approximately one-half percent (salmonids) to one percent (cyprinids and cyprinodonts) sequence divergence per one million years. The ages of some forms thought to represent ten thousand years of postpluvial evolution are more likely to be hundreds of thousands of years old, according to molecular/fossil estimates. Estimated divergence times of fishes, based upon DNA, provide unique data on the nature and timing of barriers and aquatic connections among basins.

Great Basin fish faunas exhibit high endemism, but they have lower diversity than predicted by pluvial cycles of isolation and by rapid evolution in allopatry. We hypothesize that uplift causes high stream gradients and, therefore, decreased local habitat diversity because of rapid stream runoff. Small and isolated populations on the basin floors are prone to allopatric differentiation, but they also are prone to high extinction rates; therefore, isolation and stabilizing selection in desert basins rarely produced new species that survived extinction events.

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## Dedication

This paper is dedicated to Carl L. Hubbs, Robert R. Miller, and Dwight W. Taylor, whose studies of aquatic organisms in western North American desert basins set the twentieth century standard for aquatic biogeography and conservation.

## Introduction to Great Basin Ichthyology

Carl L. Hubbs began his studies of fishes in the Great Basin in 1915 while on an expedition to the Bonneville Basin as a field assistant to J.O. Snyder (Miller and Shor, 1997). Prior to the Bonneville trip, Snyder had surveyed fishes in the Lahontan Basin and in the Oregon Lakes, Owens River, and Mohave River basins (Snyder, 1908, 1912, 1914, 1917a, 1917b, 1918, 1919, 1924). Hubbs continued to conduct exhaustive explorations of the Great Basin in 1934, 1938, and 1942; with his wife, Laura, and their children, Earl, Frances, and Clark, he collected and identified more than 118,000 specimens. Hubbs was joined by his student, Robert Miller, in 1938, and between them they

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produced about three dozen papers on Great Basin fishes. Miller's efforts resulted in numerous papers on fishes of the Death Valley system (e.g., 1946a, 1946b, 1950, 1972) and on broader issues relating to evolution and conservation of Great Basin fishes (1959, 1961a, 1961b, 1965, 1981). Miller continued conducting this field work with his wife, Frances Hubbs Miller, and their five children, and he extended the project to include a survey of the fishes of Mexico.

The landmark synthesis of the systematics and biogeography of fishes of the Great Basin was published by Carl Hubbs and Robert Miller in 1948(b), which was expanded from a symposium paper read in 1942. The monograph described the geographical limits of more than 100 hydrographic units, the elevations of ancient lake levels, and the biogeographic relationships of fishes in each basin. The authors' goal was to show how convincingly physiographic deductions are supported by knowledge of the distribution of fishes in the Great Basin.

The Hubbs–Miller team and Elliot Blackwelder (1933) both used fish distributions to infer past aquatic connections, which were based upon the principles of Jordan (1905, chapters 16, 17). The interaction of time and barriers framed the questions in the Hubbs–Miller inventory of Great Basin fish evolution. Their descriptions and classification of those fishes were intended to answer questions about hydrographic connections among basins, barriers between basins, and rapidity of evolution. Although they chose not to speculate about evolutionary mechanisms (1908b:119), they offered frequent hypotheses about amounts and rates of evolution. They later expanded upon their ideas about fish speciation (Hubbs, 1940, 1941a, 1941b; Miller, 1946a, 1950).

Hubbs and Miller's most exciting idea was declared in the introduction to their 1948 monograph (Hubbs and Miller, 1948b:24):

Some of the isolation and speciation that is dated from Pleistocene time may be much more recent. Now disconnected waters within many of the basins of western North America may have been connected and their fish fauna made uniform not many centuries ago. From a consideration of the evidences on climatic changes ... it seems likely that such connections may have been established several times during the last three millennia. We believe, however, that most of the local differentiation and endemism among the fishes of the isolated desert waters dates from the end of the Glacial period. Hutchinson (1939) concluded that the similar differentiation of now isolated fish populations in Kashmir and Indian Tibet dates from the period of maximum glaciation. ...

In correlation with Post-pluvial isolation, a limited degree of speciation has occurred here and there, but data are too meager to warrant any attempt to use the rate of species evolution in dating the Pluvial waters. ... A considerable body of observations and mathematical data indicates that small, closely inbreeding populations may speciate at a much more rapid rate than was previously thought possible (Wright, 1940a, 1940b, 1942; Huxley, 1943).

The authors treated their geological and ichthyological data in two ways: they used geological data to infer rates of fish differentiation, and they used degree of morphological divergence to infer the times of geological barriers. The usual assumption was that fish populations were uniform at the end of the most recent connection between aquatic habitats. This led to the de-

duction that rapid speciation occurred in the postpluvial interval of isolation, about 11,000 years.

Carl Hubbs, Robert Miller, and Laura C. Hubbs (1974) expanded upon their previous work and the work of others in their subsequent monograph on hydrographic history and relict fishes of the North-Central Great Basin. Laura Hubbs measured hundreds of fish specimens from different basins and calculated the mean and standard deviation for the populations in each basin, providing replicated comparisons of times and amounts of divergence. Hubbs and Miller (1948a, 1972) described many additional localized cyprinid species and subspecies, which provided further evidence for postpluvial divergence in geographic isolation (see Appendix).

Hubbs and Miller sought to answer a question that still motivates biogeographers (e.g., Ricklefs and Schluter, 1993); that is, What are the appropriate scales of the spatial and temporal interactions that bring about species production? Hubbs and Miller (1948b) emphasized differences among and within basins, namely, different taxonomic levels, numbers of endemic forms, and local diversity in relation to regional diversity as indicators of evolutionary history: "The Lahontan fauna ... comprises, we estimate, about 30 forms, as compared with perhaps 28 in the Bonneville and about 24 in the Death Valley system. The relatively high number of total forms is correlated with the isolation of local populations, for the Lahontan system has become greatly disrupted since Pluvial times" (Hubbs and Miller, 1948b:32).

Hubbs and Miller (1948b:41) also recognized an important role for hybridization in evolution: "Since the waters have dwindled, and the lake and creek types have been forced into cohabitation, the two have hybridized very extensively. We have referred to this specific breakdown in connection with our analysis of a similar case of hybridization in the Mohave Desert (Hubbs and Miller, 1943)." The effects of hybridization in reducing diversity and erasing evidence of evolutionary history are peculiarly prominent among fishes in the western United States (Smith, 1992a; Dowling and Secor, 1997).

Our goal is to continue the comparison of fish and hydrographic information so as to answer questions about timing and origins of fish diversity. Evidence presented herein for timing of fish divergence comes from the fossil record (G.R. Smith, 1981a, 1981b; Smith et al., 1982) and from molecular studies (Dowling et al., 2002; Shiozawa and Evans, unpublished). In this paper, we summarize gene sequence divergence data in the context of the fossil record of Great Basin fishes. We seek to shed light on the rates of evolutionary changes in Great Basin drainages in the spirit of the other Great Basin naturalists of 50 years ago (Hall, 1946:59–67; Durrant, 1952:490–518; LaRivers, 1962; and the vast body of literature published by Hubbs and Miller).

Our understanding of freshwater fish distributions benefits from the fact that freshwater fish are more geographically constrained than most other organisms (Cope, 1868; Jordan, 1905). The principles thought to influence distribution and evolution

of fishes have remained rather constant during the last 130 years, but estimates of timing of geological and evolutionary events vary by five orders of magnitude (compare Cope, 1868, with Hubbs et al., 1974). The Great Basin offers a unique opportunity to study the time scales of evolutionary processes because of its numerous, isolated basins that have replicated fish habitats and histories. In addition, well-documented evidence exists for environmental gradients, pluvial cycles, and ages of sediments that preserve fossil ancestors of Holocene fishes (e.g., Morrison, 1965, 1991; Benson and Thompson, 1987; Benson et al., 1990; Oviatt et al., 1992; Reheis and Morrison, 1997; Smith and Bischoff, 1997). These factors provide the basis for Cope's (1883) and Hubbs and Miller's (1948b) assumption that fish evidence can contribute much to the study of hydrographic history. Our attempts to fulfill this promise have been guided further by Dwight Taylor's methods and his principle (1960) that hydrologic, topographic, and climatic features change more rapidly than do lineages of organisms.

The Late Cenozoic fossil record in the Great Basin reflects the climatic and faunal revolution between the Paleogene and the Neogene. For example, the temperate Miocene to Holocene fish faunas of the Great Basin (as now known) share only one family (Catostomidae) with the subtropical faunas of the western North American Eocene in Wyoming, Utah, and Colorado (Grande, 1984). Transitional Great Basin fish records are Cope's (1872) *Amyzon mentalis* and *Trichophanes hians* from the Osino, Nevada, Oligocene coal beds and Early Tertiary fossils similar to *Diplomystus* in Elko County, Nevada. Our discussion herein, however, will be limited to the late Cenozoic record. Publications on fossil *Empetrichthys*, fundulids, and cyprinodontids by Miller (1945b) and Uyeno and Miller (1962) included reviews of many pre-Pleistocene records of modern lineages in the southwestern Great Basin. LaRivers (1962) compiled the first account of endemic and introduced fishes in Nevada, including what was known at that time about ecology and fossil fishes.

Newberry (1871, and references therein) was the first to study Great Basin fishes from a geological context, but he was soon followed by Jordan (1878a, 1878b, 1891), Cope (1883), Jordan and Evermann (1896), and Tanner (1936). J.O. Snyder and Hubbs and Miller, in works cited above, were the next to dominate the field. Uyeno and Miller (1962), Miller (1981), M.L. Smith (1981), and G.R. Smith (1966, 1978, 1981a, 1981b) discussed fossils and described patterns of differentiation, species density, and zoogeography of western North American fishes among basins. Minckley et al. (1986) discussed this history in detail, then compiled current geological literature on the Cenozoic tectonics of western North America and hypothesized broad aspects of zoogeographic history of western fishes. They looked for congruence between area cladograms and fish cladograms then available and concluded that the modern fauna occupied western tectonic units in the Oligocene before they were separated from Atlantic Ocean tributaries by the Miocene cycle of tectonic uplift. Minckley and

Deacon (1991) described critical conservation issues and extinction threats to the modern fauna. Behnke (1992) provided original analysis and summarized the available information on recent trouts. Sigler and Sigler (1987, 1996) summarized the modern fauna, including introduced fishes.

The fishes discussed in the present paper inhabit or inhabited the hydrographic Great Basin, as defined, for example, by Hubbs and Miller (1948b) as being the region of Holocene internal drainage bounded by barriers shared with the present drainages of the Colorado, Sacramento, Klamath, and Columbia Rivers (Figure 1). The Great Basin is not static; rather, it is a mosaic whose boundaries and external connections have shifted with tectonic, volcanic, and climatic changes across time scales ranging from 10 thousand years (Ky) to 10 million years (My) during the last 17 My (Minckley et al., 1986; and citations below). Many hydrographic connections have been hypothesized. For example, in the middle Miocene, there were large lakes in northern Nevada and Utah that drained through the Snake River Plain southwest across the Sierra Nevada to the Pacific coast drainage (Stokes, 1979). Later, the Lahontan Basin (which still drained to the Pacific Ocean) was connected to the Snake River Plain. At different times, the White River (Hubbs and Miller, 1948b), Las Vegas Creek (Haynes, 1967), Death Valley–Owens River systems (Miller, 1946a, 1948), and perhaps even the Bonneville Basin (Ives, 1948) and upper Snake River were variously connected to the Bouse Embayment of the lower Colorado River. As the Sierra Nevada was uplifted, it is possible that a north-to-south drainage system included basins in Oregon and possibly Washington (Smith et al., 2000). There is good evidence that 2.5 million years ago (Ma) the Snake River's course changed with its capture by the Columbia River through Hell's Canyon (Wheeler and Cook, 1954). At undetermined times in the late Cenozoic, there were connections from the Mono Lake basin to the Lahontan Basin, from Owens River west to the Pacific coast drainage, and later, south to Mexico. In addition, Death Valley was connected to the lower Colorado River as well as to the Basin and Range Province in Mexico (Minckley et al., 1986; Hale, 1985). Fifteen to 20 thousand years ago (Ka) the basins of internal drainage were probably restricted mainly to northern and eastern Nevada and sometimes to the Death Valley system. At about that time, the Bonneville Basin and the basins of Catlow and Fort Rock Valleys and of Harney and Malheur Lakes (hereafter, Harney–Malheur) were sometimes tributaries to the Snake River (Taylor and Bright, 1987; Bisson and Bond, 1971; Minckley et al., 1986), whereas the White River was occasionally connected to the lower Colorado River (Taylor, 1983). The sizes and connections of basins fluctuated with climatic moisture through the late Pliocene (Smith et al., 1982) and the Pleistocene (Morrison, 1991; DiGiuseppi and Bartley, 1991).

The hypotheses presented in this paper do not assume the above hydrographic outline, but they suggest that connections and disconnections, such as outlined above, were more frequent than commonly assumed. Our approach is to use fish fossils,

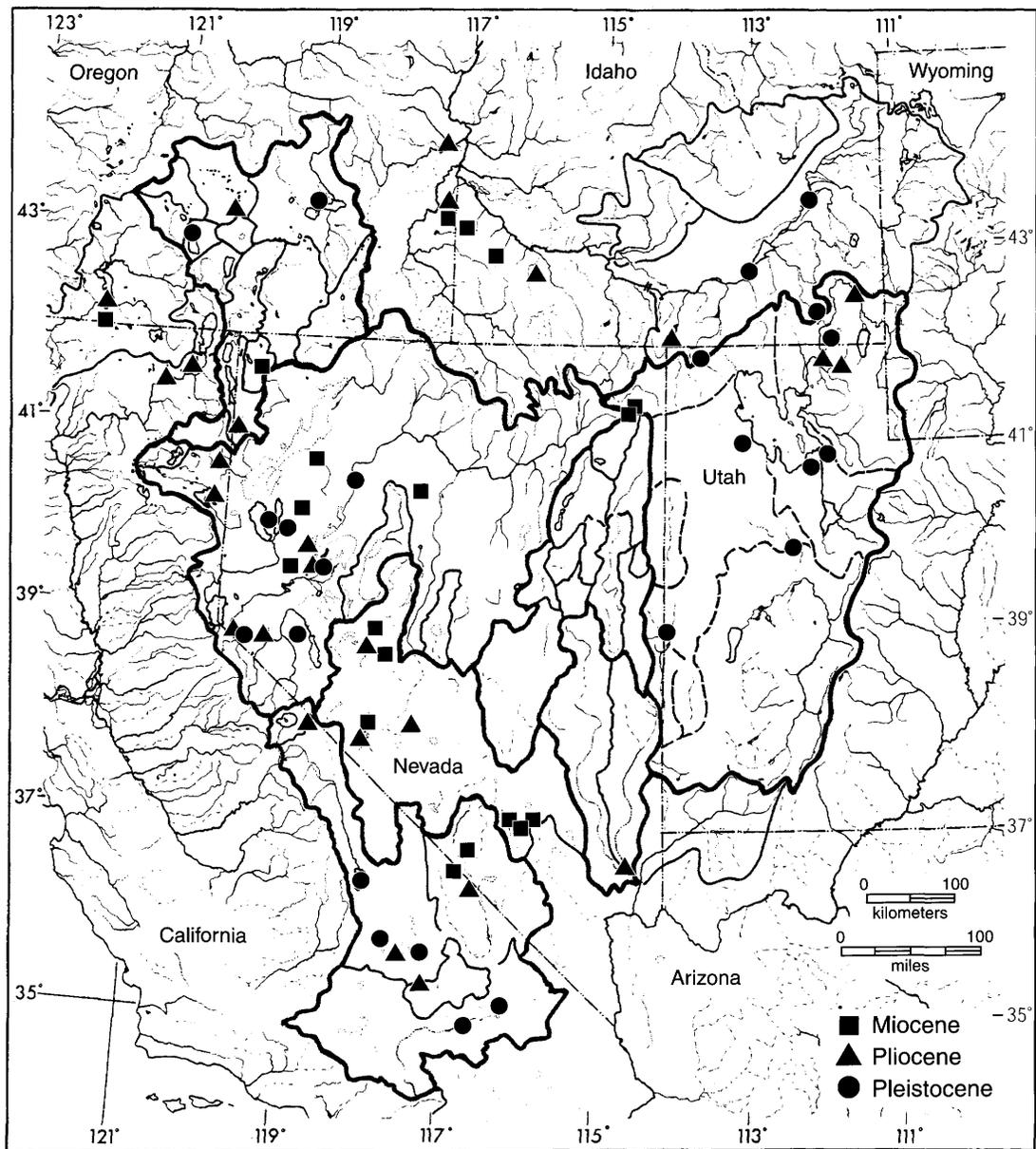


FIGURE 1.—Fossil fish localities in the Great Basin and adjacent drainages. Ages of fossil fish are indicated by symbols defined on the figure. Fossils are listed in the Appendix, where they are indicated by a cross. Heavy lines demarcate major drainage divides.

phylogenetic analysis, biogeography, and genetic distances as primary evidence for the times and locations of hydrographic change.

#### Material and Methods

Our hypothesized drainage connections are based upon distribution ranges of fish clades, species, or genetically similar populations, especially species and subspecies that span drainage divides that are no longer passable. We assume that ancient

fishes dispersed only through their habitats, because this method is supported by testable generalizations, in contrast to ad hoc hypotheses for dispersal of fish eggs, such as on birds' feet (e.g., Brown and Rosen, 1995; Spencer and Patchett, 1997). Likely geological mechanisms for transfer include lake spillover (Hubbs and Miller, 1948b), river capture, erosional beheading of streams, diversion of channels by erosion, and diversion of drainage by uplift or volcanic eruptions (Bishop, 1995). The degree of isolation of basins constrains dispersal, which leads to predictions that are testable by geographic, geo-

logic, genetic, and cladistic analyses. The large number of adjacent basins with similar habitats permits analysis of replicated histories of similar local faunas in addition to isolated case histories. It is important that we attempt to use fish data that are independent of geological assumptions, in the spirit of Hubbs and Miller (1948b) and Taylor (1960), so as to contribute non-circular conclusions useful to geology.

Records of Holocene fishes from the Great Basin were compiled primarily from the records of Hubbs (and his students and successors), which have been deposited in the Division of Fishes, Museum of Zoology, University of Michigan, and from the literature. Late Cenozoic fossil fish data (Figure 1; Table 1) were compiled from collections in the Museum of Paleontology and the Museum of Zoology, University of Michigan; the W.M. Keck Museum, Mackay School of Mines, University of Nevada, Reno; the Museum of Vertebrate Paleontology, University of California at Berkeley; the Department of Biology, California State University at Bakersfield; and the paleontological literature. (Lists of comparative material are available from authors G.R.S. and K.W.G.) Records of new distributions are noted in the species accounts in the Appendix. These accounts include information on specimen characteristics, collecting localities, and names of the collectors when the specimens were not deposited at the above-listed institutions (Appendix; Table 5). Ancestral-descendent pairs are recognized by shared apomorphies that are not shared with the next closest sister group. The probability of discovering ancestral-descendant pairs is thought to be low in marine and terrestrial systems (Foote, 1996), but in the Great Basin it is greatly enhanced by short geological time frame, highly constrained geography, the small number of taxa, and the salient osteological characteristics among fish taxa.

Cladistic methods used to estimate branching sequences for cyprinid fishes are from Dowling et al. (2002), Simons and Mayden (1997, 1998), and Cavender and Coburn (1992); for Catostomidae, Smith (1992b); for *Prosopium*, Smith and Todd (1993); for trout, Shiozawa and Evans (unpublished); and for Cyprinodontidae, Echelle and Dowling (1992). Molecular methods follow those used by Echelle and Dowling (1992), Shiozawa and Evans (1995), and Dowling and Naylor (1997). Cladograms were calculated from mitochondrial DNA (mtDNA) sequence data, using the parsimony algorithm "Phylogenetic Analysis Using Parsimony" (PAUP\*; Swofford, 1990), version 4.0 d64 by D. Swofford. Informative characters among the species of Cyprinidae are the shared base pairs of the mitochondrial cytochrome *b* gene, relative to outgroups. North American and Eurasian cyprinids were used as outgroups for the analysis of western North American Cyprinidae. Informative cladistic characters among *Oncorhynchus clarki* and among *Cyprinodon* are shared restriction-site differences in mtDNA, relative to outgroups. *Oncorhynchus mykiss* (rainbow trout) is the outgroup for the cladistic analysis of subspecies of *Oncorhynchus clarki* (cutthroat trout). *Cyprinodon macularius* and several species of southwestern *Cyprinodon* from

outside the Great Basin served as outgroups for the cladistic analysis of *Cyprinodon* species of the Death Valley system.

**DATA USED TO ESTIMATE THE RATE OF EVOLUTIONARY CHANGE PER UNIT TIME.**—The relative homogeneity of molecular distances (Tables 2–4) among species with a common ancestor suggested a source of independent evidence to break the logical circularity inherent in using geological events to date evolution and in using evolutionary differentiation to date geological events. Previous workers carefully contrasted geological and ichthyological data, but it has been difficult to find independent data to constrain the time of geographic isolation. The traditional method (Hutchinson, 1939) defines a relevant interval of evolutionary time as beginning with the last possible period of hydrographic connection. This method assumes that one panmictic and homogeneous form at the time of connection evolved into two isolated and differentiated forms in the present. For example, it is assumed that a uniform Pliocene population before the Panamanian land bridge evolved into Pacific Ocean and Atlantic Ocean populations isolated by the Panamanian isthmus during the last 3.5 My (Bermingham et al., 1997). This method is limited to investigation of only one possible time for the origin of divergence, with bias toward the most recent.

It has been deemed parsimonious to choose the time of most recent connection as the beginning of the divergence because to choose an earlier time seemed to add an unnecessary ad hoc hypothesis, i.e., more time than is minimally necessary. Discovery of the amount of time required for the observed divergence is, however, the original question, and to assume the shortest of several possible times does not test the hypothesis. It is important to test the alternative possibility, namely, that multiple populations were present prior to the time of last connection and that the forms observed in the Holocene have been accumulating genetic differences for a time period longer than since the last connection. This alternative is important for studies such as the Panamanian separation of Atlantic and Pacific marine faunas, as well as for freshwater fishes in the Great Basin. Divergence times of clades must ultimately be based upon ages determined from the stratigraphic context of fossils—usually some combination of mammalian biostratigraphy (Woodburne, 1987), potassium–argon, <sup>40</sup>argon–<sup>39</sup>argon, or other radiogenic dates (e.g., Baksi et al., 1992), magnetostratigraphy (Negrini et al., 1987), fission-track ages (Kimmel, 1982), and field studies of geomorphology and geochemistry (e.g., Allison, 1940, 1982; Hubbs and Miller, 1948b; Bright, 1966, 1967; Benson and Thompson, 1987; Benson et al., 1990; Curry, 1990; Morrison, 1991; Reheis and Morrison, 1997).

We compared data on divergence of mtDNA molecules among fishes (Kocher and Carleton, 1997) with dates of relevant fossils to calculate rates of molecular evolution (Collins et al., 1996). Molecular differences among homologous mitochondrial genes in these taxa are expressed as pairwise percent sequence divergence (Gillespie, 1991). The difference values are proportions of the specified part of the genome that differ in

TABLE 1.—Late Cenozoic fossil fish localities in the Great Basin. Numbers refer to indexed taxa mentioned in the Appendix; a question mark (?) = uncertain identification or age.

Locality, by state	Indexed taxa	Source <sup>1</sup>
MIOCENE		
Nevada		
Bullfrog Mine near Beatty, Nye County, 23 Ma?	117	Lugaski, UNRM
Esmeralda, Esmeralda County	5, 27, 28, 58, 88, 120	LaRivers, 1962, UNRM
Siebert Tuff, Nye County, 17 Ma	122	Lugaski, 1978, UNRM
Buffalo Canyon, Churchill County, 15 Ma	6, 88	T. Lugaski, UNRM
Middlegate Formation, Churchill County	88	D.I. Axelrod, UCD
Stewart Valley, Mineral County, 12 Ma	27, 88	
Virgin Valley, Humboldt County	6, 58, 124	Lugaski, UNRM
Truckee Formation, Churchill County	8, 29, 80, 89, 128	Bell, UMMP
Red Rock locality, Churchill County	87	J.R. Alcorn, UMMP
Rabbit Hole, Pershing County	88	LaRivers, UNRM
Sahwave Mountains, Pershing County	116, 128	
Humboldt Formation, Elko County, 9.5 Ma	123, 130	Lugaski, UNRM
Coal Valley, Mineral County	6, 88	T. Kelly, MVP
Alum Mine, Nye County	88	LaRivers, UNRM
Jersey Valley, Pershing County	8	Lugaski, UNRM
Brady Pocket, Churchill County, Hemphillian?	56	Charles Dailey, MVP, UMMP
Carson Valley, Douglas County	15, 30, 88	
Oregon		
Trout Creek, Harney County	129	C. Arnold, UMMP
Utah		
Cache Valley Formation, Salt Lake group	3	J.S. Williams, USU
PLIOCENE		
California		
Secret Valley, Lassen County	1, 30, 69, 91, 124	UMMZ, Wagner et al., 1997, MVP
Madeline Plains, Lassen County	1, 25, 26?, 30, 91	Wagner et al., 1993, MVP
White Hills, Airport Lake, Inyo County	12, 62	Gobalet; UMMP
Mono Basin	1, 13, 14, 30, 63, 74	Miller and Smith, 1981; Gobalet; UMMP
Honey Lake	9, 25, 60, 65, 68, 70, 91	Taylor and Smith, 1981, UMMP
Idaho		
Salt Lake group at Georgetown	3, 59	S.A. Bilby, ISU
Nevada		
Carson Valley, Douglas County, early Blancan	2, 15, 30, 64, 75	T. Kelly, Gobalet, MVP
Carson Valley, Douglas County, late Blancan	2, 15, 64, 92	T. Kelly, Gobalet, MVP
Pine Nut Ridge, Douglas County	6	T. Kelly, 1994, MVP
Duck Valley, Washoe County	10, 62	
Carson Sink, Churchill County	92	
Mopung Hills, Churchill County	9, 72, 93, 124	Taylor and Smith, 1981, UMMP
Fish Cave, Churchill County	124	R. Miller, UMMP
Oregon		
Fort Rock Lake, Lake County, Blancan	7, 59, 62, 90	Allison and Bond, 1983, OSU
Utah		
Junction Hills, Salt Lake group, Hemphillian	3, 23, 26, 30, 57, 61, 69, 81	P. McClellan, MVP
Park Valley, Box Elder County, Hemphillian?	125	T. Cavender, UMMP
PLEISTOCENE		
California		
Manix Lake, San Bernardino County	12, 129	Buwalda, 1914; Reynolds, 1991, 1994
Searles Lake, San Bernardino County	12	
China Lake, San Bernardino County	12, 62	UMMP
Lake Mohave or Soda Lake, San Bernardino County	12	Leatham, UMMP
Owens Lake Core, Inyo County	13, 73, 82, 92	G.I. Smith, UMMP
Nevada		
Humboldt River Canyon, Pershing County	10, 92	Gobalet, MVP
near Fallon, Churchill County	60, 72	J.R. Alcorn, UMMP
Carson Valley, Irvingtonian	15, 30, 64	T. Kelly, Gobalet, MVP
Sunshine Amphitheater, northwestern Walker Lake, pre-Lahontan	72, 92	M. Reheis, USGS
Lahontan Cave deposits	124	Jordan, 1924, MVP
Smith Creek Cave	23, 99	Mead et al., 1982

TABLE 1.—Continued.

Locality, by state	Indexed taxa	Source <sup>1</sup>
Oregon		
Chewaucan, Lake County	11	Gobalet and Negrini, 1992
Utah		
Hot Springs, Salt Lake County	23, 66, 84, 85, 125, 126	Smith et al., 1968, UMMP
Black Rock, Salt Lake County	23, 84, 85, 98, 125, 126	Smith et al., 1968, UMMP
Black Rock, Tooele County	23	J.H. Madsen, Jr., UMMP
Homestead Cave	23, 66, 84, 85, 87?, 98, 126	Broughton, UU
Thatcher Basin	61	Bright, UMMP
Old River Bed	62, 82, 98	Oviatt, UU
STRATIGRAPHY UNCERTAIN		
Nevada		
Nevada AEC Test Site, Nye County, Miocene?	119	Richard Wyman, UMMP
California		
Titus Canyon, Pliocene? (stratigraphy uncertain)	111, 117	Miller, 1945b
Titus Canyon Formation, Oligocene?	117	Lugaski, UNRM
Furnace Creek, Death Valley, Pliocene?	118	Miller, 1945b

<sup>1</sup>Published source and/or collector and location of specimens. Abbreviations: ISU = Idaho State University Museum, Pocatello; MVP = Museum of Vertebrate Paleontology, University of California, Berkeley; OSU = Oregon State University, Corvallis; UCD = University of California, Davis; UMMP = University of Michigan Museum of Paleontology, Ann Arbor; UMMZ = University of Michigan Museum of Zoology; UNRM = Mackay School of Mines, University of Nevada, Reno; USGS = United States Geological Survey; USU = Department of Geology, Utah State University; UU = University of Utah.

accumulated mutations, corrected for back mutation (Tamura and Nei, 1993). We were encouraged to pursue this method by the homogeneity of values of pairwise comparisons of sets of lineages, each derived from a common ancestor (Tables 2–4). This homogeneity suggested that the rate of molecular evolution was roughly constant for a given gene system in a given clade. The relative-rate test of Sarich and Wilson (1967) was used to evaluate the precision of the time estimate. It is based upon the assumption that all taxa derived from one node (branch point) on a cladogram have evolved while accumulating mostly neutral mutations for the same amount of time (e.g., Figure 2; Table 2), regardless of the number of intervening branch points; therefore, all the distances (in a homologous molecule) from the sister clade to all the members of the clade in question should be identical. This degree of similarity is a measure of the constancy of the rate of molecular change and, therefore, an estimate of the precision of a molecular estimation of geological time. In other words, the homogeneity of the measured distances between sister branches within a clade is an indication of how constant the rate of molecular change has been. It is important to stress that these distance values were tested in conjunction with ages of fossil fish that we interpret as ancestors; distance values were not converted to rates of molecular change based upon molecular clock assumptions from mammals or other organisms.

If we accept the accumulated differences (genetic distance) as numerators in a rate estimate for these fishes, we then need an independent denominator measured in millions of years to yield the amount of molecular change per one million years (Collins et al., 1996). The denominator, evolutionary time, is

estimated herein as millions of years since the time from first appearance of a fish lineage to the present. Relative times of lineage origins, recognized by possession (in fossils) of evolutionarily derived states that diagnose appropriate groups (Lundberg, 1993), are underestimated because occurrences of fossils are usually minimum estimates of the age of their lineage (Minckley et al., 1986). This problem exists because the first members of a lineage are not only rare, they are also not easily recognized (assuming that apomorphies accumulate gradually at many points along branches between nodes). Where fossils are limited to infrequently preserved depositional environments, the sample sizes are not adequate to evaluate statistical error around the estimated age of the first occurrence of a lineage. The denominator error from underestimated times of first appearance results in overestimated rates of change (rate = percent divergence/time). Errors in the numerators, e.g., from back mutations, yield underestimated rates, unless genetic distances are adequately corrected (Tamura and Nei, 1993). The potential consequences of these errors are readily apparent from inspection of Figure 14, in which numerator error is corrected, but denominator error is not; therefore, our rates of molecular change (0.5%–1%/My) are likely to be overestimates, approximating upper bounds. If the oldest of these lineages are as old as the Oligocene, as suggested by Minckley et al. (1986), correct rate estimates could be 0.3%–0.7%/1 My.

The pairwise difference values for lineages in a clade, such as the Cyprinodontidae, Salmonidae, or Cyprinidae, are regressed against geological divergence-time estimates (Figure 14). The regression coefficient then gives the percent sequence



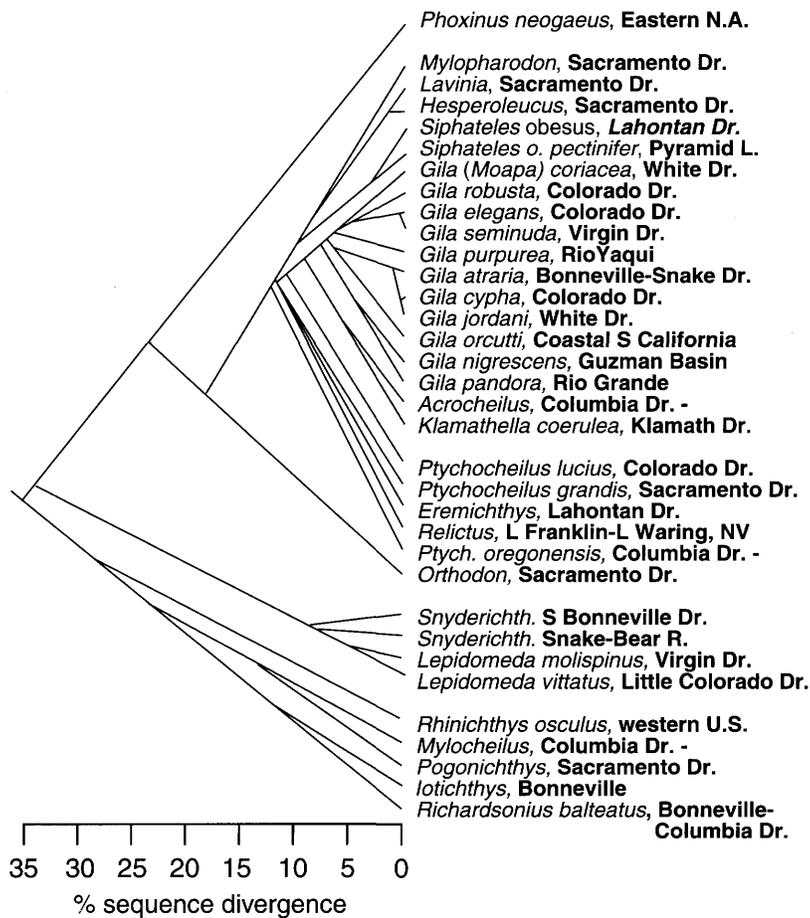


FIGURE 2.—Mitochondrial DNA phylogeny of western Cyprinidae, based upon parsimony cladistic analysis of the cytochrome *b* gene. This tree is extracted from a larger analysis of 88 cyprinid taxa (Dowling, unpublished). The relative rates test (see “Methods”) is based on the expectation that all of the sister species to any outgroup should have the same percent sequence divergence. The variation in those distances (Tables 2–4) is a measure of the variation in relative rates of change and the lack of precision in any inference. The depth to each node is scaled to age in millions of years, assuming that 1 My corresponds to 1% average distance between clades (Table 2). Rank order of cladistic nodes and distances is preserved within 1%, except that the *Relictus*–*Eremichthys* distance is 15%.

divergence per one million years for that gene and that clade (Figure 14), with an indication of the reliability of that estimate (Table 2). Once we have estimated the rate of change for a gene in a taxon, we can return to the cladogram and can estimate the amount of absolute time elapsed between sister clades in different basins, as estimated by genetic differences. Cladograms (without time) can then be recast as phylogenies (with estimates of time), as in Figures 2, 10, and 11. The estimated rate depends upon the correction factor for back mutations at all base pair sites. For example, the Tamura–Nei correction, used herein, gives 50 percent higher sequence-divergence values and older branch times (for the older cyprinids) than *p* distances or the Kimura two-parameter correction (Tamura and Nei, 1993).

In the analyses below, both morphological and molecular cladistic estimates of rates of change are presented for the Cyprinidae (Figures 2, 3), but the molecular cladistic estimate is used to frame the relative-rate test. Correlations between the node sequences of the molecular trees and percent sequence divergence are positive and significant; correlations between node sequences of the morphological trees and percent sequence divergence are not significant.

Different kinds of hydrographic connections between basins affect molecular-rate estimates differently. For example, lacustrine spillovers of lakes into rivers that transferred low-elevation suckers, minnows, pupfishes, lacustrine trouts, and whitefishes occurred in sometimes datable pluvial times during

glacial cycles (e.g., Lake Bonneville’s spillover, McCoy, 1987), but headwater stream captures that transferred cold-water, high-gradient mountain suckers, salmonids, and sculpins occurred more frequently (e.g., between the Bear, Snake, and Green Rivers). Therefore, large, lowland fishes will generally contribute to older time estimates, whereas headwater fishes contribute to younger estimates. This is independent of the question of whether headwater fishes evolve more rapidly (Smith, 1992b).

There are two alternative general hypotheses for times of divergence of Great Basin fishes. The first alternative is that a population was devoid of genetic structure prior to the most recent connection. Alternatively, differentiation may date not from the most recent connection and disconnection, but from a previous period of high water in the Pleistocene or Pliocene (see discussions of Whitehorse and Bonneville cutthroat trout and Death Valley pupfishes, below). Consideration of a broader range of possible isolation phenomena, along with dated fossils and molecular data, enable us to test alternative hypotheses about timing of divergence.

Several additional problems may detract from the generality of these methods. In particular, fish fossils are limited, and some possess few apomorphic characters. More complete molecular cladograms for more taxa are also needed. In addition, mtDNA data may have suffered introgressive loss of evolutionary information in basins that frequently changed connections

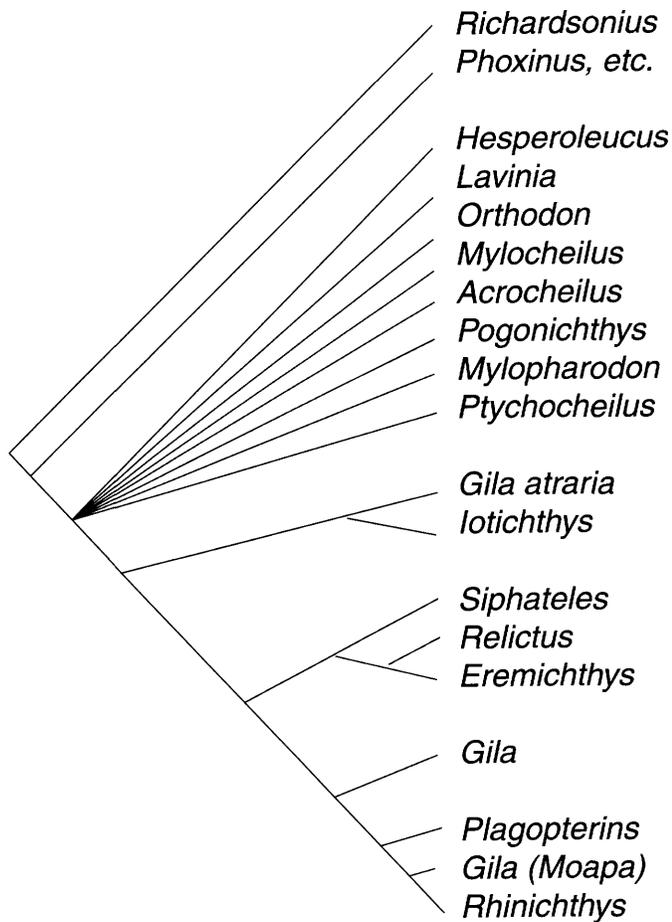


FIGURE 3.—Morphological phylogeny of western Cyprinidae after Coburn and Cavender (1992). This tree was extracted from a consensus tree, which was based upon 100 equally parsimonious trees representing a larger sample of cyprinid fishes.

among allopatric populations (Smith, 1992a; Echelle and Dowling, 1992; Dowling and Secor, 1997).

Cladistic patterns and estimated amounts of molecular divergence are presented in the "Results." Distinct population units are listed and indexed in the Appendix, with their diagnostic characters, location, fossil ages, and brief history. Statements about the kinds of characters and the qualitative degree of differentiation seen between sister units are included to enable comparisons with our molecular- and fossil-based hypotheses about rates of evolution.

Authors of recent species and subspecies names are given in the Appendix, following Robins et al. (1991). Citations and authors of species names of fossils are given in the Appendix. Institutional abbreviations are defined in Table 1.

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Robert Miller and his family and students collected thousands of fossil fish bones. Dwight W. Taylor was important in

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#### Results

Fifty-two recent species—19 Cyprinidae, 12 Catostomidae, eight Salmonidae, five Cyprinodontidae, four Goodeidae, and four Cottidae—comprise the Holocene Great Basin fish fauna. Twenty-seven of these species are endemic. Four species among the cyprinids, goodeids, and cottids have been driven to extinction, and two species or subspecies of salmonids have been extirpated from the Great Basin as a result of habitat destruction caused by human activities (Minckley and Deacon, 1991). Among the 52 species (especially cyprinids, salmonids, and cyprinodonts), more than 50 additional isolated populations have been recognized as separate subspecies. Sixty-four fossil forms, from the late Miocene to the present, represent many recent lineages and several clades that are now locally extinct (for example, Gasterosteidae and Centrarchidae). Fossil

fishes are now known from 55 Great Basin localities (Figure 1; Table 1); several hundred additional fossil localities occur at the northern edge of the Great Basin, on the Snake River Plain. Extensive analyses of mtDNA divergence have been carried out on recent representatives of these fossil forms: Dowling et al. (2002) on Cyprinidae (minnows), Echelle and Dowling (1992) on Cyprinodontidae (pupfishes), and Shiozawa and Evans (1995) on Salmonidae (trouts).

CYPRINIDAE.—Minnows, family Cyprinidae, are the most diverse and widespread fishes in the Great Basin; the 19 Holocene lineages include 10 endemic species and more than 20 endemic subspecies. Three species of minnows, *Gila atraria*, *Siphateles bicolor*, and *Rhinichthys osculus*, have been especially persistent and have differentiated into many distinct subspecies and local populations. Unfortunately, small minnows are under-represented in the Great Basin fossil record, so they contribute little to our estimates of rates of molecular evolution. At least five lineages, *Ptychocheilus*, *Mylocheilus inflexus*, *M. robustus*, *Mylopharodon*, and *Lavinia* (exclusive of *Hesperoleucus*), lived in the Great Basin in the Pliocene and Miocene but are absent there today. *Siphateles* is the best represented genus in the fossil record, occurring in the Miocene to Pleistocene of the Lahontan Basin and Mohave River drainages.

Fossil and living Cyprinidae in the Great Basin are herein assigned to three ancient clades, which are based on our molecular analyses (Figure 2; see also Simons and Mayden, 1997, 1998). These three clades are older than the Great Basin, and molecular evidence indicates that they probably date back to the Oligocene (Table 2; Appendix). The first of the three clades (Figure 2) in the Great Basin (including fossils) is the large western North American chub group that includes *Mylopharodon*, *Lavinia*, *Hesperoleucus*, *Siphateles*, *Gila*, *Acrocheilus*, *Klamathella*, *Ptychocheilus*, *Eremichthys*, and *Relictus* (Appendix, numbers 1–32). These are related to *Orthodon* in the Sacramento drainage system and to *Phoxinus* in eastern North America. This “Western Chub clade” has four subgroups in the Great Basin: (1) the *Mylopharodon*–*Lavinia*–*Hesperoleucus* and *Siphateles* clade (Appendix, numbers 1–22); (2) the *Gila*–*Acrocheilus*–*Klamathella* clade, with *Ptychocheilus lucius* as its sister group (Appendix, numbers 23–29); (3) the *Relictus*–*Eremichthys* clade, including *Ptychocheilus grandis* (Appendix, numbers 31–32); and (4) the *Ptychocheilus oregonensis* clade (Figure 2; Appendix, number 30). Whether or not *Ptychocheilus* is actually paraphyletic, as indicated by Figure 2, is problematical. *Ptychocheilus* cf. *oregonensis* is one of the oldest cyprinids in the region (Smith et al., 2000).

The second major cyprinid group in the Great Basin is the *Snyderichthys*–*Lepidomeda* (spinedace) clade (Appendix, numbers 33–35). It is related to the other spinedaces, which inhabit tributaries of the Bouse Embayment (see below). Sister groups of this clade include *Margariscus* and *Couesius* of northern and eastern North America.

The third major minnow clade includes western American outliers of the huge eastern North American shiner clade. Western forms include *Iotichthys* (Appendix, number 36), *Richardsonius* (Appendix, numbers 37–39), *Rhinichthys* (Appendix, numbers 40–55), and *Mylocheilus* (Figure 2; Appendix, numbers 56–58). This group also includes *Pogonichthys* of the Sacramento drainage system. An alternate cladistic hypothesis (Figure 3), based upon morphological analysis, shows different interpretations of relationship (Coburn and Cavender, 1992).

Great Basin cyprinids are listed (Tables 1, 2), numbered, and reviewed in the Appendix in approximately the sequence given in Figure 2. Typical distribution patterns of minnows (illustrated by *Gila* and *Siphateles*) are shown in Figure 4.

Fossil minnows in the Great Basin date back to the middle Miocene or earlier (Cavender, 1986; Reynolds, 1994). Many cyprinid genera are early members of the Great Basin fauna (Appendix, numbers 5, 14, 15, 26–28, 30, 56–58). The *Gila* group is widespread and especially diverse in all of the Great Basin as well as in the Colorado River drainage, the Rio Grande, and northern Mexico. *Siphateles* is centered in the Lahontan Basin and Sacramento River drainages, and *Gila* is in the drainages surrounding the Lahontan Basin. The Great Basin part (White River) of the lower Colorado River (Bouse Embayment) drainage is inhabited by *Lepidomeda*, *Moapa*, and *Gila*, as well as by *Catostomus clarki* and the empetrichthyine good-eids. *Snyderichthys copei* of the Bonneville Basin and upper Snake River drainages is cladistically part of the Plagopterin group and provides evidence of Pliocene and Pleistocene drainage connections (Dowling et al., 2002). The southern California coastal form, *Gila orcutti*, is the sister group to *Gila atraria* of the Great Basin and to *G. jordani* and *G. cypha* of the Colorado River drainage.

Electrophoretic variation in *Gila atraria* of the Bonneville Basin was studied by Rosenfeld (1991), who concluded that accumulated differences were influenced more by natural selection in local springs, lakes, and streams than by vicariance and time. He estimated that 14,500 years was too short an interval for the accrual of qualitative differences between hierarchical groups of vicariant populations. Populations of *Gila atraria* from northern and southern Bonneville basins and from the Bear River have diverged extensively in their mtDNA; they have not remained uniform during the last 2 My (sequence divergence = 0.009–0.024) despite recent and probably frequent sympatry. The northern Bonneville form of *G. atraria* shares an unexpectedly high proportion of its mtDNA with *G. cypha* and *G. jordani* of the Colorado River (percent sequence divergence = 1.1% and 0.7%, respectively; Table 2), supporting the hypothesis that a connection existed from Lake Bonneville through Meadow Valley Wash, Nevada, to the Colorado River drainage (Ives, 1948).

A separate biogeographic pattern encompasses the northern Great Basin and the Columbia River and Snake River drainages. This pattern is marked by the distributions of *Klamathella*, *Siphateles*, *Acrocheilus*, *Lavinia*, *Mylopharodon*, and

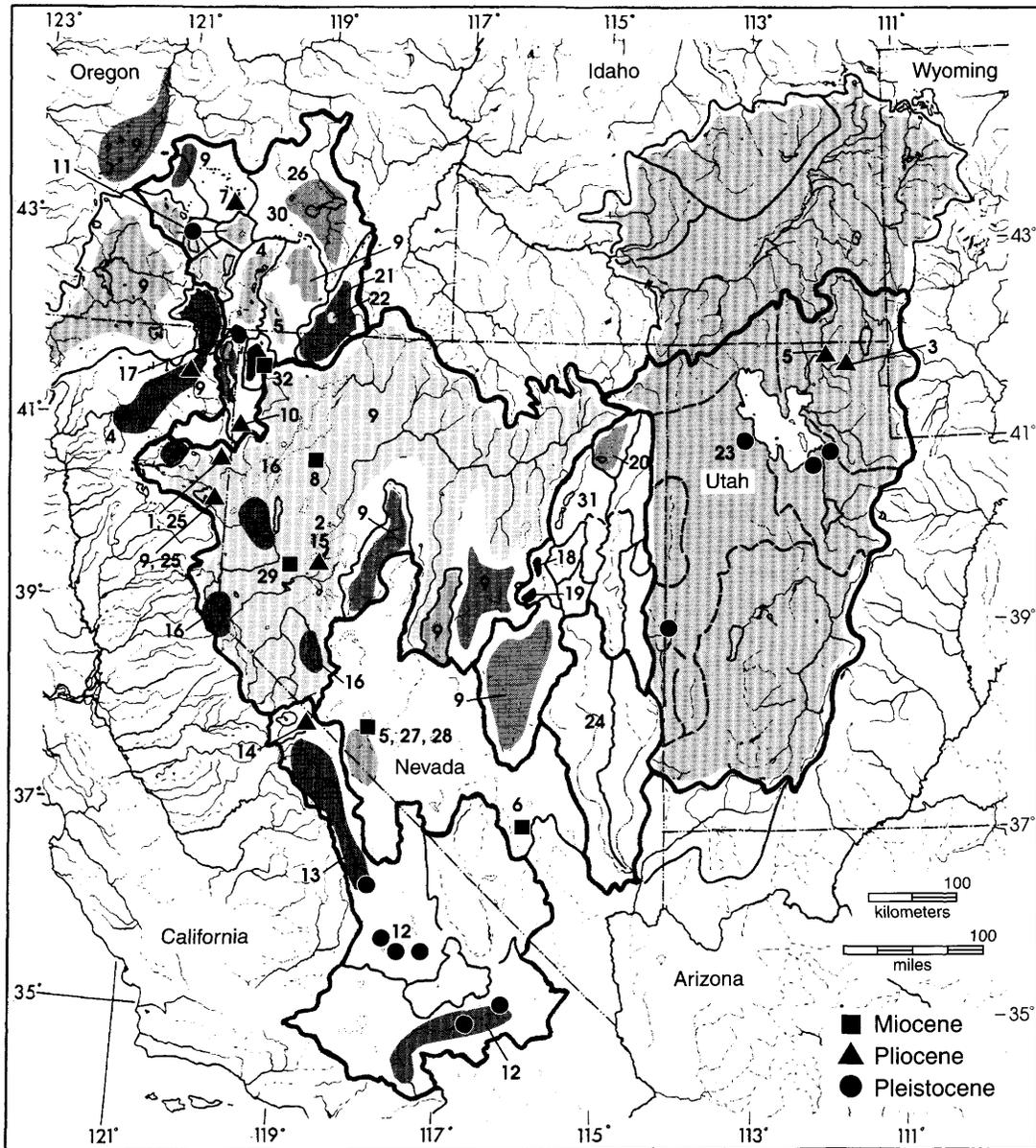


FIGURE 4.—Distribution of Holocene and fossil *Siphateles*, *Gila*, and certain relatives in the Great Basin. Map shading indicates different species or subspecies ranges. Ages of fossil fish are indicated by symbols defined on the figure. Numbers refer to species or subspecies listed in the Appendix.

*Mylocheilus* in a Columbia–northern Great Basin–Pit River track. At a lower cladistic hierarchical level, this biogeographic pattern broadens to include the Sacramento River drainage, with *Ptychocheilus grandis*, *Hesperoleucus*, and *Orthodon* (Figures 2, 3), and the Colorado River drainage, with *Ptychocheilus lucius*. The several Great Basin records of *Mylocheilus* and *Mylopharodon* are evidence of a late Miocene connection between west-central and northwestern Nevada and the Snake River Plain. *Mylocheilus caurinus* (Table 2, number 58) is the closest living relative to *Mylocheilus robustus* of the Mio–Pliocene Snake River Plain (Appendix, number 58) and to

*Mylocheilus heterodon* from the Ringold Formation of Washington (Smith et al., 2000).

Pairwise distances among clades that are based upon a parsimony cladistic analysis enable evaluation of relative rates of molecular change (Table 2). The homogeneity of these rates among minnows can be evaluated by comparing the standard deviation (s.d.) around the mean distances. The 26 species estimated to share a common ancestor with *Phoxinus* have a mean distance between each of them and *Phoxinus* of 0.22 (s.d. = 0.022). The 66 combinations of sister species to *Mylopharodon*, *Lavinia*, and *Hesperoleucus* have a mean distance of 0.15

(s.d. = 0.02); the 38 combinations of *Siphateles* sister species have a mean distance of 0.12 (s.d. = 0.02); the 30 species of the *Gila orcutti*-*G. atraria* group have a mean distance of 0.08 (s.d. = 0.02); the 26 sister species to *Acrocheilus* and *Klamathella* have a mean distance of 0.08 (s.d. = 0.02); the 216 combinations of the spinedaces have a mean distance of 0.34 (s.d. = 0.03); and the 210 combinations of the western representatives of the shiner clade have a mean distance of 0.35 (s.d. = 0.05). With the rate of divergence estimated at about 1% per one million years, the standard deviations of group or barrier ages is usually on the order of 10%, but rarely more than 25%, of the estimated age (Table 2). The distances and inferred

timing of cyprinid patterns span the time from Miocene to the last postglacial period.

CATOSTOMIDAE.—Catostomids are the most ancient of the fish groups present in the Great Basin (Cope, 1872; Smith, 1966, 1992b; Minckley et al., 1986). They are also among the largest and hardiest aquatic survivors of the Great Basin's historically variable climate and ecology. Catostomidae are the second most diverse and abundant family in the Great Basin, with 12 species, but the maximum number of sympatric forms is three or four. Great Basin suckers are part of a primarily western American monophyletic group (Figure 5), the Catostomini, whose sister group (and outgroup in the analysis) is the

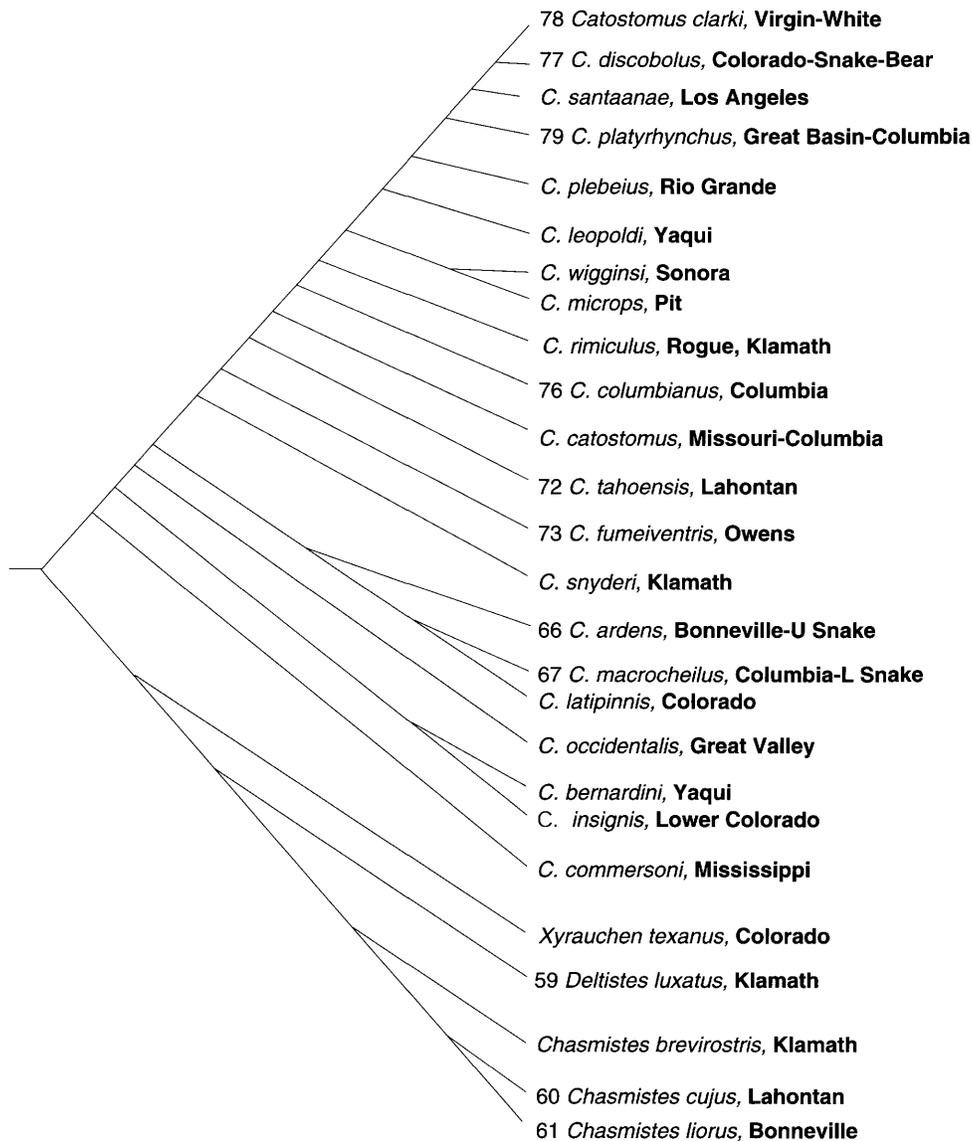


FIGURE 5.—Estimate of the phylogenetic tree for *Chasmistes*, *Deltistes*, and *Catostomus* in the Great Basin and their relatives in the Catostomini (from Smith, 1992b). Not all species of *Chasmistes* were included in the cladistic analysis. Numbers refer to the species accounts in the Appendix.

Moxostomatini of the eastern United States and Mexico (Smith, 1992b).

The Catostomini range from medium-sized, benthic, head-water species in the subgenus *Pantosteus* (genus *Catostomus*) (Figure 7), to large-sized benthic predators in low-gradient streams (other *Catostomus*, Figure 6), to large-sized planktivores in large lakes (*Chasmistes*, Figure 7). The fossil record of catostomids is diverse; it includes plesiomorphic forms as well as forms that were morphologically more specialized than present-day species. Fossil *Catostomini* are known from the

Miocene (10 Ma) to the Holocene, with Great Basin diversity reaching a peak of four species in the northern Bonneville Basin (and upper Snake River and upper Colorado River basins) in the late Pleistocene (see Appendix, numbers 59–79). Catostomids are tetraploid fishes that show abundant hybridization and extreme variation, but no indication of rapid speciation (Smith, 1992b).

There are two clades of Catostomini in the Great Basin (Smith, 1992b). The first is the genus *Chasmistes*, the lake suckers. Four Holocene species of *Chasmistes* are localized in Utah

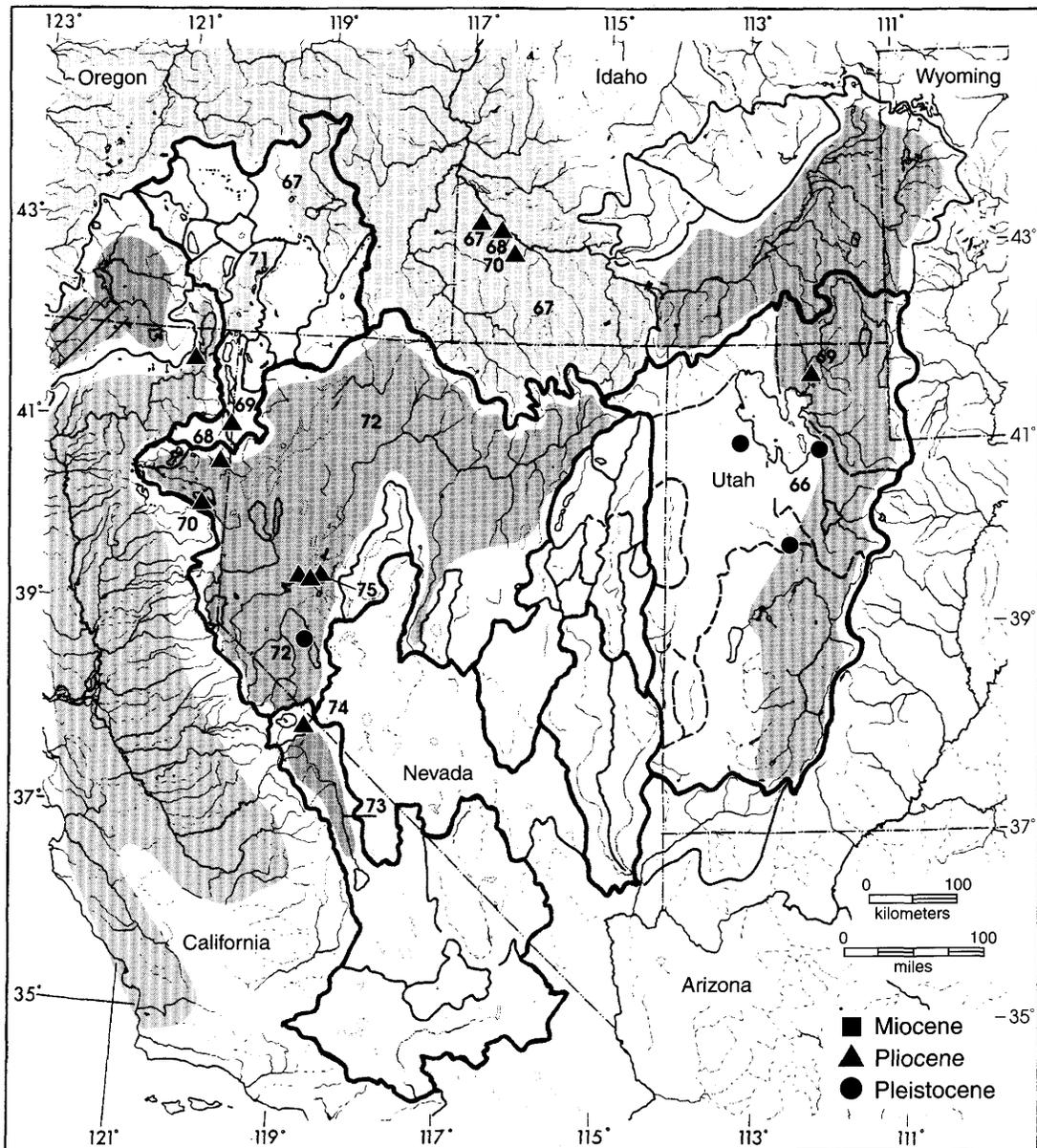


FIGURE 6.—Native distribution of *Catostomus ardens* (Utah, 66), *C. macrocheilus* (Idaho, 67), *C. fumeiventris* (southern California, 73) and *C. tahoensis* (Nevada, 72) in the Great Basin and some of their relatives outside the Great Basin. Shading indicates drainage basins occupied by species (as numbered in the Appendix). Fossil records and Holocene occurrences are indexed to the numbered species accounts in the Appendix. Ages of fossil fish are indicated by symbols defined on the figure. These are low-gradient fishes that required a major river or lake connection to cross a drainage divide.

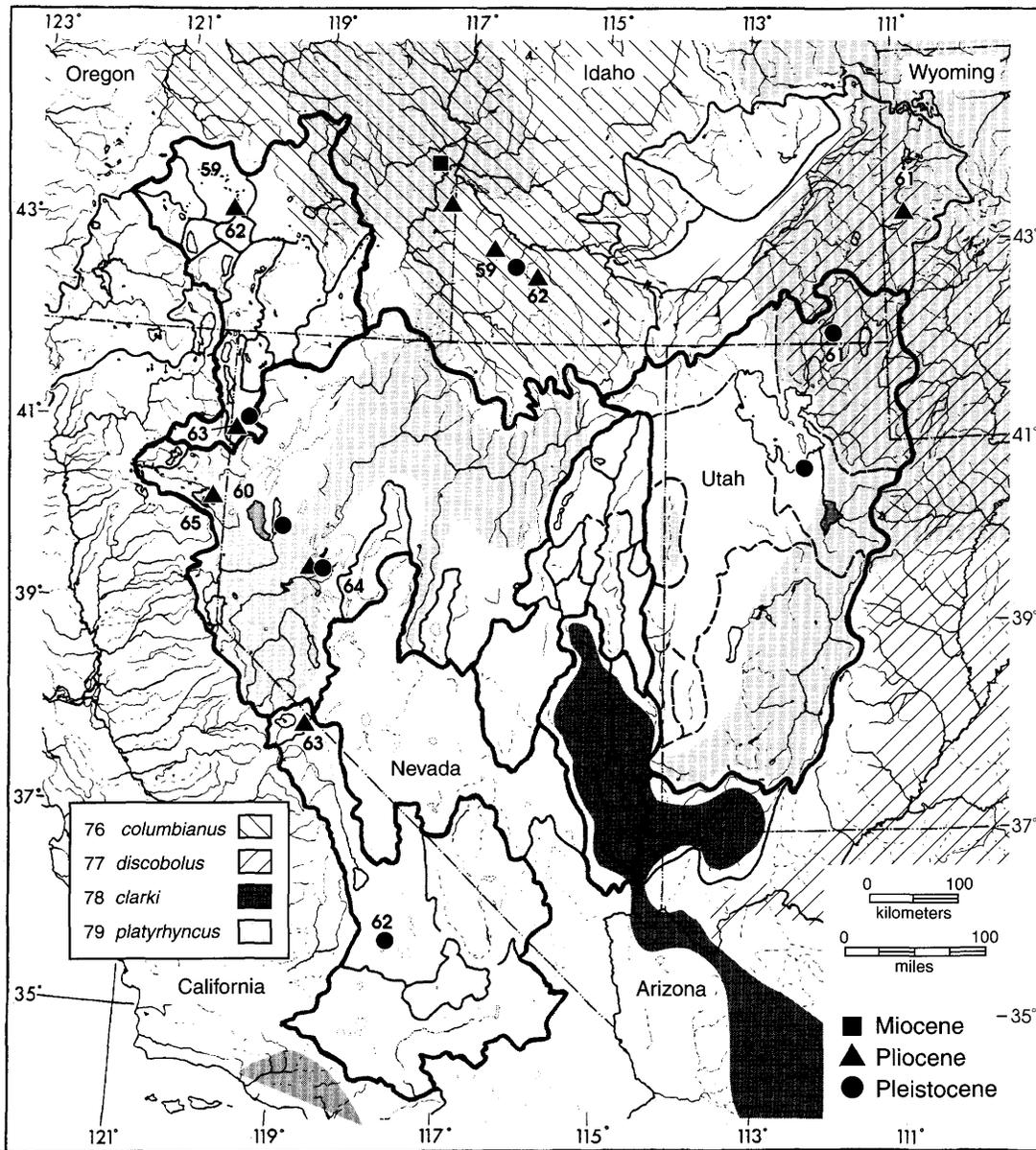


FIGURE 7.—Distribution of the mountain suckers: *Catostomus platyrhynchus* (Utah, Idaho, Wyoming, Nevada, 79), *C. columbianus* (Idaho, Oregon, 76), *C. clarki* (southern Nevada, 78), and *C. discobolus* (Utah, Wyoming, Idaho, Colorado, 77) in the Great Basin and of their relatives (*C. rimiculus*, Oregon; *C. santaanae*, California) outside the Great Basin. Ages of fossil *Chasmistes* and *Deltistes* in the Great Basin are indicated by symbols defined on the figure. Numbers refer to the species accounts in the Appendix.

and Pyramid Lakes, in Klamath River (Figure 7), and in the headwaters of the Snake River. There are also numerous Miocene to Holocene fossil *Chasmistes* specimens in the Great Basin (Miller and Smith, 1981; Figure 7). Silicified gill-raker plates with fimbriate distal ends have been found in the Mono Lake basin. Fimbriate distal ends are an apomorphy for *Chasmistes*. Their presence in Mono Lake deposits indicates this adaptation to planktivory occurred 4–3 Ma (Gobalet, unpublished data). The sister genera to *Chasmistes* are *Xyrauchen* and *Del-*

*tistes* (Appendix, number 59) of the Colorado River and the Klamath system, respectively. The modern lake sucker in Utah Lake, *Chasmistes liorus mictus* Miller and Smith (1981), shows intense introgression from *Catostomus ardens*. The introgressive event is remarkable because *Chasmistes* and *Catostomus* diverged 10–4 Ma (both genera are morphologically distinct in Pliocene sediments of the Snake River Plain; Smith et al., 1982).

The second clade is the genus *Catostomus*, which includes two ecological groups that were formerly classified as subgenera

(Smith, 1966; Smith and Koehn, 1971). As now understood, the subgenus *Pantosteus* (mountain suckers) (Appendix, numbers 76–79) is monophyletic, but recognition of *Pantosteus* makes the subgenus *Catostomus* paraphyletic (Smith, 1992b). The more plesiomorphic species of catostomids are usually restricted to lowlands in basins (Figure 6), where they inhabit low-gradient rivers or lakes in a vicariant pattern. These species are *C. ardens* in the Bonneville Basin, *C. macrocheilus* in the Harney–Malheur Basin (and Columbia River basin), *C. warnerensis* in the Warner Lakes basin, *C. tahoensis* in the Lahontan Basin, *C. fumeiventris* in the Owens River basin, and *C. shoshonensis* in Wall Canyon of Surprise Valley (Appendix, numbers 66–75; Figures 5, 6). Fossil *Catostomus* (10 Ma to Holocene) are known from the north edge of the Great Basin, which is along the southern margin of the Snake River Plain.

The mountain suckers (*C. columbianus*, *C. platyrhynchus*, *C. discobolus*, *C. clarki*) are morphologically derived (Smith, 1992b). They inhabit high-gradient streams and stream headwaters, and they have been broadly dispersed by many headwater transfers (Figure 7; Smith, 1966). *Catostomus platyrhynchus* has been transferred from the Bonneville Basin to the Lahontan Basin and to the drainages of the Snake/Columbia, Colorado, and Missouri Rivers. *Catostomus discobolus* is native to the upper Colorado River, including the Grand Canyon, and has been transferred among the Colorado River and Snake River drainages to the Bear and Weber Rivers in the northern Bonneville Basin. *Catostomus clarki* is found in the drainages of the Gila, Virgin, and White Rivers, but not the Colorado River in and above the Grand Canyon, and it helps define the Pliocene drainage of the Bouse Embayment of the Gulf of California during the time when it might have been blocked from its connection with the upper Colorado River drainage (Taylor, 1983). *Catostomus santaanae*, in the Los Angeles area (Figure 7), is the sister species to the Colorado River species, *C. discobolus* and *C. clarki*. *Catostomus santaanae* represents the population that lived in the lowest Colorado Paleoriver when it flowed to its Los Angeles delta, prior to 9 Ma. *Catostomus columbianus* inhabits both the Harney–Malheur Basin and the Columbia River drainage and helps to define the overflow through the South Fork of the Malheur River to the Snake River across the Voltage lava flow (Piper et al., 1939), which occurred as recently as about 9000 years B.P. (Gehr and Newman, 1978).

ICTALURIDAE.—North American catfishes of the genus *Ameiurus* were rare in the Great Basin. Two Miocene forms are known (Appendix, numbers 80, 81), one from the Truckee Formation in Nevada and one from formations in the Salt Lake group in northern Utah. Their relatives include fossils in the Pliocene Columbia River, Miocene and Pliocene Snake River, and Miocene to Holocene rivers in eastern North America (Lundberg, 1992; Smith et al., 2000). These occurrences provide additional evidence for former Great Basin connections to the Snake River Plain and to south-central Washington before the formation of the modern Columbia drainage. The Miocene

form from northern Utah is most similar to bullheads of the Snake River Plain, supporting a Hemphillian or older connection between the Salt Lake group and Lake Idaho (Taylor, 1966; Stokes, 1979). No *Ameiurus* are known from the southwestern United States or Mexico, despite the diversity of other genera of catfishes in Mexico (Lundberg, 1992).

SALMONIDAE.—Eight native species of salmonids apparently inhabited the Great Basin in recent times: rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*, with many subspecies), bull trout (*Salvelinus confluentus*), four whitefishes (*Prosopium* spp.), and possibly the Arctic grayling (*Thymallus arcticus*). Additional trouts and char are represented in the fossil record. Salmonids are cool-water fishes that inhabit mountain streams and deep lakes. Their distribution patterns indicate that they dispersed among basins via headwater-stream captures as well as by discharge from pluvial lakes. During interglacial times (such as the present), desiccation and warming of aquatic habitats restricts these fishes to small populations in a few cool lakes, rivers, and headwaters. During pluvial stages of the last 3 My, however, there were numerous, large populations (see Appendix) in large, deep lakes and large rivers. Salmonids from the Miocene, Pliocene, and Pleistocene are known to have occurred in lake basins, such as the Salt Lake group, Fort Rock Lake basin, Lahontan Basin, Honey Lake basin, Bonneville Basin, and Owens Basin. Holocene salmonids are found in drainages west, north, and east of the Great Basin, and in a few drainages at high elevations in Mexico.

COREGONINAE: There are six recent species of whitefishes in the genus *Prosopium* of the subfamily Coregoninae. Four live in the Great Basin; three of these are endemic to Bear Lake in Utah and Idaho (Appendix, numbers 82–85). The other two, *P. cylindraceum* and *P. coulteri*, inhabit eastern to northwestern North America and Siberia (Smith and Todd, 1993). At least one fossil species, *P. prolixus* Smith (1975), is common in Pliocene sediments of the Snake River Plain. The morphologically based, cladistic estimate of relationships of the species in the group is shown on a distribution map (Figure 8). Unpublished molecular data (Shiozawa) indicates a more complicated pattern than that depicted in Figure 8. *Prosopium* illustrates intralacustrine as well as allopatric speciation in Bear Lake and in subbasins of the Bonneville–Bear system. As predicted by the intralacustrine speciation hypothesis, the differentiated characters among the species of *Prosopium* are mostly associated with feeding: the shape of the mouth and jaw and the numbers of teeth, gill-rakers, and pyloric caeca (Smith and Todd, 1993). The phylogenetic pattern indicates that the most-derived forms in the genus evolved in the Bonneville Basin and Bear Lake.

THYMALLINAE: Grayling (*Thymallus*) have not been regarded as part of the Great Basin fauna. There are no fossil or Holocene specimens documenting their presence. Inclusion in the present list is based upon the apparently knowledgeable identifications in the journal of John Townsend (1978), who recorded collecting grayling in the Bear River in 1834 (Appendix, number 86).

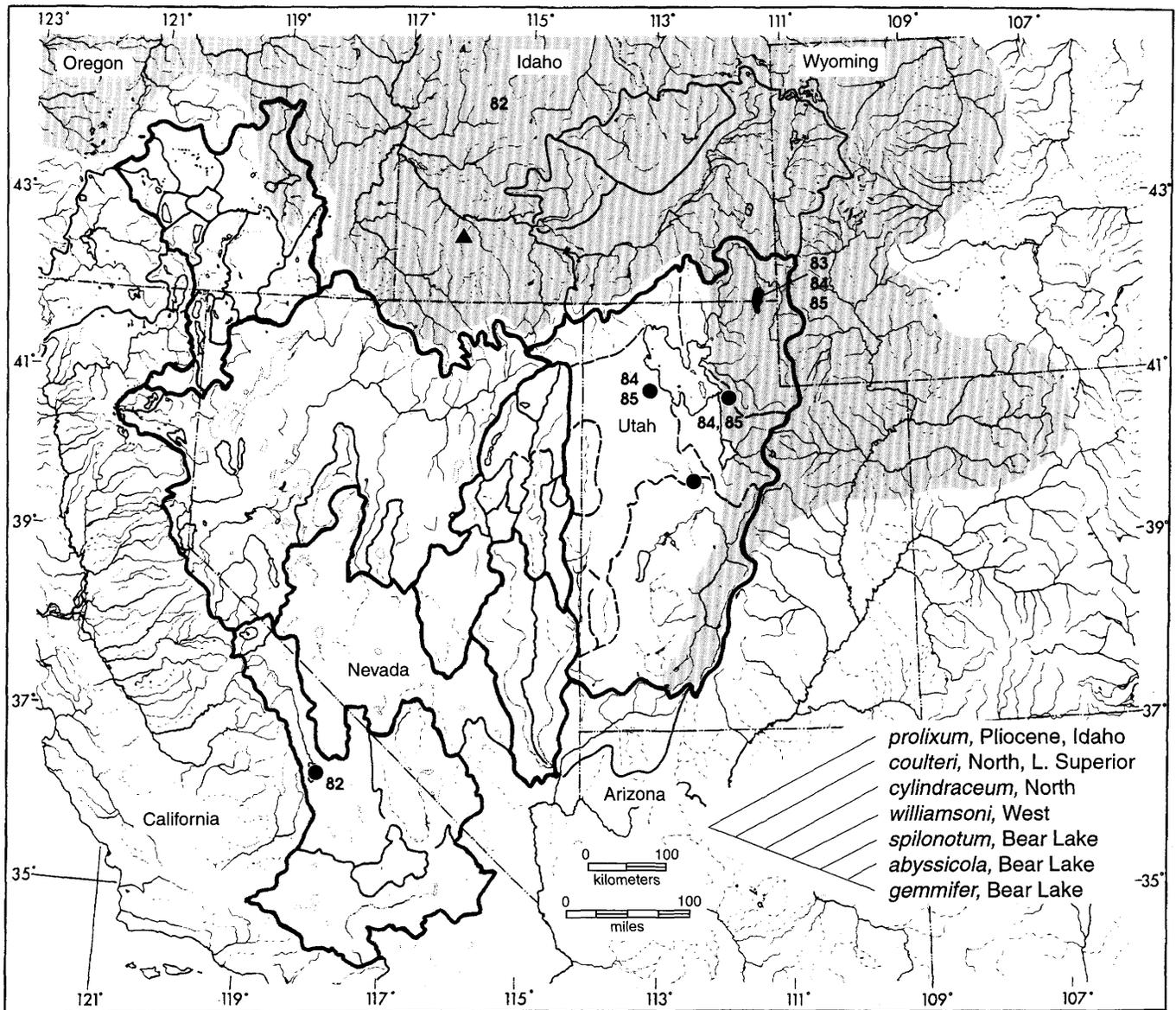


FIGURE 8.—Native distribution of *Prosopium* (shown with shading) in the Great Basin and nearby drainages, with estimate of the phylogenetic tree (from Smith and Todd, 1993). Shading indicates drainage basins occupied by species (as numbered in the Appendix). Symbols representing fossil ages are defined in Figure 1.

**SALMONINAE:** Settlers in the nineteenth century found abundant trout in many northern Great Basin lakes and streams (map, Figure 9), but these were quickly overexploited (Behnke, 1992). By the 1930s, introduced hatchery fish began to cloud the possibilities for interpreting salmonid and hydrographic history (Behnke, 1981, 1992), and unfortunately museum specimens that predate these introductions are sparse. Modern protein and mtDNA studies are, however, discriminating native from introduced stocks and are adding considerable historic information (Leary et al., 1984, 1987). Trouts are adapted to cold lakes and streams and to high gradients. Stream forms survived arid times at high elevations and gla-

cial times in large lakes. There are indications that, in addition to trouts (*Oncorhynchus*), at least two char (*Salvelinus*) were native to the northern Great Basin; this evidence is reviewed in the Appendix (number 87). The fossil record of *Salvelinus* is older than the fossil record of *Oncorhynchus*. *Salvelinus* was in the Great Basin (central Nevada) and northern Idaho in the middle Miocene and in the Snake River Plain in the late Miocene.

The late Miocene *Oncorhynchus* of the Truckee Formation differs in many characters from modern species of *Oncorhynchus*. It possesses synapomorphies that are shared by *O. clarki*, indicating it is more advanced than the basal Mexican golden

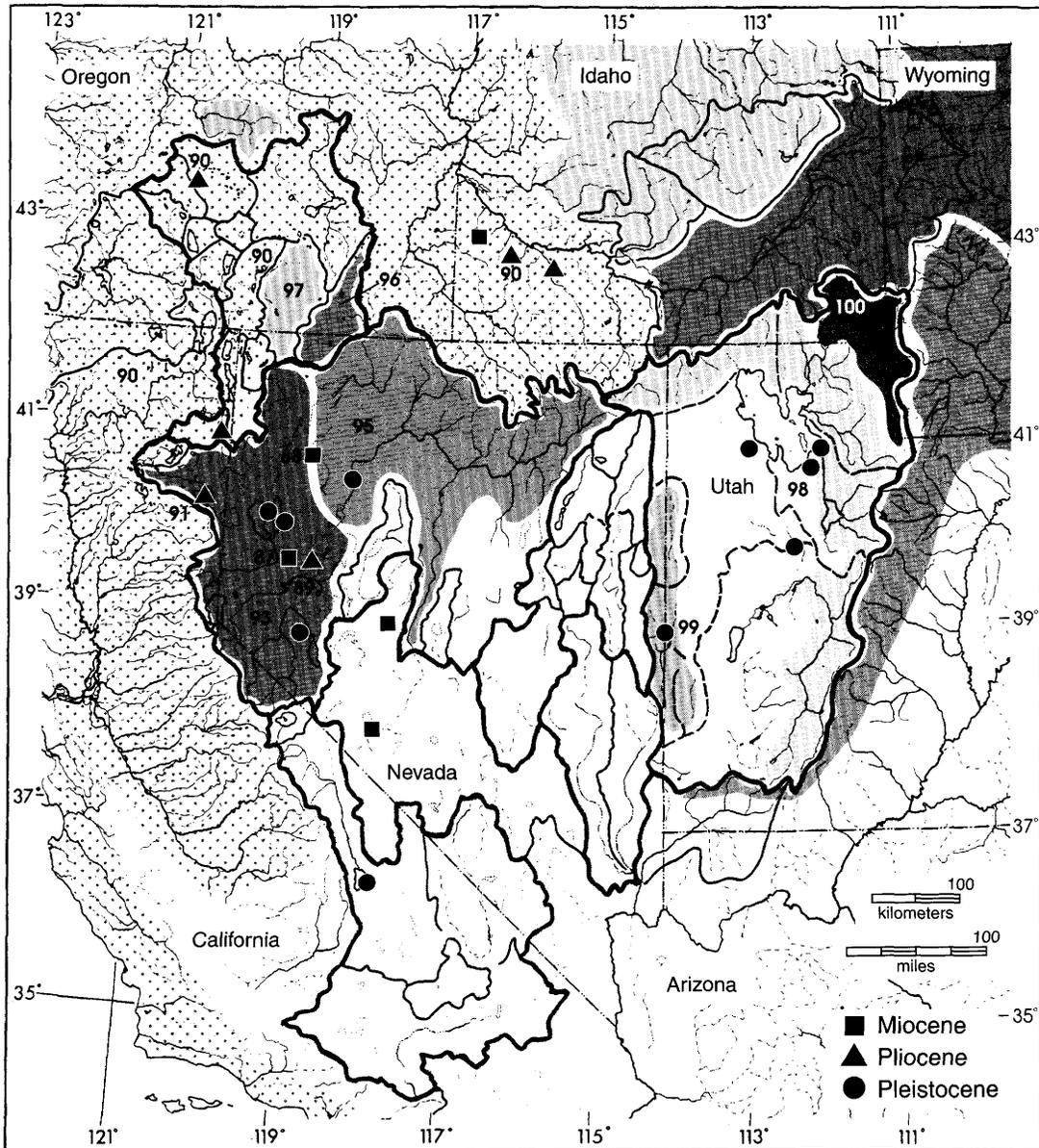


FIGURE 9.—Distribution of Holocene and fossil species and subspecies of rainbow trout (*Oncorhynchus mykiss*, stipple pattern) and cutthroat trout (*O. clarki*, shaded patterns) in the Great Basin and adjacent drainages. Shading indicates drainage basins occupied by species and subspecies (as numbered in the Appendix). Squares = Miocene; triangles = Pliocene; bullets = Pleistocene.

trout, *O. chrysogaster*. The characteristics of the Truckee trout indicate that it existed before the differentiation of rainbow trout and cutthroat trout (Stearley and Smith, 1993), while its habitat was connected to the Pacific Ocean. As early as late Miocene and throughout the Pliocene, the trout, †*Oncorhynchus* (“*Rhabdofario*”) *lacustris* (Cope), of the lower Snake River drainage and northwestern Nevada, shows a composite of *O. clarki* (cutthroat trout) and *O. mykiss* (rainbow trout) characters, e.g., *O. clarki* dentaries, intermediate maxillae, and *O. mykiss* premaxillae. These characters diagnose either the ancestor prior to the *clarki*–*mykiss* divergence or the ancestral

redband trout (*Oncorhynchus mykiss gairdneri*). The distinction cannot be made at this time because intermediates between *O. clarki* and *O. mykiss* still exist, especially in the Columbia Basin. Characters of these trout subsequently sorted into *O. mykiss* and *O. clarki* elsewhere, but they continue to be introgressed or unsorted in redband trout throughout their range in the lower Columbia River, Klamath River, and Sacramento River drainages (Leary et al., 1984, 1987; Berg, 1987; Allendorf and Leary, 1988), possibly throughout much of the last 3 My. A sample of hatchery-produced *O. mykiss* differs from *O. clarki* by 3.7% mtDNA (Table 3).

TABLE 3.—Sequence divergences, based on mtDNA restriction-site data, for *Oncorhynchus clarki* populations and their outgroup species, *Oncorhynchus mykiss*. (Cr. = Creek, R. = River.)

Species or population	<i>O. mykiss</i>	Trout	Deaf Smith	Sevier	Bear	Yellow-stone	Snake	Sedge	Current	Sheep	Mack	Flynn	Fish	Wing	Cougar	Wash-burn	Humbolt	Silver-king	Willow	White-horse	
<i>O. mykiss</i>	0																				
Trout Cr.	0.039	0																			
Deaf Smith Cr.	0.057	0.023	0																		
Sevier R.	0.036	0.008	0.023	0																	
Bear R.	0.041	0.014	0.035	0.015	0																
Yellowstone R.	0.036	0.014	0.035	0.015	0.004	0															
Snake R.	0.037	0.012	0.035	0.013	0.003	0.002	0														
Sedge Cr.	0.037	0.012	0.035	0.013	0.003	0.002	0	0													
Current Cr.	0.033	0.012	0.032	0.010	0.009	0.008	0.007	0.007	0												
Sheep Cr.	0.033	0.012	0.032	0.009	0.009	0.008	0.007	0.007	0	0											
Mack Cr.	0.040	0.018	0.040	0.017	0.018	0.018	0.018	0.018	0.014	0.014	0										
Flynn Cr.	0.040	0.018	0.040	0.017	0.018	0.018	0.018	0.018	0.014	0.014	0	0									
Fish Cr.	0.037	0.018	0.040	0.016	0.016	0.016	0.016	0.016	0.010	0.010	0.011	0.011	0								
Wing Cr.	0.036	0.019	0.040	0.016	0.014	0.014	0.014	0.014	0.008	0.008	0.013	0.013	0.003	0							
Cougar Cr.	0.037	0.020	0.042	0.017	0.013	0.013	0.012	0.012	0.009	0.009	0.014	0.014	0.004	0	0						
Washburn Cr.	0.042	0.022	0.036	0.020	0.018	0.018	0.018	0.018	0.012	0.012	0.018	0.018	0.009	0.007	0.008	0					
Humbolt R.	0.042	0.022	0.036	0.020	0.018	0.018	0.018	0.018	0.012	0.012	0.018	0.018	0.009	0.007	0.008	0.001	0				
Silverking Cr.	0.042	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.017	0.017	0.009	0.007	0.008	0.001	0.001	0			
Willow Cr.	0.041	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.016	0.016	0.009	0.007	0.008	0.001	0.001	0.001	0		
Whitehorse Cr.	0.041	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.016	0.016	0.009	0.007	0.008	0.001	0.001	0.001	0.001	0	0

*Oncorhynchus clarki*, the cutthroat trout, has been in the Great Basin longer than proposed by Behnke (1981, 1992), according to the Miocene fossil record. Molecular data indicate that interbasin differentiation of *O. clarki* subspecies goes back nearly 5 My, into the Pliocene (Table 3).

The Great Basin trouts form three clades. The Bonneville Basin clade is cladistically basal, being the sister group to the remainder of the species (Figure 10). The Snake River clade is the next-most basal group, and it includes the Bear River form. Although the Bear River is now a tributary to the northern Bonneville Basin, it was part of the Snake River drainage prior to 20–15 Ka (McCoy, 1987; Curry, 1990; Bouchard et al., 1998). The Lahontan Basin and southern Oregon subspecies are a sister group to the westslope trout subspecies, *O. c. lewisi*. Coastal cutthroat trouts, *O. c. clarki*, are an intermediate clade between the Colorado River plus Snake River groups and the Westslope plus Oregon–Lahontan groups (Figures 9, 10).

Fort Rock Valley, west of the Harney–Malheur Basin in Lake County, Oregon, was the site of Fort Rock Lake, also called Fossil Lake, which was a tributary to the Deschutes and Columbia Rivers prior to blockage of the outlet by postpluvial lava flows (Allison, 1940, 1982). Pliocene and Pleistocene sediments in the Fort Rock Valley contain trouts, minnows, and suckers. A Pliocene salmon from diatomaceous sediments of the Fort Rock Formation, *Oncorhynchus* sp. (either *nerka*, *keta*, or *gorbuscha*), was reported by Cavender and Miller (1972). The trout specimens in this basin (*Oncorhynchus* sp.; Appendix, number 90) are osteologically similar to redband trout and were considered to date from the late Pleistocene by Allison and Bond (1983). They based their conclusion upon shared characters of the palatine, maxilla, hyomandibular, and orbitosphenoid. More than 50 dentaries from Fossil Lake were examined for the present study. Forty-seven maxillae have a mixture of modern *O. clarki* (from Pyramid Lake before introductions) features and features of Pliocene *O. lacustris* (pre-*clarki* and pre-*mykiss*) of the Snake River Plain, whereas seven maxillae resemble *O. m. gairdneri* (redband trout). One premaxilla resembles that of *O. clarki* and seven resemble that of *O. mykiss*, but it is not clear whether the differences represent variability in one species. Palatines from Fossil Lake are deep, like that of *O. lacustris*, and the hyomandibular is angled posteroventrally, also like that of *O. lacustris*.

The Pliocene fish fauna of Secret Valley, Modoc County, California (*Oncorhynchus* (Appendix, number 91), *Klamathella*, *Ptychocheilus*, *Lavinia*, *Chasmistes*, and possibly *Acrocheilus* and *Cottus*), and the Pliocene fish fauna of the Snake River Plain are very similar; this suggests the two drainages were connected prior to the Pliocene (Wheeler and Cook, 1954; Miller and Smith, 1981; Wagner et al., 1997). A similar fauna from the nearby Alturas Basin, Modoc County, California, contains *Klamathella*, *Ptychocheilus*, *Chasmistes*, and *Catostomus* (Wagner et al., 1997). These similarities suggest former hydrographic connections (not necessarily contemporaneous) among the Pit River, the Snake River, and the Klamath Basin.

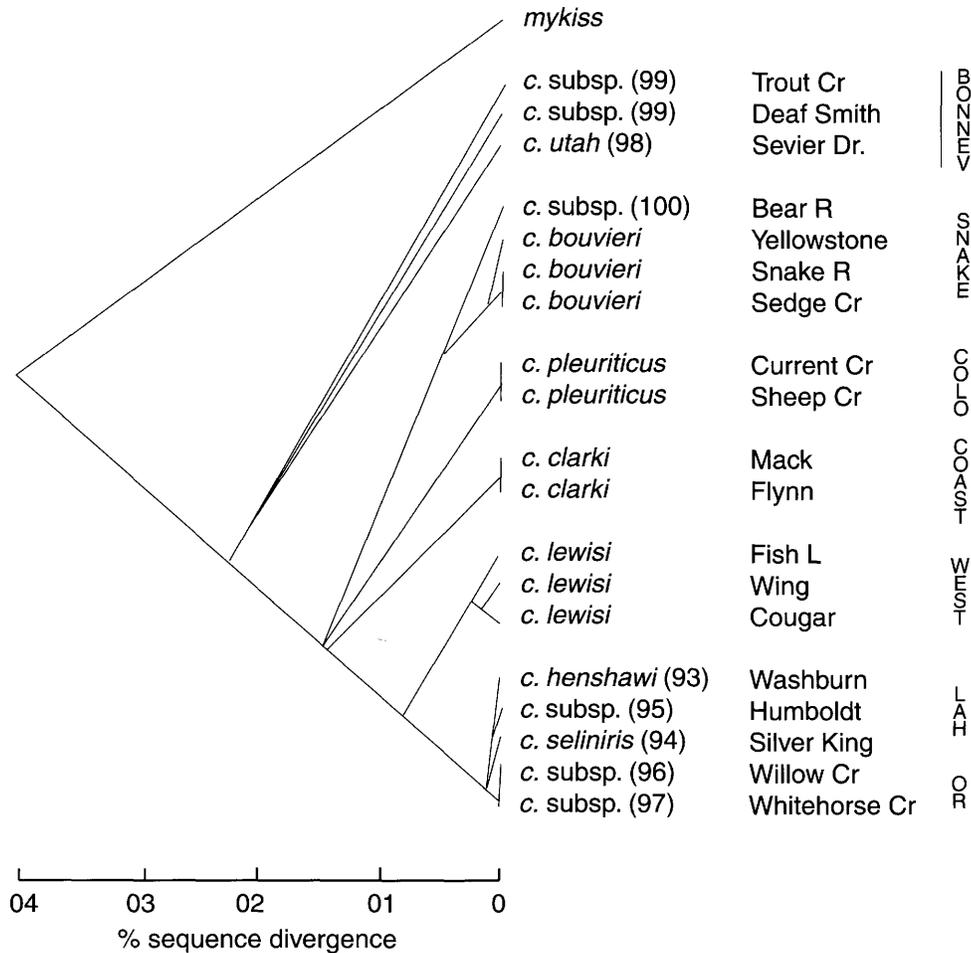


FIGURE 10.—Estimate of the phylogenetic tree of *Oncorhynchus clarki* (cutthroat trout) and its outgroup, *Oncorhynchus mykiss*, based on restriction fragment analysis of mtDNA. Branch lengths may be read as estimated time if divided by the calculated rate of 0.5% sequence divergence per 1 My. Abbreviations: BONNEVE = Bonneville Basin, SNAKE = Snake River drainage, COLO = Colorado River drainage, COAST = Coastal drainages, WEST = west slope drainages, LAH = Lahontan Basin, OR = Oregon Lakes drainages, southeast Oregon.

CYPRINODONTIDAE.—The Great Basin pupfishes are the showpiece of Great Basin ichthyology. They were the focus of R.R. Miller's doctoral research, the results of which were published in his 1948 monograph. This monumental systematic and experimental work illustrated the relationship between isolation and differentiation in relict waters. Pupfishes of the Great Basin's Death Valley system (Miller, 1946a) have been the subject of extensive ecological and physiological studies (Brown and Feldmeth, 1971; Soltz and Naiman, 1978; Feldmeth, 1981), behavioral observations (Liu in Turner, 1974), biochemical comparisons (Turner, 1984; Echelle and Echelle, 1993), and molecular analyses (Echelle and Dowling, 1992; Parker and Kornfield, 1995). Relationships of these species are now understood to be more complex than formerly thought. *Cyprinodon radiosus* (Appendix, number 101) of the Owens River is the sister species to *C. macularius* of the lower

Colorado River, and these two species are the sister group to the clade that includes *C. salinus*, *C. nevadensis*, *C. diabolis*, and relatives, in the Salt River, the Amargosa River, Devil's Hole, and Ash Meadows (Figure 11; Appendix, numbers 102–110). This Death Valley and Ash Meadows clade possibly includes *Cyprinodon fontinalis* of northern Chihuahua, Mexico (Figure 11), but this is not consistent with geography or scale morphology (Miller and Smith, 1986; Minckley et al., 1986). Hydrographic connections among basins and with drainages in Mexico are indicated by *Cyprinodon* mtDNA analysis (Figure 11; Table 4; Echelle and Dowling, 1992; Echelle and Echelle, 1993) and molluscan data (Hershler and Pratt, 1990). Study of the data usually regarded as indicative of the relationship between isolation and divergence reveals interesting conflicts—molecular, biochemical, and morphological divergence and reproductive isolation are incongruent

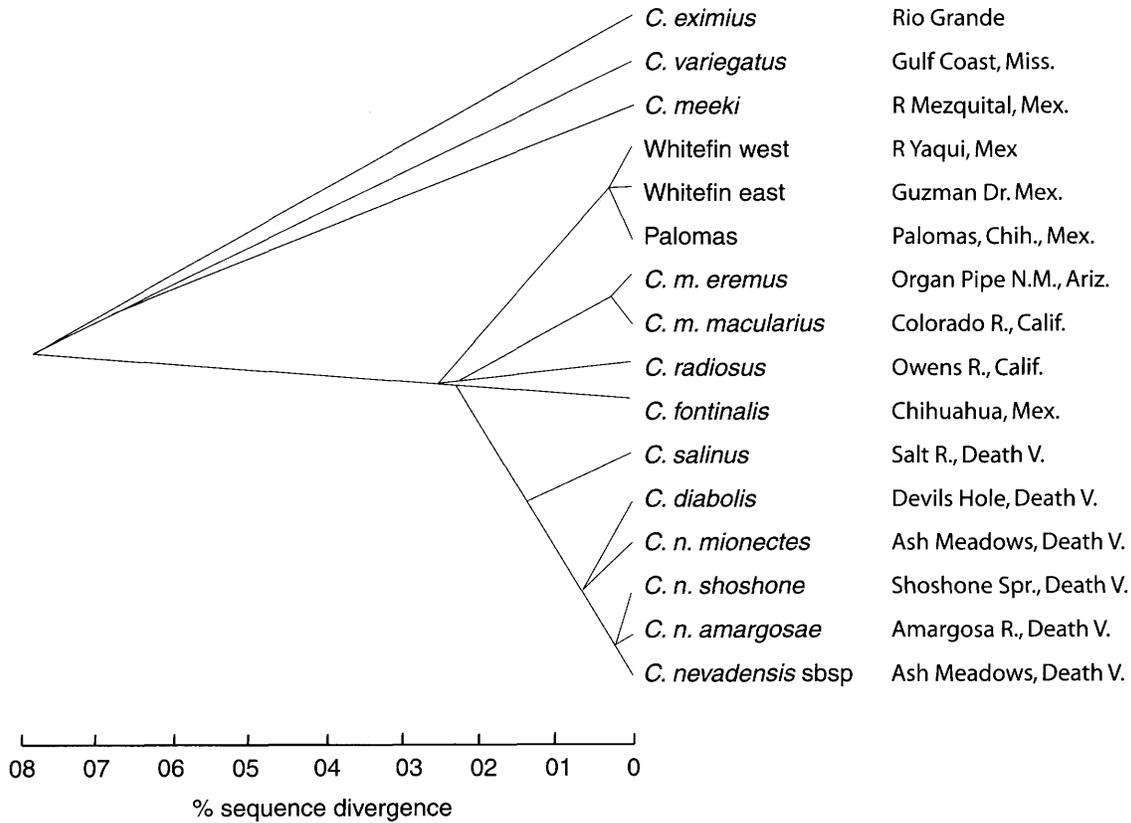


FIGURE 11.—Phylogenetic relationships (strict consensus tree) of certain western North American *Cyprinodon*, based upon parsimony analysis of mtDNA restriction site data (Data and trees from Echelle and Dowling, 1992). The Death Valley species are *C. C. nevadensis*, *C. salinus*, and *C. diabolis*; *C. milleri* has *C. salinus* mtDNA. *Cyprinodon radiosus* is the Owens River species, and *C. macularius* is in the lower Colorado River and vicinity. The other species are primarily from Mexico (Echelle and Dowling, 1992). The depth to each node may be scaled to age in millions of years, assuming that 1 My corresponds to 1% of the average percent sequence divergence between clades.

with each other and with evidence for timing of divergence (Turner, 1974; Echelle and Dowling, 1992; Echelle and Echelle, 1993). Cladistically analysed molecular data indicate that *Cyprinodon* has been in the Death Valley system for about 3 My. Biogeographic relationships of *Cyprinodon* (and good-eids) of the Great Basin are to the south, in Mexico, especially if *C. fontinalis*, from Chihuahua, is related to the Death Valley clade (Figure 11). The diversity of *Cyprinodon* species within the Great Basin, taken with its sister species, *C. macularius* Baird and Girard, displays a geographic pattern that extends from Death Valley and the Owens River to across the Gila River and the lower Colorado River drainages (Minckley et al., 1986).

Pliocene connections from the lower Colorado River to the Owens, Mohave, and Amargosa Rivers occurred about 3 Ma, according to molecular data (Figure 11; Table 4). The connections possibly involved China Lake, Searles Lake, Panamint Valley, and Wingate Pass to Lake Manly, now Death Valley, according to fish and other evidence (Miller, 1946a; Hubbs and Miller, 1948a; Benson et al., 1990). The Pliocene Owens–Mo-

have drainage connected to the lower Colorado River drainage (Blackwelder, 1933, 1954; Hale, 1985) near the region of Ludlow Pass (at 594 m), Bristol Lake, and Cadiz Lake. Brown and Rosen (1995) found no evidence of a through-flowing connection across the present topography, and they suggested alternative dispersal processes, routes, or times; however, rounded boulders in a large paleochannel, which are evidence of a through-flowing stream, are present near Ludlow (Hale, 1985; G.I. Smith, pers. comm. to G.R.S., 1999). Encroachment of the Gulf of California toward Death Valley (Durham and Allison, 1960) and the presence of foraminifera correlated with the Bouse Formation in cores taken from the dry lakes of Danby and Cadiz in southeastern San Bernardino County, California (P.B. Smith, 1960, 1970), suggest a connection existed to the estuary of the lower Colorado River. The most compelling fish evidence for a connection between the Mohave and Colorado Rivers is the distribution of *Cyprinodon macularius* of the lower Colorado drainage and *C. radiosus* of the Owens River. Mitochondrial DNA of these two species indicates they had a common ancestry between 2 and 3 Ma (Table 4).

TABLE 4.—Sequence divergences, based on mtDNA restriction-site data, for selected western North American *Cyprinodon* (Figure 11). See text for localities.

Species or subspecies	<i>C. eximius</i>	<i>C. variegatus</i>	<i>C. meeki</i>	Whitefin pupfish(w)	Whitefin pupfish(e)	Palomas pupfish	<i>C. m. eremus</i>	<i>C. m. macularius</i>	<i>C. r. radiosus</i>	<i>C. f. fontinalis</i>	<i>C. s. salinus</i>	<i>C. d. diabolis</i>	<i>C. n. mionectes</i>	<i>C. n. shoshone</i>	<i>C. n. amargosae</i>
<i>C. eximius</i>	0														
<i>C. variegatus</i>	0.083	0													
<i>C. meeki</i>	0.073	0.068	0												
Whitefin pupfish (west)	0.060	0.068	0.069	0											
Whitefin pupfish (east)	0.056	0.068	0.069	0.006	0										
Palomas pupfish	0.059	0.066	0.068	0.002	0.002	0									
<i>C. m. eremus</i>	0.074	0.073	0.069	0.019	0.022	0.021	0								
<i>C. m. macularius</i>	0.076	0.075	0.071	0.019	0.023	0.021	0.003	0							
<i>C. r. radiosus</i>	0.077	0.095	0.082	0.028	0.028	0.027	0.027	0.028	0						
<i>C. f. fontinalis</i>	0.063	0.061	0.068	0.015	0.015	0.013	0.021	0.021	0.035	0					
<i>C. s. salinus</i>	0.082	0.082	0.087	0.033	0.033	0.032	0.036	0.033	0.039	0.024	0				
<i>C. d. diabolis</i>	0.075	0.075	0.080	0.028	0.028	0.026	0.031	0.036	0.037	0.019	0.012	0			
<i>C. n. mionectes</i>	0.075	0.080	0.075	0.029	0.029	0.027	0.032	0.036	0.038	0.020	0.013	0.005	0		
<i>C. n. shoshone</i>	0.072	0.082	0.077	0.022	0.022	0.020	0.028	0.033	0.035	0.028	0.013	0.005	0.006	0	
<i>C. n. amargosae</i> (Tecopa)	0.077	0.077	0.077	0.026	0.026	0.024	0.032	0.037	0.035	0.024	0.013	0.005	0.006	0.003	0
<i>C. nevadensis</i> subsp.	0.074	0.078	0.078	0.024	0.024	0.022	0.030	0.035	0.032	0.022	0.012	0.003	0.005	0.002	0.002

GOODEIDAE.—The poolfishes and springfishes, *Empetrichthys* and *Crenichthys*, respectively (Appendix, numbers 112–115), are Great Basin endemics in the subfamily Empetrichthyinae (Webb, 1998) of the family Goodeidae (Parenti, 1981; Grant and Riddle, 1995). *Empetrichthys* and *Crenichthys* are oviparous and were formerly classified as cyprinodontids, but Parenti's (1981) phylogenetic evidence demonstrated their relationship to the live-bearing goodeids of the Mexican Plateau. Empetrichthyines resemble fundulids in osteology, numbers of fin rays, and tooth form, which distinguish them from the cyprinodontids, but unlike fundulids, they lack pelvic fins. Fossil *Empetrichthys* were discovered from the Pliocene near Los Angeles, California, and from the Pleistocene in southern Nevada (see Appendix, number 112). Paleontological studies by M.L. Smith (in Miller and Smith, 1986) and molecular studies by Webb (1998) indicate middle to late Miocene goodeid vicariance between the White River and the lower Colorado River drainages and the Mexican Plateau, probably involving tributaries of the Bouse Embayment and the Gulf of California. The distribution of fossil and Holocene *Empetrichthys*, *Fundulus*, and *Gasterosteus*, along with species of *Pyrgulopsis* (hydrobiid snails), provide evidence that late Miocene lowland Pacific coast tributaries flowed westward from west-central Nevada and Death Valley across a lower, proto-Sierra Nevada (Bell, 1979; Hershler and Pratt, 1990) about 6 Ma, perhaps through the (reversed) Mohave River valley (Weldon, 1982).

FUNDULIDAE.—Most species of killifish in the family Fundulidae live in eastern North America, but there are representatives in Mexico and California. Several fossil forms were described (Miller, 1945b) before it was recognized (Parenti, 1981) that the Goodeidae of the Mexican Plateau, relatives of Fundulidae, are represented in the Great Basin. The Nevada fossils (Appendix, numbers 116–123) have some observable characters that suggest they could be related to the Empetrichthyinae or the Goodeidae (Miller, 1948:100), except that none of the Nevada fossils lack pelvic fins, as do the empetrichthyines.

The ancient diversity of fundulids in the southwestern Great Basin is remarkable, considering the paucity of other genera (except *Siphateles* and *Gasterosteus*) in the fossil record from there (M.L. Smith, 1981) and the absence of *Fundulus* in the Great Basin today. The presence of fundulids from northeast (Humboldt Formation) and west-central (Truckee Formation) Nevada and Death Valley through most of the Miocene and Pliocene establishes a benchmark of antiquity that is important, given that the ages of origin of Great Basin fish groups are underestimated (see "Material and Methods" and the Appendix).

COTTIDAE.—The Cottidae, like the Salmonidae, are low-temperature, usually high-gradient fishes. They occupy mountain streams and cold lakes. Their fossil record in the Great Basin goes back to the Pliocene and Pleistocene in the Lahontan Basin (*C. beldingi*) and to the late Pleistocene in the Bonneville Basin (*C. bairdi*, *C. extensus*). Their phylogenetic relationships are to the north and west. More species of northwestern

sculpins occur in the northern Bonneville Basin and Bear River drainages than are currently acknowledged in the literature, according to new discoveries by Shiozawa and others (unpublished). Sculpins are not found with cyprinodontoids in western North America, unlike their occasional sympatry in the eastern United States, reflecting the more extreme habitat gradients (temperature and stream profiles) in the west.

**GASTEROSTEIDAE.**—The Miocene three-spined stickleback (*Gasterosteus doryssus*; Appendix, number 128) occurs in the Great Basin from the Truckee Formation in west-central Nevada from Hazen (Bell, 1974) to the Sahwave Mountains (LaRivers, 1964). It represents a fauna that colonized the basin prior to final elimination of the drainage outlet to the Pacific coast by the Sierra Nevada uplift (Bell et al., 1985). The Nevada *Gasterosteus* is the most significant fossil fish lineage in the Great Basin, if not in Cenozoic ichthyology in general, because of the abundant, beautifully preserved samples in annual laminae of diatomite and the detailed studies of these samples by Bell and his students (Bell and Haglund, 1982; Bell, 1994, and references therein). In brief, the study of more than 8000 specimens from a 110,000-year time sequence has shown rapidly fluctuating but gradual change, with no stasis (Figure 12). Bell (1994) concluded that much of the change can be attributed to selection, but some seems uncorrelated with environmental change.

*Gasterosteus aculeatus aculeatus* (Appendix, number 129), the modern, anadromous, fully plated, three-spined relative, was reported from the late Miocene Monterey Formation at Lompoc, California, by Bell (1977), strengthening the hypothesis that inland freshwater populations of sticklebacks were independently derived from a widespread anadromous form (Bell, 1979). Comparison of these sticklebacks demonstrates that new species can arise repeatedly, as restricted peripatric and paraphyletic derivative populations, without effects on the ecology, morphology, or long-term history of the widespread, ancestral species. Bell's point demonstrates the logical difficulties attending Hennig's rule (1966), which requires changing a

species name with each branching event in a clade's history, if the parent species did not change while daughter lineages were produced (Bell, 1979).

**CENTRARCHIDAE.**—Sunfish occupied lakes and streams in western North America from Idaho, Washington, and Oregon to Nevada and northern Utah (Salt Lake group) during the Miocene and Pliocene. The Nevada specimens suggest that the climate during the middle to late Miocene was warm and that the basin floor was at low elevations, but floristic data indicate the floor was at higher elevations (Wolfe et al., 1997). The combination suggests local topographic extremes. There was more diversity during the Miocene than is recognized in the currently defined genera *Archoplites* and *Plioplarchus*. An undescribed form existed in the Miocene of Oregon (Appendix, number 130). Modern centrarchids are restricted to *Archoplites* of the Great Valley, California, and to a radiation of nine genera and more than 30 species in the Atlantic coastal drainages of North America.

## Discussion

### FISH BIOGEOGRAPHY AND GEOLOGICAL TIME

**RELATIONSHIP BETWEEN PHYSIOGRAPHIC AND BIOLOGICAL EVIDENCE.**—Hubbs and Miller's search for congruence between physiographic and ichthyological histories is evident throughout their 1948b monograph. They noted, for example, the local morphological distinctiveness of *Siphateles*, *Rhinichthys*, and *Cyprinodon* as evidence of postpluvial separation of previously uniform gene pools (Hubbs and Miller, 1948b:66, 83, 91). The seemingly parsimonious assumption that faunas were uniform at the time of the last habitat connection has rarely been questioned (Kocher and Stepien, 1997), but even in 1948, it was in conflict with the fossil record of modern fishes, which, when known, extended back beyond Pleistocene events to the Pliocene or Miocene (Hubbs and Miller, 1948b:25–27).

Taylor (1960) noted the antiquity of many modern lineages of mollusks and fishes and suggested that they are much older than modern physiography, ice ages, and pluvials. The corollary of this suggestion is that the tectonic, volcanic, and glacial changes in the landscape occur more rapidly than the evolving changes in lineages on that landscape. Taylor's principle suggests that we cannot assume that the observed amount of species and subspecies evolution automatically occurred in the interval since the most recent possible geological changes and vicariance events. Multiple possible vicariant times should be among the tested alternatives. For example, the assumption that cladogenesis of Holocene birds originated in the Pleistocene was refuted by Klicka and Zink (1997), who demonstrated that numerous supposedly Pleistocene species date back to the Pliocene. Our interpretations of fossil fish specimens combined with DNA analyses and phylogenetic analyses of Holocene species indicate that the ages of clades and vicariance barriers have usually been underestimated, thereby challenging the frequent assumption that the most recent possible connection was the operative one.

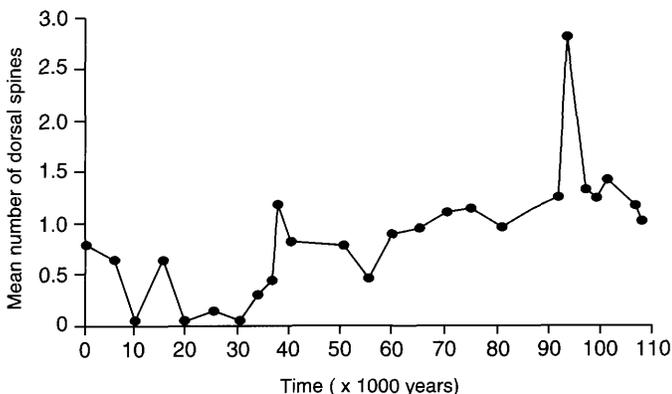


FIGURE 12.—Variation in mean number of dorsal spines in *Gasterosteus doryssus*. Variation shows rapid short-term changes and slow long-term trend (after Bell et al., 1985).

Phylogenetic estimates for the Cyprinidae (Figures 2, 3), Catostomidae (Figure 5), Coregoninae (Figure 8), *Oncorhynchus* (Figure 10), and Cyprinodontidae (Figure 11) are presented in the figures with key words for taxon geography to provide background for examining the relative timing of historic hydrographic connections among basins. Traditional studies (Hubbs and Miller, 1948b; Smith, 1966, 1978; Hubbs et al., 1974; Minckley et al., 1986) and the new phylogenies enable the formulation of hypotheses concerning the relative ages of barriers.

According to the phylogenies, moderately old and prominent barriers separated the Great Basin from its neighboring drainages to the east and the Sacramento Basin to the west. Phylogenetic indicators of the barrier between the Great Basin and the Colorado Basin, for example, are the relative antiquity of the nodes between the *Gila atraria* group and the *G. robusta* group (Figures 2, 3), between *Xyrauchen* and *Chasmistes*, between *Catostomus ardens* and *C. latipinnis*, between *C. platyrhynchus* and *C. discobolus* (Figure 5), and between *Oncorhynchus clarki utah* and *O. c. pleuriticus* (Figures 9, 10). The importance of the Sierra Nevada as a barrier is indicated by the separation of *Catostomus occidentalis* and *C. microps* from *C. tahoensis* (Figure 5), and by *Oncorhynchus mykiss* from *O. clarki* (Figures 9, 10). A strong barrier separated the Bonneville and Lahontan Basins along the original line of separation in the Great Basin, as illustrated by the relative distance between nodes, for example, between nodes for *Gila* and *Siphateles* (Figures 2, 3), *C. ardens* and *C. tahoensis* (Figure 5), and *O. c. utah* and *O. c. henshawi* (Figures 9, 10). The moderately strong separation of the Lahontan Basin and Colorado Basin drainages is illustrated by the nodal distances between *Gila* and *Siphateles* (Figures 2, 3), *C. tahoensis* and *C. latipinnis* (Figure 5), and *O. c. henshawi* and *O. c. pleuriticus* (Figures 9, 10). The weakest, most recent barriers separated the Lahontan Basin and Death Valley systems, and the subdrainages within the Bonneville, Lahontan, White River, and Death Valley systems (most examples are similar species or subspecies not shown on the phylogenies), but all of these barriers have been breached by headwater-stream captures, indicated by some of the examples below and in Figures 2, 3, 5, and especially Figure 10.

Fish distributions suggest that much of the drainage from the area of the Great Basin flowed to the Pacific Ocean at times during the Miocene, Pliocene, and Pleistocene, even though the Basin and Range topography began forming more than 15 Ma. The fish data presented herein indicate that these hydrologic confluences probably had an episodic history that began much earlier than the most recent known connection.

**MIOCENE.**—Geological and paleontological studies indicate that at times during the Miocene, the Death Valley, Lahontan, and Bonneville systems drained westward to the Pacific Ocean (Bell, 1974, 1994; Stokes, 1979; Taylor, 1985; Minckley et al., 1986; G.I. Smith, pers. comm. to G.R.S., 1999). Some Miocene biogeographic patterns, however, were dominated by north–south systems (Taylor, 1985) that were congruent with

the north–south structures that resulted from convergence of the west coast of North America with the Pacific Plate (Figure 13). Early hydrographic connections occurred between the Humboldt lacustrine system and the western Snake River Plain and southeastern Oregon, according to Stokes (1979) and evidence from the distribution of Centrarchidae. Later in the Hemphillian, the Salt Lake group, with a relatively rich fish fauna in the northern Bonneville Basin, was probably connected to the eastern Snake River Plain (McClellan, 1977). The fish fauna was related to, but specifically different from, that of the western Snake River Plain (McClellan and G.R. Smith, In press). The presence of *Lavinia* in the lower Salt Lake group indicates there were earlier connections to the western Snake River Plain and the Pacific coastal drainages. *Lavinia* is now restricted to the Sacramento drainage. The mixture of lowland fish faunas and upland floras in Nevada during the Miocene (Wolfe et al., 1997) suggests that evolution of regional topographic relief took place subsequently (Orr, 1982; Pierce and Morgan, 1992).

**LATE MIOCENE TO PLIOCENE.**—The southern Lahontan Basin fossils from the late Miocene and Pliocene are indicative of low elevations, but the northern Lahontan Basin fossils are indicative of higher elevations. Elevations of the Snake River Plain were low in the late Miocene, but uplift of the eastern Snake River Plain at this time occurred in the path of the Yellowstone hot spot (Pierce and Morgan, 1992).

A connection from the Mono Lake area of the Great Basin to the San Joaquin River ended when basalt dammed the V-shaped channel near Deadman Pass in the Devil's Postpile quadrangle (Huber and Rinehart, 1965, 1967), causing cessation of river flow 3.2 Ma (Dalrymple, 1964; Huber, 1981). The channel is now at about 8400 ft (2580 m) elevation, having been raised 3120 ft (950 m) by uplift of the Sierra Nevada (Dalrymple, 1964; Huber, 1981), so the estimated elevation of the active channel was 5280 ft (1620 m; G.I. Smith et al., 1983; G.I. Smith, pers. comm. to G.R.S., 1999). The outlet possibly continued from the Great Valley across the Diablo Uplift to deposit the Monterey Fan (Cole and Armentrout, 1979). Cyprinid and gasterosteid fish connections require lower elevations during the late Miocene, based upon their present elevational restrictions.

**PLIOCENE.**—Our phylogenetic data suggest the occurrence of some ancient drainage connections that had not been previously noted (Figure 13). For example, the similarity of morphology and DNA (see below) of *Lepidomeda* from the Virgin River drainage and *Snyderichthys* from the upper Snake River and the Bear River drainages suggests there were connections from the upper Snake River to the Virgin River–White River drainage (Dowling et al., 2002). Keyes (1917), in a discussion of the origins of Lake Bonneville, proposed that the headwaters of the Snake River were formerly a tributary to the Virgin River. Ives (1948) presented evidence that Lake Bonneville drained from its Escalante arm to Meadow Valley Wash (a tributary to the Virgin River) prior to its drainage through Red

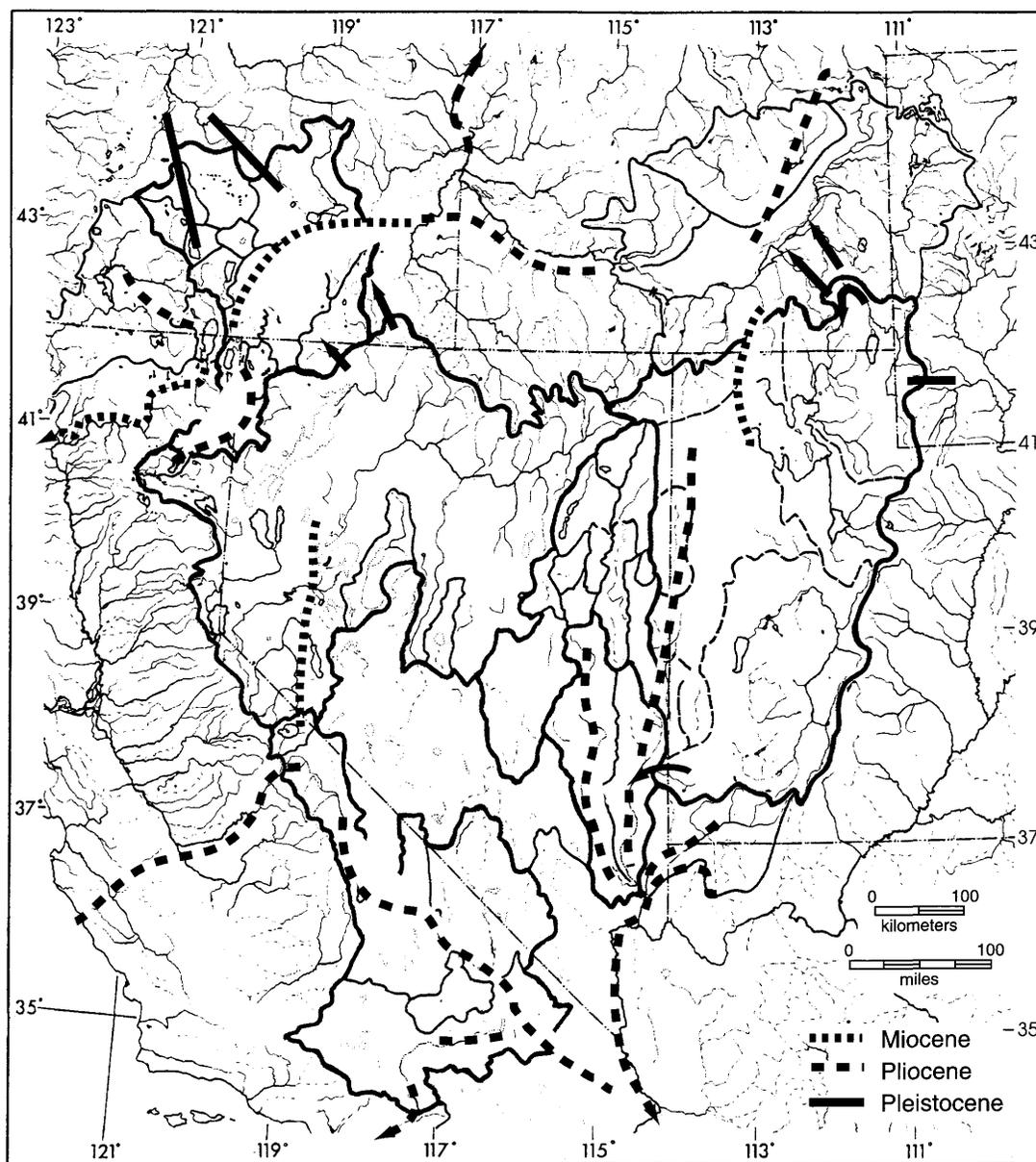


FIGURE 13.—Paleogeographic map showing major Miocene, Pliocene, and Pleistocene hydrographic connections, based upon our current interpretations of age and location and supplemented by the conclusions of Cole and Armentrout (1979), Taylor (1985), Taylor and Bright (1987), Ives (1948), and G.I. Smith (pers. comm. to G.R.S., 1999). Heavy dashed lines and arrows represent captures, overflows, or rivers. See "Discussion" and Appendix for the estimated timing of some of the barriers represented by lightweight lines.

Rock Pass to the upper Snake River. Hubbs and Miller (1948b) rejected these hypotheses as unsupported by fish evidence. Possible connections require serious consideration now because of new cyprinid and molluscan evidence. Miocene and Pliocene distributions of freshwater snails, namely, *Valvata idahoensis* Taylor, *Lutralimnea dineana* (Taylor), *L. gentilis* Taylor, and *Tryonia protea* (Gould), led Taylor (1985:285, 296, 317) to propose late Miocene and possibly Pliocene connections (not necessarily contemporaneous) from the upper Snake

River, through the Bonneville area, to the lower Colorado River drainage.

The White River canyon in southern Nevada is surrounded by possible drainage connections, as indicated generally by Taylor (1985, figs. 15, 25), leading to the Bouse Embayment of the Gulf of California in the late Miocene or early Pliocene (Shaffiqullah et al., 1980; Buising, 1990) and in the Pleistocene (DiGuseppi and Bartley, 1991). The Colorado Paleoriver was diverted from its delta in the Los Angeles Basin to

the Salton trough about 9 Ma (Howard, 1996). The depositional elevation of the Bouse Formation (near the Arizona–Nevada border) is usually cited as at sea level, constraining the time of uplift of the Colorado Plateau, but this is currently in dispute. Bouse Formation sediments and shells show ratios of strontium isotopes intermediate between values expected for marine and freshwater, indicating this area had a mixture of water sources with different strontium isotopes, according to Spencer and Patchett (1997). These authors' contention that the formation was deposited in a lake, possibly at an elevation of 400–700 m, is rejected on the basis of fossil and biogeographic data; the Bouse Formation contained a fauna of foraminifera, barnacles, brackish-water fishes, and marine mollusks (Metzger, 1968; Smith, 1970) that could not have been supported for 3 My by dispersal on birds' feet, as suggested by Spencer and Patchett (1997). The hypothesis that the Bouse Formation was lacustrine (Spencer and Patchett, 1997) has been tested and, by inference, rejected by the absence of any such marine faunas in saline lakes today (Kidwell in Spencer and Patchett, 1997).

Pliocene fluvial connections between the northern pre-Lahontan Basin and the Alvord Basin of Oregon are indicated by geological data (Reheis and Morrison, 1997) and fish distributions (Appendix, numbers 9, 22, 91, 96, 97). DNA divergence data (below; Table 3) suggest that reconnections 0.2 Ma allowed trout populations in these basins to once again mix.

**PLIO–PLEISTOCENE.**—Connections among the Mono Lake, Owens River, Death Valley, Mohave River, and lower Colorado River drainages are indicated by cyprinodontid fish distributions (Miller, 1948) and geological data (Gale, 1915; Morrison, 1965; G.I. Smith, 1978; Benson et al., 1990). The connection between the Mohave River and the Colorado River basins through Bristol, Cadiz, and Danby Basins lacks support from geomorphology, according to Brown and Rosen (1995), but the connection suggested by present *Cyprinodon* distribution is supported by sedimentary data (Hale, 1985) and by marine or saline-lake foraminifera from cores in Danby and Cadiz dry lakes (Smith, 1960). The foraminifera occur in green clays that are currently within a few hundred feet above or below sea level.

**PLEISTOCENE.**—Pleistocene connections occurred on a landscape more like that of the present (Figure 13). Additional evidence for exchange between the Lake Bonneville and Virgin River drainages, possibly in the Pleistocene, is seen in *Catostomus clarki* from the headwaters of the Virgin River. These fish have unique predorsal scale and gill-raker counts that increase clinally toward their relatives across the divide in the Bonneville Basin (Smith, 1966). Numerous possible stream captures are associated with the major north-to-south valley west of Hurricane Fault (Averitt, 1964; Anderson and Mehnert, 1979) in southern Utah (along Highway 91). The drainage connection between the Bonneville Basin and the Colorado River drainage is also suggested by intergrades between *Catostomus platyrhynchus* and *C. clarki* in Shoal Creek (Smith and Koehn,

1971), which is in the southernmost part of the Bonneville Basin near the outlet proposed by Ives (1948).

Small headwater-stream captures are required to explain the broad northern distributions of headwater inhabitants, such as *Catostomus platyrhynchus*, *C. discobolus* (Figure 7), *Onco-rhynchus clarki* subspecies (Figure 9), and *Cottus* spp. (Appendix, numbers 124, 125). Numerous examples of northern connections can be recognized on topographic maps and in the field. For example, in Wyoming, two such possible connections may be related to the distribution of *Catostomus platyrhynchus*, *C. discobolus*, and *Cottus bairdi* in the Green, Bear, and Snake Rivers. Willow Creek, formerly tributary to Muddy Creek of the Green River (T.13 N., R.119 W., Ogden sheet, United States Geological Survey (USGS) 1:250,000 series), was captured by the headwaters of the Bear River 11 mi (17 km) south-east of Evanston, Wyoming. Twin Creek, of the Bear River between Fossil Butte and Kemmerer, Wyoming (T.21 N., R.117 W., Ogden sheet), apparently captured the head of Hams Fork of the Green River. We hypothesize that these captures could have carried *Catostomus discobolus* from the Green River drainage to the Bear River, from whence they could have transferred to the Snake River at Soda Springs (Bright, 1967) and to the Weber River in upper Chalk Creek (Hansen, 1969, 1985).

#### MITOCHONDRIAL DNA EVIDENCE FOR THE TIMING OF PHYLOGENETIC AND HYDROGRAPHIC EVENTS

Analysis of DNA divergence data from fishes offers a means of constraining ages of barriers and uplift in the Great Basin. Estimated rates of evolution of mtDNA genes in Cyprinidae, Salmonidae, and Cyprinodontidae (Figure 14) vary from about 0.5% sequence divergence per one million years in salmonids to about 1% per one million years in cyprinids and cyprinodontids. These values are similar to those reported for snails of the marine gastropod genus *Nucella* (see Collins et al., 1996) and for goodeid fishes (Webb, 1998) but differ from the estimate of Martin and Palumbi (1993). The relative-rate tests (e.g., Table 2) show standard deviations of 10%–25% of the mean values of percent sequence divergence, or roughly 2–5 My for mean ages of 7–38 My (Table 2) for basal branches in the cyprinid data. Standard deviations are 15%–30% in the salmonid data, allowing a rough idea of the imprecision of the estimates. These are overestimates of rates of molecular change because the fossil ages in the denominators of the rate calculations are underestimated. If the rates are underestimated by 10%–30%, elapsed times inferred from rates of molecular change are expected to be underestimated (by as much as 0.5–1.2 My in 4 My for spinedaces, for example). This means that the connection indicated by the Snake River *Snyderichthys* relationship to the Virgin River *Lepidomeda* (percent sequence divergence = 4%) probably occurred within the range of 4–5 Ma.

In general, divergence times based upon the rates calculated herein are old, as predicted by Minckley et al. (1986). Great Basin cyprinids in the sister clade to *Phoxinus* of eastern North America differ from *Phoxinus* by an average of 22%

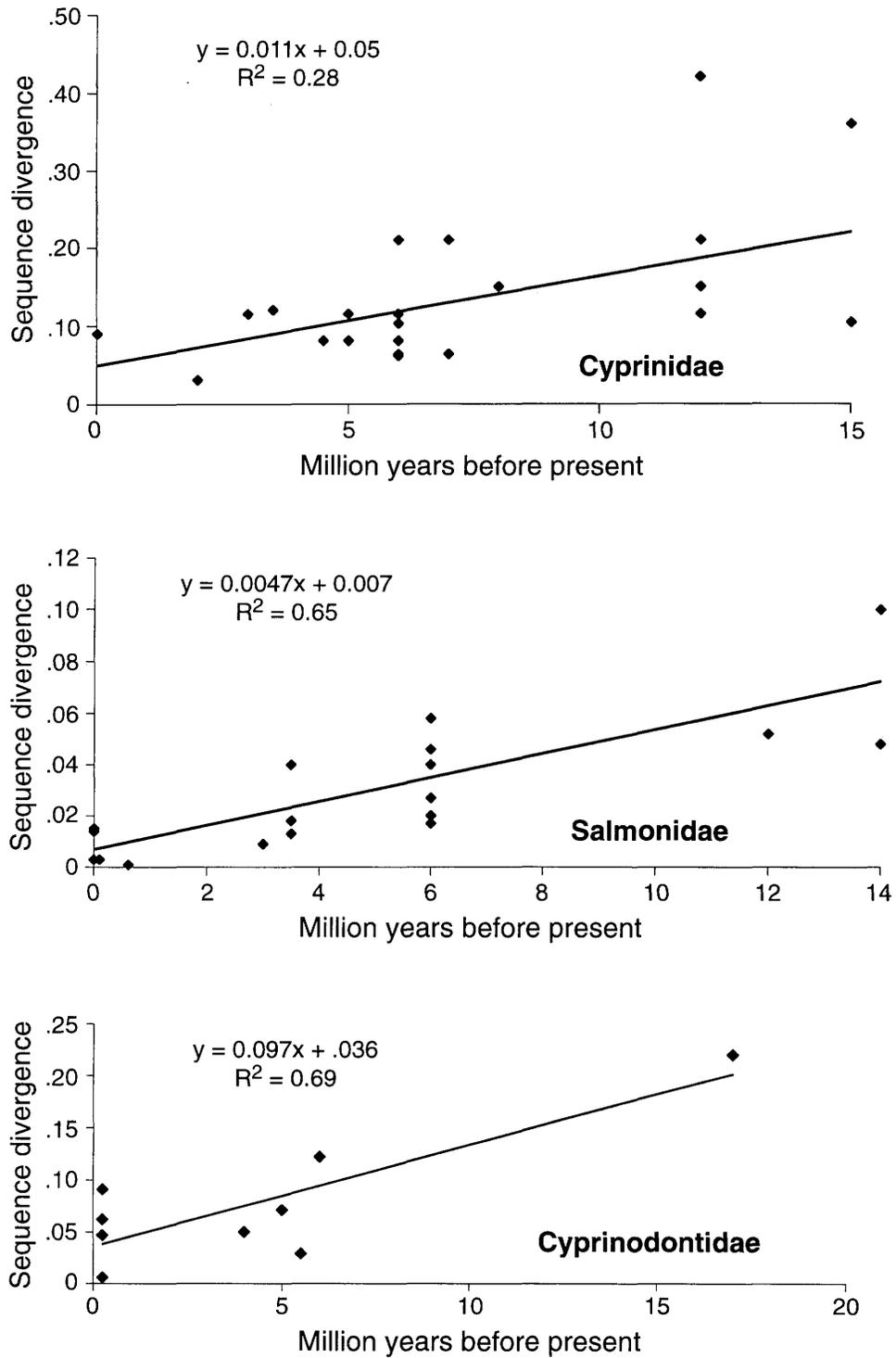


FIGURE 14.—Rates of molecular change in Great Basin and Snake River plain Cyprinidae, Salmonidae, and Cyprinodontoi. Estimated ages of fossils are given in the Appendix and Table 5. DNA sequence divergences are from Tables 2–5;  $R^2$  is an estimate of the percent of the variance explained by the regression.

sequence divergence (Table 2), implying that separation occurred 22 Ma, or in the early Miocene. *Rhinichthys osculus* from the Virgin River and *R. atratulus* of eastern North America differ by 22%. *Snyderichthys* and the *Lepidomeda* group

differ from *Semotilus* of eastern North America by 20%. Closer relatives across the continental divide generally differ by less. For example, *Clinostomus* and *Richardsonius* differ by 12% sequence divergence, and eastern and northern North

TABLE 5.—Fossil cyprinid, salmonid, and cyprinodontoid taxa and ages of samples of first appearances used in the estimations for the rates of molecular change in Figure 14. Fossil taxon numbers correspond to numbers in the Appendix; unnumbered taxa are from outside of the Great Basin. Ages in parentheses are additional fossil records for that taxon. (Fm. = formation.)

Fossil taxon	Sister taxon	Age (My)	% seq. div.
CYPRINIDAE			
1. <i>Lavinia</i>	<i>Mylopharodon</i>	6 (3.5,3)	8.1
2. <i>Lavinia</i>	<i>Mylopharodon</i>	5 (3)	8.1
3. <i>Lavinia</i>	<i>Mylopharodon</i>	6	8.1
5. <i>Mylopharodon</i>	<i>Siphateles</i>	12	15.0
5. <i>Mylopharodon</i>	<i>Lavinia</i>	4.5	8.1
5. <i>Mylopharodon</i> ?	Eastern minnows	12	42
6. <i>Siphateles</i>	<i>Gila</i>	6 (6)	11.5
6. <i>Siphateles</i> ?	Eastern minnows	15	36
7. <i>Siphateles</i>	<i>Gila</i>	3	11.5
8. <i>Siphateles</i>	<i>Gila</i>	6 (6)	11.5
9. <i>Siphateles</i>	<i>Gila</i>	3 (3)	11.5
10. <i>Siphateles bicolor obesa</i>		2 (0.6)	3.1
14. <i>Siphateles</i> sp.	<i>Mylopharodon</i>	8	15.0
15. <i>Siphateles</i> sp.	<i>Gila</i>	5 (3,1)	11.5
23. <i>Gila a. atraria</i>	<i>Gila atraria</i> subsp.	0.01	0.9
25. <i>Klamathella</i>	<i>Gila</i>	6	6.2
26. <i>Acrocheilus</i>	<i>Klamathella</i>	6	6.4
26. <i>Acrocheilus</i>	<i>Klamathella</i>	7	6.4
27. <i>Gila</i>	<i>Siphateles</i>	12	11.5
28. <i>Gila</i>	<i>Siphateles</i>	12	11.5
29. <i>Gila</i>	<i>Siphateles</i>	12	11.5
<i>Gila</i> spp.	<i>Ptychocheilus</i>	6	10.3
30. <i>Ptychocheilus</i>	<i>Gila</i>	15 (6,6,8)	10.4
37. <i>Richardsonius</i>	<i>Clinostomus</i>	3.5	12.0
56. <i>Mylocheilus</i>	<i>Richardsonius</i>	7	21
57. <i>Mylocheilus</i>	<i>Richardsonius</i>	6	21
58. <i>Mylocheilus</i>	<i>Richardsonius</i>	12	21
SALMONINAE			
87. <i>Salvelinus</i>	<i>Hucho</i>	14	4.8
88. <i>Oncorhynchus</i>	<i>O. clarki</i> + <i>O. mykiss</i>	14	10
89. <i>O. clarki</i> (Truckee Fm.)	<i>O. mykiss</i>	6	4
90. <i>O. clarki</i> (Ft. Rock Basin)	<i>O. mykiss</i>	3.5	4
91. <i>O. clarki</i> (Honey Lake)	<i>O. mykiss</i>	3.5	4
92. <i>O. clarki</i> (Carson Sink)		3.5	1
92. <i>O. clarki</i> (Mopung Hills)		3	1
92. <i>O. clarki</i> (Humboldt River Canyon)	<i>O. clarki</i>	0.7	0.1
97. <i>O. clarki</i> (Whitehorse Basin)	<i>O. clarki</i>	0.15	0.1
97. <i>O. clarki</i> (Sunshine Amphitheater)	<i>O. clarki</i>	1	0.1
98. <i>O. clarki</i> (Sevier Basin)	(Snake River)	0.01	1.3
98. <i>O. clarki</i> (Trout Creek)	(Sevier River)	0.01	1.0
<i>O. nerka</i> <sup>1</sup>	<i>O. gorbuscha</i>	6	5
<i>O. keta</i> <sup>1</sup>	<i>O. gorbuscha</i>	6	3
<i>O. rastrosus</i> <sup>1</sup>	<i>O. nerka</i>	12	5
<i>O. keta</i> <sup>1</sup>	<i>O. nerka</i>	6	6
CYPRINODONTOIDEI			
<i>Chapalichthys encaustus</i> <sup>2</sup>	<i>Chapalichthys pardalis</i>	0.25	0.6
<i>Ameca splendens</i> <sup>2</sup>	<i>Xiphophorus variatus</i>	0.25	4.7
<i>Allophorus robustus</i> <sup>2</sup>	<i>Ameca</i> , etc.	0.25	6.2
<i>Goodea atripinnis</i> <sup>2</sup>	<i>Ataeniobus. toweri</i>	0.25	9.1
<i>Girardinichthys multirad</i> <sup>2</sup>	<i>G. viviparus</i>	5.0	7.1
<i>Tapatia</i> <sup>2</sup>	other <i>Girardinichthyini</i>	6.0	12.2
111. <i>Cyprinodon breviradius</i>	<i>C. spp.</i>	5.5	2.9
113. <i>Empetrichthys erdisi</i>	<i>Crenichthys</i>	4.0	7.0
122. <i>Fundulus lariversi</i>	Goodeidae	17	22

<sup>1</sup>Data from G.R. Smith (1992a).

<sup>2</sup>Data from M.L. Smith (1980) and Webb (1998).

American *Couesius* differ from *Lepidomeda* by 16% (Dowling et al., 2002), implying that separations occurred in the early to middle Miocene. Great Basin *Gila* differ from Colorado River and Rio Grande *Gila* by 4%–9% (except for northern *Gila atraria*, *G. jordani*, and *G. cypha*, which differ by 0.4%–1.1% sequence divergence, implying there have been relatively recent introgressive transfers of mtDNA; Table 2). Similarly, Great Basin *Gila* and their relatives in the Colorado River, Rio Grande, Rio Yaqui, and in waterways in nearby valleys in the Basin and Range Province of northern Mexico differ among themselves by 5%–9%, implying lower elevations and more connections existed to the south 5–9 Ma (Table 2; Dowling, unpublished data). Great Basin *Gila* differ from Columbia–Snake *Acrocheilus* and *Klamathella* by 6% sequence divergence, but Great Basin *Siphateles* differ from the same taxa by 10%–11%, implying separation occurred well back in the Miocene. Differences between conspecific populations of *Gila* and *Snyderichthys* within the Bonneville Basin range up to 2.4%, indicating subspecific divergence began in the late Pliocene.

Populations of *Oncorhynchus clarki* (cutthroat trout, Table 3) differ from *O. mykiss* (rainbow trout and redband trout) by about 4% sequence divergence, implying separation occurred about 8 Ma (assuming rates of molecular evolution of about 0.5% sequence divergence per 1 My). Populations of *Oncorhynchus clarki* in the Great Basin (except for Deaf Smith Creek and Bear River) differ from populations of the west slope (Columbia River) and the Snake–Yellowstone–Bear Rivers by 1%–2% sequence divergence, implying separation occurred about 4–2 Ma. Bonneville Basin populations are heterogeneous. The Deaf Smith Creek (northern Bonneville) population differs from all other trouts by about 2% more than do other Bonneville trout populations (indicating rapid change occurred in the Deaf Smith Creek population because it is not cladistically basal, Figure 10). The Bear River (most northern Bonneville) population differs from the upper Snake River population by only 0.3%–0.4% sequence divergence, which implies separation took place about 0.7 Ma, which is roughly consistent with part of the Bear River chronology of Bouchard et al. (1998). Populations of the Bonneville and Lahontan Basins differ from each other by an average of 2% sequence divergence, implying they have been separated for about 4 My. Outside the Bonneville Basin, variation within basins is usually less than 0.1%. Lahontan Basin populations differ from those from the Oregon Lakes by only 0.1% sequence divergence, implying they have been separated for about 200 Ky.

Great Basin pupfish populations are related to *Cyprinodon macularius* and its relatives of the Colorado River and Mexico (Echelle and Dowling, 1992; Echelle and Echelle, 1993; Figure 11, Table 4). The Owens pupfish, *C. radiosus*, is a member of the *C. macularius* clade but not the Death Valley clade; *C. radiosus* differs from *C. macularius* by 2.7%–2.8% sequence divergence. Death Valley pupfishes differ from *C. macularius*

and *C. radiosus* by about 3% sequence divergence, implying separation occurred about 3 Ma. *Cyprinodon fontinalis* of Mexico may be a member of the Death Valley clade. These relationships require multiple connections between the Death Valley system and drainages in Mexico, through the Colorado River drainage in the Plio–Pleistocene. *Cyprinodon salinus* of the Salt River in Death Valley differs from other Death Valley pupfishes by 1.3% sequence divergence, implying separation took place a little more than 1 Ma. *Cyprinodon diabolis* and several subspecies of *C. nevadensis* form a clade whose populations differ from each other by about 0.2%–0.6% sequence divergence, implying separations occurred 0.2–0.6 Ma. Miller (1948:85–86) concluded that the divergences of *C. salinus*, *C. diabolis*, and *C. nevadensis* date from about the middle Pleistocene, which is consistent with the molecular differences given above (Table 4). For divergence of some Death Valley populations to have been as rapid as hypothesized by Hubbs and Miller (1948b:82)—as short as 10 Ky—would require unrealistically high rates of sequence divergence.

#### SPECIES DIVERSITY

Fishes of the Great Basin are not diverse, except in endemic species and subspecies (Hubbs and Miller, 1948b). Most of these taxa are explainable as relicts of repeated cycles of extinction or introgression during dry periods between Pleistocene pluvials. The subspecies are the product of rapid change in morphology in isolated, small populations in rapidly changing environments (Hubbs and Miller, 1948b). But low diversity in a landscape so divided by barriers (permitting divergence and recolonization following divergence) is not consistent with most hypotheses about geographic and climatic control of speciation processes (Hubbs and Miller, 1948b; Mayr, 1963; Vrba, 1993). Great Basin fossil and Holocene fish data indicate, however, that periods of aridity and insularity, coupled with high barriers that prevent recolonization after local extinctions, have eliminated more species than were produced by the numerous stages of isolation; therefore, the processes that cause species divergence have not matched extinction at the spatial and temporal scales of isolation that have occurred in the Great Basin. High extinction rates have been predicted for small, isolated populations (MacArthur and Wilson, 1967; Jablonski, 1980). To determine whether speciation has been influenced by these factors, we considered the processes that have operated in Great Basin fish populations in relation to isolation by pluvial cycles.

Two unusual kinds of data lend themselves to empirical analyses of these two problems. First, the Basin and Range Physiographic Province is divided into dozens of pseudo-replicated fish habitats isolated by mountain ranges, making a highly constrained physiographic region. This permitted us to trace lineages with rather well-controlled histories. Second, the region has a more detailed fossil fish record (Figure 1) than is available for most modern fish faunas, and this record is supported

by a reasonably well-known stratigraphic context (e.g., Benson et al., 1990; Morrison, 1991; Oviatt et al., 1992) and by mammalian stratigraphy (e.g., Stirton, 1936; Lindsey et al., 1984; Lundelius et al., 1987; Repenning, 1987; Tedford et al., 1987; Woodburne, 1987). These circumstances enabled us to begin to address some of the most difficult problems in evolutionary biogeography: Over what time scales do speciation processes occur? How long does it take for differentiation of races, subspecies, and species to occur in isolation? Are the rates of differentiation interval-dependent (Gingerich, 1986), i.e., is the concept of a general rate inappropriate (Bookstein et al., 1978; Bookstein, 1986; Bell, 1994)? Consideration of questions about species and their origins requires a species concept that is open to testable hypotheses concerning processes of origination.

**SPECIES CONCEPTS AND SPECIATION HYPOTHESES.**—Three species concepts stand out as most relevant to models of freshwater fish speciation in the Great Basin: phylogenetic, biological, and evolutionary. The phylogenetic species concept (Cracraft, 1983) focuses on diagnosable, monophyletic, and irreducible units that maximize the recognition of biotic diversity. Many more phylogenetic species could be recognized than are currently acknowledged in the Great Basin. The phylogenetic species concept is often rejected because its lower limits are not well constrained (Mishler and Donoghue, 1982) and because many species are not monophyletic. Local demes, such as the subspecies and races of *Cyprinodon nevadensis*, *Siphateles bicolor*, and *Rhinichthys osculus*, could be recognized as species under this model. Moritz et al. (1995) argued for use of mutually and reciprocally unique differences as species criteria. This concept requires no information about time, monophyly, or reproductive isolation, so it is independent of evolution of reproductive isolation. The addition of reproductive and historical tests to proposed species enables more complete evaluation of speciation models.

The biological species concept (Mayr, 1963) recognizes groups of populations that are reproductively isolated from other such groups. The focus on reproductive isolation makes this concept central to most speciation process models. Species so defined often contain geographically variant populations, so that in the Great Basin the concept is realistic and objective but is operational only by inference. This definition is sometimes applied too restrictively to accommodate some Cyprinidae, Catostomidae, and Salmonidae, for which there is evidence of gene flow between historically well-differentiated lineages that diverged several million years ago (Smith, 1992a). The biological species concept is improved for our purposes by integration with the ecological species concept of Van Valen (1976, 1988), that is, accommodation of limited gene exchange between long-term, ecologically independent lineages.

The evolutionary species concept (Simpson, 1951; Wiley, 1981; Mayden and Wood, 1995) requires evidence that lineages have separate evolutionary histories, usually diagnosed in a cladistic context. This concept does not require (or rule

out) evidence for reproductive isolation as evidence for lineage independence. The evolutionary species concept is applicable to Great Basin fish lineages to the extent that introgressed but still-separate lineages are not excluded because of non-monophyly or temporary lapses in independence.

The time required for acquisition of genetically based ecological or reproductive isolation as a guarantor of lineage independence is a matter of special concern in the study of speciation in the Great Basin because of the large number of diagnosable, but possibly ephemeral, allopatric populations. Western North American fishes show a high degree of allopatry, but they also provide unusually frequent examples of gene exchange between species of long-standing independence (Hubbs, 1955). Great Basin species of minnows, suckers, trouts, pupfishes, and sculpins are especially consistent with species concepts and origination models that require reproductive independence, but not necessarily isolation. Modest introgressive influence does not contradict this definition, if the morphologically and ecologically different lineages are not amalgamated through hybrids with high fitness. Reproductive independence and reproductive isolation are often assumed to be synonymous and mutually required for species recognition, but in many species, it is worth making a distinction. Evidence for introgression is usually taken to be evidence against independence (by zoologists, not botanists; Wagner, 1983; Rieseberg and Wendel, 1993), but if forms are ecologically different enough to be disruptively selected, introgression does not necessarily reduce two lineages to one.

For example, the ecologically distinct pairs *Catostomus ardens* and *Chasmistes liorus* of Utah Lake belong to clades that diverged 3–6 Ma. Introgression occurred in the Provo River at the time of the drought in the early 1930s (Miller and Smith, 1981), but morphological stability of *C. ardens* and ecological persistence of (modified) *C. liorus* indicate sufficient reproductive separateness between these forms to warrant species rank. In contrast, some pairs of populations of *Siphateles bicolor obesus* and *S. b. pectinifer* in the Lahontan Basin failed to stay separate through recent times (Hubbs and Miller, 1948b). These different outcomes are ecology dependent (Van Valen, 1976, 1988) in that the reproductive isolation is maintained only by spawning-site selection based upon ecological characteristics—depth, current, light, temperature, and substrate. Evolution of lineage independence, therefore, is partly a function of ecological context (Smith, 1992a; Smith et al., 1995). The introgression hypotheses of Hubbs and Miller (1948b) and Smith (1992a) suggest a Pleistocene history of alternation between habitat-rich pluvials and habitat-poor, arid interpluvials, which could have resulted in cyclic adaptation to special habitats in wet times, followed by selection of morphologically generalized phenotypes during times of reduced habitat diversity. The result is introgressive destruction of some (but not all) independent lineages.

We therefore define species as lineages whose separate history can be reasonably inferred from diagnostic morphological,

ecological, genetic, or behavioral apomorphies. This definition recognizes that species are individuals (Ghiselin, 1974, 1997), and it is meant to be consistent with Ghiselin's general definition (1997:99): "Biological species are populations within which there is, but between which there is not, sufficient cohesive capacity to preclude indefinite divergence." Our wording acknowledges extrinsic properties and emphasizes history. It might also be peculiarly ichthyological—D.S. Jordan (quoted by Joseph Grinnell, 1924:225) said that "a species is not merely a group of individuals distinguished from other groups by definable features;" it is "a kind of animal or plant which has run the gauntlet of the ages and has persisted." The intrinsic bases for maintaining historical lineage separateness may be ecological (different habitats), reproductive (different times or places of spawning), or developmental (different genes for growth), but they are ultimately genetic and controlled by long-term selection (Fisher and Ford, 1947; Wright, 1948). The traits that we focus upon herein are associated with reduced hybrid fitness because of high mortality or low fertility (Dowling et al., In prep.). Tests of intrinsic reproductive separation are usually inferred from (1) the presence or absence of traits unique to sympatric relatives, (2) apomorphic courtship displays, (3) assortative mating, (4) failure to produce fertile or viable offspring, or (5) reduced fitness of hybrid products. Tests of long-term persistence require paleontological or molecular biogeographic data that provide a time context in which to evaluate persistence or stability for a period longer than a post-glacial fragment of a glacial cycle. We suggest that molecular divergence measures can contribute to this test, although a sharp, defining demarcation in time or sequence divergence is not suggested. The criteria presented above provide appropriate evidence for accepting or rejecting species assignment under both the evolutionary and the biological species concepts. These considerations provide a context for analyzing the temporal scale of morphological and genetic differentiation in relation to speciation.

The above definition and the patterns of Great Basin fishes through geologic time suggest avoidance of the chronospecies concept, which is popular in paleontology but incompatible with cladistic, evolutionary, or biological views of species (Krishtalka and Stucky, 1985; Ghiselin, 1997). Great Basin species are interpretable as individuals that may change through time, sometimes anagenetically, and sometimes through recombination of genes from related populations. In either case, the individuality of ancestral-descendant lineages through time is paramount (Ghiselin, 1974, 1997), and it seems unhelpful to the study of speciation to change lineage names to indicate anagenetic changes. To name chronological species recognizes only stratigraphic diversity, not species diversity. Similarly, it seems unhelpful to change the name of a sister taxon that has given rise to a peripatric daughter taxon without any change in the morphology of the original population (Bell, 1979).

**SPECIES FORMATION IN THE GREAT BASIN.**—The Great Basin fishes are a product of cycles of expanded and contracted habitats, resulting in cycles of differentiation of local populations but only modest persistence of lineages through time. Here the speciation process involves three steps (Smith et al., 1995): (1) separation of populations by hydrographic or habitat barriers (or microhabitat difference in lakes); (2) accumulation of genetic differences in growth, development, physiology, ecology, or behavior; and (3) accumulation of some minimum combination of genetically based differences sufficient to cause hybrids to suffer reduced fitness. Operationally, the products of these process are recognized when lineage independence seems reasonably supported by reciprocally nonoverlapping molecular, morphological, or ecological apomorphies that indicate an intrinsic basis for lineage separateness. Confidence in and predictions from these hypotheses are subject to tests by paleontological or biogeographic circumstances that indicate persistence through more than one environmental cycle.

The Cenozoic tectonic and Pleistocene hydrographic history of the Great Basin created hundreds of allopatric isolates with the potential to become species, as demonstrated by Hubbs and Miller (1948b) and Hubbs et al. (1974). We conclude, however, that the same conditions (small isolates) and processes (long isolation and short cycles of habitat fluctuation) that caused the initial differentiation also caused extinction of the majority of potential species. Evidence of this extinction is seen in the declining late Cenozoic fish diversity, depauperate local faunas, and absence of the vast species numbers expected from scores of so-called "species-pump" cycles.

Examples of surviving vicariant pairs in the Great Basin are nevertheless notable. They include *Lepidomeda albivallis* and *L. altivelis* in the White River Valley and in Pahrangat Valley, Nevada; *Richardsonius egregius* and *R. balteatus* in the Lahontan and the Bonneville–Columbia Basins; *Catostomus tahoensis* and *C. fumeiventris* in the Lahontan and Owens Basins; *Cyprinodon salinus*, *C. milleri*, *C. nevadensis*, and *C. diabolis* in the Death Valley system; *Crenichthys baileyi* and *C. nevadae* in the White River valley and in Railroad Valley; *Empetrichthys latos* and *E. merriami* in Pahrump Valley and Ash Meadows; and *Cottus extensus* and *C. echinatus* in Bear Lake and Utah Lake. Most of the other species in the Great Basin have sister taxa outside the basin or have complex distribution patterns requiring dispersal. Examples of stages of differentiation similar to the above are found among the subspecies and races of *Siphateles bicolor*, *Rhinichthys osculus*, *Gila atraria*, and *Oncorhynchus clarki*. These forms are early and perhaps temporary examples of vicariant speciation, as described above. Our DNA divergence data and the hypothesis that speciation usually involves the long-term accumulation of multiple genetic differences suggest that, on average, species-level differentiation (beyond the subspecies and races of Hubbs and Miller) requires a longer time than the duration of the Pleistocene.

Lacustrine speciation requires special explanation. Examples include the species of *Prosopium* in Bear Lake and the Bonneville Basin, and *Siphateles bicolor pectinifer* in the Lahontan Basin. The trophic and lacustrine adaptations of these sympatric forms indicate that they might have differentiated in intralacustrine micro-allopatry (Smith and Todd, 1984) involving evolution of different habitats and spawning times. Independent evidence suggests that intralacustrine speciation is much more rapid than speciation in most other circumstances (Mayr, 1984; McCune et al., 1984; Smith et al., 1995), possibly because it is driven by competitive selection (Rosenzweig, 1978). Variability also might be enhanced by relaxed selection during lake transgression and population expansion (McCune, 1990).

There is a widely cited hypothesis that lacustrine speciation is driven by cyclic allopatry, with low stages that separate allopatric populations, which diverge, and high stages, which foster dispersal and widespread sympatry (e.g., Mayr, 1963; McCune et al., 1984). The history of the Great Basin includes numerous pluvial cycles (dozens, if pluvial cycles tracked glacial cycles) during the last 3 My (Imbrie and Imbrie, 1979; Benson et al., unpublished data; G.I. Smith et al., unpublished data). The pattern of species abundance and distribution in Great Basin fishes does not conform to the lacustrine fluctuation model of lacustrine speciation (Mayr, 1984; Smith and Todd, 1984) because extinction, not speciation, has dominated Great Basin history (Smith, 1978), perhaps because the arid parts of the cycle have been so extreme.

The fossil and molecular evidence for an ancient presence (a criterion suggested by Ricklefs and Schluter, 1993) of most of the species in the Great Basin also suggests that extinction has been more frequent than species production. The abundance of races and subspecies in the Great Basin suggests that frequent origin and extinction jointly act on populations with limited ranges. Species with stable habitats or large geographic ranges, by contrast, tend to be long-term survivors (Jablonski, 1980).

The pattern of morphological change through time, if viewed on the million-year time scale, would appear to be consistent with the hypothesis that most morphological changes in species occurred at the time of initial divergence (Stanley, 1975; Gould and Eldredge, 1977). Viewed on the thousand-year time scale, we see early morphological response to changing environments, but slow accumulation of characters that may be capable of sustaining long-term individuality.

**TEMPORAL SCALE OF SPECIES DIFFERENTIATION IN THE GREAT BASIN.**—These cases suggest a model in which Great Basin fish differentiation was distributed broadly across pluvial cycles of the last 3 My. Through time, some fraction of the new forms went extinct, and some species and subspecies introgressed into relatives during extinction episodes. Some of these diverged again during pluvial and early postpluvial episodes. The net result is abundant geographic variation cycling through time, as seen in the fossil record, combined with low species diversity, as seen in Great Basin fishes today (Miller, 1959).

The fossil record indicates that throughout the million-year time scale, net changes have been slow. Geographic variation shows that during the thousand-year time scale, some morphological changes in oligogenic and ecophenotypic traits have been rapid (Hubbs and Miller, 1948b; Bell, 1994). It is possible that bony characters seen in the fossil record are multigenic and evolve more slowly than oligogenic meristic, color, and shape characters that differentiate subspecies. It is also likely that body shape, scale, and fin characters fluctuate, perhaps ecophenotypically, which is consistent with the random-walk hypothesis (Bookstein et al., 1978). Fluctuating variations observed during a time scale of hundreds of years (Bell and Haglund, 1982; Bell et al., 1985; Bell, 1994) and decades support this hypothesis (Figure 12). Small, rapid changes are expected in short-term studies, in contrast to slow changes expected in long-term studies (Gingerich, 1986), in part because genetic variation is consumed by selection (Lewontin, 1974).

These differences in amounts of change as a function of time are observed in empirical studies in the laboratory as well as in comparisons of paleontological rates (Gingerich, 1986). Random fluctuation was not one of the hypotheses considered by early students of Great Basin fishes: Hubbs (1940:211) saw “orderly adjustment under the control of environment” not “aimless wandering of genes through the organic world.” Studies of morphological fluctuations in the fossil record (Figure 12; Bookstein et al., 1978; Chernoff, 1981; Bookstein, 1986; Bell, 1994) and complex biogeographic patterns in the Great Basin suggest a model of rapid adaptive response to changing environments but minimal long-term trends because of the high amplitude and periodicity of the fluctuations.

## Conclusions

The Great Basin fish fauna is the most depauperate ichthyofauna in North America, despite being situated on a landscape ideal for allopatric speciation. Comparison of morphological subspecies differences (Hubbs and Miller, 1948b; Hubbs et al., 1974) with paleontological studies of populations through time indicates that abundant, newly differentiated forms usually fail to become long-term members of Great Basin biodiversity. This fauna has not significantly diversified despite repeated Pleistocene fluctuations in lake levels. The absence of the diversity predicted by repeated environmental change leads to two conclusions: (1) extinction of small populations is a more potent long-term force than speciation in fluctuating environments, such as occurred in the Pleistocene Great Basin; and (2) speciation processes are favored in small populations (Wright, 1940a; Mayr, 1963; Gould and Eldredge, 1977), but during a time scale of thousands of years, most of this diversity becomes extinct if individuals in small populations cannot disperse among drainages.

A related aspect of these fishes is that western salmonids, catostomids, cyprinids, and cyprinodontids are unexpectedly lacking in intrinsic reproductive isolation among morphologi-

cally and ecologically differentiated lineages, some of which have separate evolutionary histories going back several millions of years (Smith, 1992a). Fluctuations in abundance have caused frequent hybridization (Hubbs and Miller, 1943; Hubbs, 1955). The frequent exchange of genes through introgression appears to have maintained some genetic compatibility, even as it provided variation for adaptations to environmental change.

The extreme isolated allopatry and resulting divergence of Great Basin fishes permit some calibration of the chronology of hydrologic history of basins, as sought by Hubbs and Miller. Molecular divergence estimates, in conjunction with ages of fossil ancestors, enable the calculation of DNA divergence-rate estimates in salmonids (0.5% per 1 My) and in cyprinids and cyprinodontids (1% per 1 My). These results permit percent sequence divergence to be used to calculate a rough chronology of hydrologic barriers between individual basins, groups of basins, and drainages neighboring the Great Basin. The Rocky Mountain barrier between Great Basin and eastern North American fishes was crossed at low elevations multiple times between 22 and 12 Ma, according to cyprinid sequence divergences. Major connections among Great Basin, Colorado River,

Rio Grande, Rio Yaqui, and adjacent drainages in the Basin and Range Province of northern Mexico date from 9 to 5 Ma, based upon cyprinid divergences. Great Basin and Columbia–Snake divergences of cyprinids imply that separations occurred early, 11–6 Ma, but that many reconnections occurred during the interim. Two levels of differences between lowland and upland taxa of the Lahontan and Bonneville Basins imply that major confluences existed prior to 12–6 Ma and minor headwater connections occurred 4–0.2 Ma. Estimates based upon trout DNA sequence divergences imply that the Lahontan Basin headwaters were connected to the Columbia River drainage about 0.2 Ma, but Lahontan Basin populations were connected to each other more recently than 0.2 Ma. The Bear River populations were connected to the Snake River populations 0.3 Ma, but the trouts of the Bonneville and Lahontan Basins were connected 4–2 Ma. Cyprinodontoids of the Death Valley system were connected to the lower Colorado River basin and to Mexico several times in the last 2–3 My and were among basins in the Death Valley system during the last 0.1–1.3 My. In summary, paleontological and molecular evidence indicates that most Great Basin fish lineages are older than previously thought.

## Appendix

The fish species and subspecies of the hydrographic Great Basin, both fossil and Holocene, are listed below in approximate phylogenetic sequence and are numbered to correspond to references to them in the text, tables, and figures. Forty-one forms known only from fossils are indicated by a dagger (†). An asterisk (\*) indicates that the account of the Holocene lineage contains a pertinent fossil record.

### CYPRINIDAE

#### Western Chub Group

##### *Mylopharodon*–*Lavinia*–*Hesperoleucus* Subgroup

1. †*Lavinia* sp. (Secret Valley hitch). This small species is diagnosed by pharyngeal teeth with corrugated grinding surfaces and by dentaries with flared lateral edges (Smith, 1975, fig. 19B). *Idadon* of the Snake River Plain is herein interpreted as a synonym of *Lavinia* of the Great Valley (“1” in Table 2). *Idadon* and *Lavinia* share the unique features of corrugated pharyngeal teeth and flared dentaries, although these features are more extremely developed in *Idadon*. Flared dentaries collected from elsewhere on the Madeline Plains, northeastern California, have been identified as *Lavinia* and *Acrocheilus* by Wagner et al. (1997). The Secret Valley dentaries are more flared than those from the Snake River Plain. Although highly variable, the Secret Valley dentaries are more similar to *Acrocheilus* than to *Lavinia* (Wagner et al., 1997), but they lack the

abrupt angles of *Acrocheilus*. (*Acrocheilus* teeth are not present among UMMZ specimens from Secret Valley.) The Secret Valley fossils are assigned an age of ~3.5 Ma; this assignment was based on their correlation with specimens from the Snake River Plain.

*Lavinia* + *Hesperoleucus* is the sister group to *Mylopharodon* in the cladogram (Figure 2). *Lavinia* and *Mylopharodon* are known from apparent first appearances on the Snake River Plain about 6 Ma and 4 Ma, respectively; these ages correlate with the sequence divergence value of 8.1% (Tables 2, 5) in Figure 14.

Molecular evidence (Table 2) indicates a sequence divergence of 15% between *Siphateles bicolor* and *Lavinia*. (See number 14, below.)

2. †*Lavinia* sp. (Carson Valley hitch). A partial left dentary from late Blancan sediments (~3 Ma) and three caudal vertebrae from early Blancan sediments (~5 Ma) were collected in Carson Valley by T. Kelly. The dentary is 10.5 mm long and represents a fish about 18 cm in standard length (SL). The specimen is diagnosed as *Lavinia* by the flared gnathal ramus, coronoid process at midpoint of the bone, mesially curved anterior end, and position of eight lateralis pores. The caudal vertebrae are dorsoventrally compressed, with a thick, single longitudinal ridge on the lateral surface of the centrum.

3. †*Lavinia* sp. (Cache Valley hitch). Specimens collected from Cache Valley near Logan, Utah, by J. Stewart Williams of Utah State University, appear to be large *Lavinia*. This conclusion is based upon the slightly corrugated grinding surfaces on

the pharyngeal teeth, the flared dentaries, and the high fin-ray counts. The distinct morphology and the absence of Pliocene indicators with these fossils suggest a pre-Blancan, late Miocene age (~6 Ma). McClellan (1977) reported *Idadon* (herein treated as a synonym of *Lavinia*) from the Junction Hills fauna of the Salt Lake group, near Fielding, Box Elder County, Utah. The fossils appear to be Hemphillian in age by correlation with adjacent faunas. Cyprinids similar to *Lavinia* or *Mylopharodon*, but not to *Gila*, have been collected from the Bear River valley near Georgetown, Idaho, by Sue Ann Bilby and have been deposited in the collections of the Idaho State Museum of Natural History. This record supports the age estimate of 6 Ma assigned to the sequence divergence value of 8.1% in Figure 14.

4. *Hesperoleucus symmetricus* (Baird and Girard) (California roach). This species lives in the Great Basin only in the Warner Lakes system, near Adel, Lake County, Oregon. It is most similar to *Hesperoleucus* sp. in Goose Lake and the Pit River drainage (from where it might have been introduced (Miller, 1959)). Although sometimes placed in *Lavinia* because of protein and molecular similarities, the morphological differences and fossil record suggest that *Lavinia* and *Hesperoleucus* are long-different lineages that share molecular similarity (they differ by only 1.3% sequence divergence) probably because of introgression.

5. *\*Mylopharodon* Ayres (western chubs). Chubs with molariform teeth occurred in the Great Basin and in the Snake River Plain from the middle Miocene through the Pliocene, and they remain in the Great Valley of California. Fossils of this genus are rare in the Great Basin. †*Mylopharodon*(?) *doliolus* Smith and Kimmel was a large chub with widely spaced, rounded molariform teeth (Smith et al., 1982, fig. 4E). It was placed in *Mylopharodon* because of its molariform teeth, elongate posterodorsal process of the pharyngeal arch, and general shape of the pharyngeal arch. This form is from the Esmeralda Formation in Silver Peak Quadrangle, Nevada, and may be as old as  $12 \pm 2$  My. It lacks the derived characters of all *Mylocheilus* and *Mylopharodon* (of the Snake River Plain, Great Basin, Sacramento Basin, northeastern California, and southeastern Oregon) and, therefore, could represent the stem group leading to *Mylopharodon* and *Siphateles*. *Mylopharodon* lived in the Honey Lake basin (collected by Todd Yeoman of Sierra College) and the Snake River Plain during the Pliocene. †*Mylopharodon hagermanensis* Uyeno first appeared at Hagerman, Idaho, on the Snake River Plain about 4.5 Ma. *Mylopharodon conocephalus* (Baird and Girard) of the Great Valley (number 5 in Table 2) and *Siphateles* (of the Lahontan Basin) differ by 10.2% sequence divergence (Figure 2; Table 2). The Miocene fossil could also be the earliest western relative of eastern cyprinids, from which *Mylopharodon conocephalus* differs by 42% sequence divergence (Table 2; Dowling, unpublished data).

### *Siphateles* Subgroup

6. *\*Siphateles* sp. (chub). Chubs with a single row of pharyngeal teeth on each arch are widespread in the late Miocene to Holocene fossil record of Nevada. Whole fossils and numerous separate bones similar to *Siphateles* were discovered in Barstovian (middle Miocene, ~15 Ma) beds of Buffalo Canyon, Churchill County, Nevada, by Ron and Zachary Jones. These are the oldest known cyprinid bones in the Great Basin, so they provide an estimate (underestimate) of the time of vicariance with the eastern clade of North American shiners, from which *Siphateles* differs by more than 30% sequence divergence (Table 2; Dowling, unpublished data). A complete but undescribed specimen similar to *Siphateles* is known from the Nevada Test Site in southern Nye County, Nevada. It is believed to be Miocene in age. Several complete specimens and numerous bones are known from the late Miocene beds of the Virgin Valley Formation, Humboldt County, Nevada. Unidentified cyprinid fossils are known from Pine Nut Ridge (Douglas County, late Hemphillian to Blancan) and from the Coal Valley Formation. The late Hemphillian fossils are estimated to be 6 My old and may indicate the branch point with *Gila*, which differs from *Siphateles* by an average of 11.5% (s.d. = 2.2%) sequence divergence (Figure 14; Table 2).

7. †*Siphateles breviarchus* (Cope) (Fort Rock chub). This is the common cyprinid in the Pliocene sediments of Fossil Lake, Lake County, Oregon. It has robust pharyngeals that are similar to those of *Mylopharodon*. It represents a stage of evolution prior to diversification of the *Siphateles bicolor* complex. The date of its divergence from *Mylopharodon* is probably about 10 Ma based on sequence divergence (Figure 14; Table 2).

8. †*Siphateles traini* (Lugaski) (chub). This fossil form, from the late Miocene lacustrine beds in Jersey Valley, Pershing County, Nevada (Lugaski, 1979), is morphologically somewhat similar to *S. bicolor*. The zeolite beds in which *S. traini* occurs suggest that the fish lived in a shallow, saline, alkaline lake of pH 9, much like Pyramid Lake, Washoe County, Nevada, in which *S. b. obesus* currently lives (Lugaski, 1979). Michael Bell and others have collected a large cyprinid from the late Miocene part of the Truckee Formation, near Hazen, Nevada (see number 29, below), with robust proportions and fin-ray counts that suggest a relationship to this group. These late Miocene sites are estimated to be 6 My old (Figure 14).

9. *\*Siphateles bicolor* (Girard) (tui chub). This polytypic species is widespread in the Lahontan Basin drainage as *S. bicolor obesus*, and it also extends into Oregon's lake basins as *S. b. bicolor*, and into the Harney Lake and lower Columbia River basins, where it has been referred to *S. b. columbianus*. *Siphateles bicolor* is diagnosed by a single row of pharyngeal teeth. Cyprinid bones found in indurated sediments of Pyramid and Winnemucca Lakes and other areas of the Lahontan Basin are probably *Gila bicolor obesus*. Fossils related to this species are

known from the Pliocene of Honey Lake, Lassen County, California, and Mopung Hills, Churchill County, Nevada, and from numerous Holocene Indian middens reported in the archaeological literature. The Blancan fossils occurred before Pleistocene tectonism began at the Honey Lake site, possibly 3 Ma. Samples from the Lahontan Basin, from the Owens River, Mono Lake, Mohave River, and Oregon Lakes basins, and from the Columbia River, analyzed by Dowling, differ from each other by 3.1% of the cytochrome *b* sequence (Table 2).

*Siphateles bicolor obesus* is widespread throughout the streams and springs in the Lahontan Basin system, where it typically has 10–19 short gill rakers, a 5–4 pharyngeal tooth formula (Hubbs et al., 1974), and distinctive scales. Many unnamed, geographically distinct forms, in addition to the named taxa summarized below, vary in gill raker number or morphology, scale counts, size, proportions, nuptial characters, and color patterns. For example, Sulfur Spring, in Diamond Valley, Eureka County, Nevada, contains a dwarf form with long gill rakers, complete lateral line, long pectoral fins, and distinctive colors; it is included with *S. b. obesus* because a downstream population has features that are intermediate between it and the Humboldt drainage forms (Hubbs et al., 1974).

Hubbs and Miller (1948b) reported distinct subspecies in the valleys of Lake Dixie and Lake Toiyabe, in Big Smokey Valley, and in Railroad Valley in central Nevada, south of the Lahontan Basin drainage (Figure 4). Another distinct form lived on the east side of the valley of pluvial Lake Toiyabe in Lander and Nye Counties, Nevada, along with *Rhinichthys osculus lariversi* (Lugaski, 1972). (Forms on the west side of the valley were apparently transplanted into the springs around the turn of the century; both populations of *S. bicolor obesus* are now extinct.)

Just about every isolated population of *S. bicolor* in the Oregon Lakes has a distinctive combination of characters involving size, body shape, fin shape, gill raker length and number, and color (Hubbs and Miller, 1948b; Hubbs et al., 1974). *Siphateles bicolor eury soma* (Williams and Bond, 1981) was named from the Guano Basin, Nevada. The Catlow Valley chub in Malheur County and the Guano Valley chub in southeastern Lake County, Oregon, are recognized as *Siphateles bicolor eury soma* Williams and Bond (1981) (Hubbs and Miller, 1948b). *Siphateles bicolor* in the Oregon basins vary from forms with more than 16 gill rakers (Catlow Valley, Guano Lake, and Warner Lakes basins) to forms with fewer than 16 gill rakers (basins of the lower Columbia River, of Harney, Klamath, Fort Rock (Fossil), Alkali, and Summer Lakes, and of Lakes Abert and Chewaucan) (Minckley et al., 1986).

10. †*Siphateles* sp. (chub). Pliocene(?) fossil *Siphateles* from Duck Valley, Washoe County, Nevada, is estimated herein to date from 2 Ma. Specimens like the modern *Siphateles* of the Lahontan Basin occur in Humboldt Canyon below the Lava Creek tephra, which was deposited  $665 \pm 10$  Ka (Izet, 1981; Izet et al., 1992) and the Brunhes–Matuyama geomagnetic reversal, 780 Ka (Baksi et al., 1992). Oregon and Nevada speci-

mens differ by 3.1% sequence divergence (Table 2). G.I. Smith and colleagues of the United States Geological Survey (USGS) recovered a specimen from the Searles Lake core (R.R. Miller, pers. comm. to G.R.S., 1999).

11. †*Siphateles bicolor* subsp. (chub). Gobalet and Negrini (1992) reported a distinct but undescribed fossil form of *S. bicolor* from the Chewaucan Basin of southern Oregon; the form was stated to be more than 10 Ky old. Modern specimens of *Siphateles* from Oregon and Nevada differ from each other by 3.1% sequence divergence (Table 2). Modern representatives in the Chewaucan, Alkali, and Fort Rock Basins (Figure 4) are similar to each other (Hubbs and Miller, 1948b).

12. \**Siphateles mohavensis* Snyder (Mohave tui chub). This distinct chub was originally described as a species from the Mohave River in the valley of pluvial Lake Mohave. It has eight anal-fin rays, uniserial teeth, and 18–29 gill rakers. Its numerous gill rakers characterize a plesiomorphic condition retained from its lacustrine ancestor (Hubbs and Miller, 1948b). Otherwise, it is similar to tui chubs (Miller, 1973). Fossils related to this form were reported from sediments of China, Manix, and Searles Lakes by Buwalda (1914), Blackwelder and Ellsworth (1936), and Flint and Gale (1958). Numerous isolated bones collected by D.F. Hewett and D.W. Taylor from Lake Manix beds represent this species and have osteological characters like the *Siphateles* figured by Miller (1973). Teeth and vertebrae recovered by B. Leatham from “Lake Mohave” (also called Soda Lake) north of Baker, California, dated at 20 Ky B.P., are most likely from this species. Late Pliocene tui chub bones associated with *Catostomus* and *Chasmistes* from the White Hills near Airport Lake, Inyo County, California, may be the same as the Soda Lake form.

13. \**Siphateles bicolor snyderi* (Miller) (Owens tui chub). This chub inhabits springs and creeks of the Owens River drainage, Inyo and Mono Counties, California. Small lateral line scales, distinctive lateral radii on the scales, few dorsal- and anal-fin rays, a distinctively shaped pharyngeal arch, and usually 10–14 gill rakers diagnose this form. It is most similar to *Siphateles bicolor obesus* in the East Walker River, from which Miller (1973) presumed it was derived. Fragments assumed to represent the Owens River *Siphateles* were recovered throughout the Pleistocene Owens Lake core (Firby et al., 1997). Holocene Indian middens along the nearby Alabama Hills in Inyo County, California, contain abundant remains of this tui chub and *Catostomus fumeiventris*, but no other fishes.

14. †*Siphateles* sp., (Mono Basin chub). Pliocene fossil bones from Mono Lake basin and Miocene to Pleistocene sediments of Carson Valley are clearly plesiomorphic *Siphateles*. The dentaries from both sites are similar to each other and are sufficiently distinct from other *Siphateles* to be regarded as a single, different species (see number 15, below; to be described by K. Gobalet). The Mono Basin sample of *Siphateles* now includes hundreds of identifiable specimens. They are similar to *Gila crassicauda* but are different from other *Gila* and other *Siphateles* in the distinct robustness of the anterior ramus of the

dentary and in the anterior position of the dorsal mental foramen; the anterior edge of the coronoid process is angled more posteriorly in *Gila*. The masticatory platform of the basioccipital is similar to *Mylopharodon* in the obtuse angle of the posterolateral processes at the origin of the caudal process; this part of the bone matches *Siphateles* rather than *Mylopharodon*. The pharyngeal arches bear a single row of teeth, which are robust, somewhat rounded, and reach large size (to 9 mm). These teeth indicate the fossil species had a larger maximum size than the modern record of 42 cm in total length for this species (Sigler and Sigler, 1987). We estimate the age of these fossils to be about 8 My old (based upon the morphological differences described here), which places them closer to the branch point with *Mylopharodon* than with *Gila*. A large, straight dentary and molariform pharyngeal teeth attributed to *Mylopharodon* by Miller and Smith (1981) might be large *Siphateles* with long jaws and rounded teeth.

15. †*Siphateles* sp. (Carson Valley tui chub). Abundant Carson Valley materials are known from the early Blancan Buckeye Creek local fauna, the late Blancan Fish Spring Flat local fauna, and the early Irvingtonian Topaz Lake local fauna, Douglas County, Nevada. They are distinctive in their robust and posteriorly angular pharyngeals, somewhat like the Mono Basin forms. The dentary shows a more anterior position of the dorsolateral mental foramen than other forms, except those from Mono Basin. The masticatory plates of the basioccipitals are rounded ventroposteriorly, like fossil *Siphateles* from the Mono Basin and Humboldt River canyon and from Holocene forms from some Lahontan Basin localities and the Sacramento River drainage. The Carson Valley forms are estimated to have lived 5, 3, and 1 Ma.

16. \**Siphateles bicolor pectinifer* (Snyder) (lake minnow). This lacustrine tui chub was described by Snyder (1917a) and placed in the distinct genus *Leucidius*. It can be distinguished by its long, numerous gill rakers (29–36) and by its usually 5–5 pharyngeal-teeth pattern. It is sympatric with *S. obesus* (Snyder, 1917a; Hubbs et al., 1974:143–150). Extensive introgression has eliminated recognizable individuals of this form in Eagle Lake and has reduced its distinctiveness in Lake Tahoe, Walker Lake, and Pyramid Lake. The presence of hybrid pharyngeals in ancient Indian middens (Hubbs, 1961; Smith, 1985) is evidence that the parental forms hybridized but maintained their differences for thousands of years (Hubbs, 1961). Remnant populations of *S. b. pectinifer* in different, unconnected habitats suggests that the ecologically significant differences are genetically based (Hubbs, 1961; Hubbs et al., 1974).

17. *Siphateles bicolor vaccaiceps* (Bills and Bond) (Cowhead Lake tui chub). This unique population was discovered by Hubbs and Miller (1948b) in Cowhead Lake, Modoc County, California. It is characterized by its small size (less than 12 cm SL), numerous, short gill rakers (19–25), and small scales. It is most similar to the unnamed chub in Warner Valley (to which Cowhead Lake was tributary in pluvial times), but that form has longer gill rakers (Bills and Bond, 1980).

18. *Siphateles bicolor newarkensis* (Hubbs and Miller) (Newark tui chub). This chub is the only native fish in the springs of the main basin of pluvial Lake Newark, in White Pine County, Nevada. It is characterized by having few, short, thick gill rakers, a usually complete supratemporal canal, long pectoral fins, and small size (less than 10 cm SL) (Hubbs and Miller, 1972; Hubbs et al., 1974).

19. *Siphateles bicolor euchilus* (Hubbs and Miller) (big-mouth tui chub). This is the sister form to *S. b. newarkensis*, with which it shares many features. It is found in springs of Fish Creek (Little Smokey) valley in the southwestern part of the valley of pluvial Lake Newark (southeast corner of Eureka County, Nevada). It is characterized by relatively large size (10–15 cm SL), especially anteriorly; large fins, especially the pectorals; and large scales (Hubbs and Miller, 1972; Hubbs et al., 1974).

20. *Siphateles bicolor isolatus* (Hubbs and Miller) (Clover tui chub). This represents one of two species found in Independence Valley, Elko County, Nevada, in the valley of pluvial Lake Clover. *Siphateles b. isolata* is small, with intermediate-length gill rakers reduced to about 11. It shares characteristics with *S. b. newarkensis* and *S. obesus* of nearby Bishop Creek of the Lahontan Basin drainage (Hubbs and Miller, 1972; Hubbs et al., 1974).

21. *Siphateles alvordensis* (Hubbs and Miller) (Alvord chub). This species inhabits creeks in the Alvord Basin of Malheur County, Oregon, and adjacent Humboldt County, Nevada. It is characterized by uniserial teeth, small, embedded scales with radii in all fields, usually seven dorsal and anal fin rays, and numerous, short gill rakers (16–22) (Hubbs and Miller, 1972).

22. *Siphateles boraxobius* (Williams and Bond) (Borax Lake chub). This small fish occurs in Borax Lake, Alvord Basin, Malheur County, Oregon. The diagnosis includes a large head, large eyes, small caudal peduncle, and a reduced lateral line. The species shares general characters with *S. alvordensis*, but it has fewer gill rakers, fewer lateral line scales, and fewer pectoral-fin rays, like many dwarf populations of *Siphateles* (Williams and Bond, 1980).

#### *Gila-Acrocheilus-Klamathella* Subgroup

23. \**Gila atraria* (Girard) (Utah chub). This variable, abundant species is widespread in the Bonneville Basin and upper Snake River above Shoshone Falls. It is distinctive in its 2,5–4,2 pharyngeal teeth with grinding surfaces, 9 dorsal-fin rays, 8 anal-fin rays, and 8–16 gill rakers. It is locally divergent and polymorphic in its mtDNA. The Bear River population diverged from the Bonneville Basin populations more than 2 Ma, well before the complex Late Quaternary interactions between the Bear River and Lake Bonneville (Bouchard et al., 1998). The fossil record of *Gila atraria* is known back only to the late Pleistocene Black Rock Canyon, Smith Canyon, and Homestead Cave faunas in the Lake Bonneville drainage basin, Utah

and Nevada (Smith et al., 1968; Mead et al., 1982; Broughton, 2000a, 2000b).

**24.** *Gila jordani* Tanner (Pahranagat roundtail chub). This species lives in Ash Springs, Crystal Lake, and (formerly) Hiko Springs, all in Pahranagat Valley, pluvial White River system, Lincoln County, Nevada (Tanner, 1950). It has the unique combination of *Gila robusta* morphology and *G. cypha* and *G. atraria* mtDNA (Table 2); this unique combination is diagnostic for the species. *Gila jordani* is sympatric with *Lepidomeda altivelis*, *Rhinichthys osculus*, *Catostomus clarki*, and *Crenichthys baileyi grandis* (LaRivers, 1962). It has been regarded as a subspecies of *Gila robusta*, with which it was presumably connected via the pluvial White River during the last 10 Ky (Hubbs and Miller, 1948b). The principle of individuality of distinct forms of hybrid origin, as applied to *Gila seminuda* (DeMarais et al., 1992), suggests that although *Gila jordani* has been separated for only 35 Ky, it should be recognized as a species with a unique history because of its unique combination of apomorphies.

*Gila* (or *Moapa*) *coriacea*, the Moapa dace, is a localized relative of *Gila robusta* (Figure 2) and *G. intermedia* that inhabits warm springs in the Moapa River, which is the former lower course of the pluvial White River channel in northern Clark County, Nevada. It is not a current member of the Great Basin fauna, but it is geographically peripheral and is a relative of *Gila jordani*. *Moapa* was named by Hubbs and Miller (1948b) who considered it to be related to *Agosia*, *Rhinichthys*, and *Gila*. According to the molecular cladogram (Figure 2), it is a member of the *Gila* clade. A Pliocene or Pleistocene fossil opercle of the *Gila* group was collected by G.R. Smith from sediments exposed in a roadcut near the town of Moapa, Nevada.

**25.** \**Klamathella* sp. (chub). *Klamathella* fossils are found in Pliocene sediments at Honey Lake, Madeline Plains, and Alturus, California. The fossils are diagnosed by their *Gila*-like pharyngeal bones with two rows of pharyngeal teeth. Fossils from the Salt Lake group (~6 Ma) at Junction Hills, Box Elder County, Utah, were reported by McClellan (1977); they are similar to fossil *Klamathella* from the Snake River Plain. *Klamathella* was formerly a subgenus of *Gila*, which was erected for *G. coerulea*. We hereby raise it to generic rank on the basis of molecular evidence that *Klamathella* and *Acrocheilus* are sister groups (Figure 2). Separation of *Klamathella* from *Gila* makes *Gila* monophyletic.

**26.** \**Acrocheilus alutaceus* Agassiz and Pickering (chiselmouth). This is a Snake River and Columbia River species that also lives in the Harney–Malheur Basin. The basin was cut off from the Malheur River, a tributary to the Snake, by rather young volcanics (less than 1 Ma, Luedke and Smith, 1982). McClellan (1977) found *Acrocheilus* teeth in sediments of the Salt Lake group in the Junction Hills, Box Elder County, Utah. Fossils reported as *Acrocheilus* from the Madeline Plains in northeastern California (Wagner et al., 1997) may be highly variable *Lavinia*.

In the molecular phylogeny (Figure 2), *Acrocheilus* is the sister of *Klamathella coerulea*, and together they are sister to the *Gila* clade. *Acrocheilus* and *Klamathella* differ by 6.4% in their cytochrome *b* sequence (Table 2); fossils show that the apomorphic jaw-shape of *Acrocheilus* was well established on the Snake River Plain 7 Ma (Smith et al., 1982), indicating divergence from *Klamathella* (plesiomorphic) occurred prior to that date.

**27.** †*Gila turneri* (Eastman) (chub). This fossil form is known from the Miocene Esmeralda Formation of south-central Nevada. Specimens are also known from slightly older (~12 Ma) lacustrine beds of Stewart Valley, Mineral County, Nevada. It is characterized by a slender caudal peduncle and 10 anal-fin rays. *Gila turneri* was assigned to *Richardsonius* by LaRivers (1962), but, based upon the large anal fin, it could be related to Colorado River *Gila*, which differ from other *Gila* by an average of about 6% sequence divergence.

**28.** †*Gila(?) esmeralda* LaRivers (chub). This species from the Miocene (~12 Ma) Esmeralda Formation may be related to *Siphateles*. It has 8 anal-fin rays, the dorsal fin in advance of the pelvics, and a deep caudal peduncle (Lugaski, 1977, 1979; Smith and Miller, 1985). *Gila* and *Siphateles* differ by an average of about 11% sequence divergence (Table 2).

**29.** †*Gila(?)* sp. (chub). A large chub, greater than 40 cm long, with 8 anal-fin rays, 9 pelvic-fin rays, long dentaries, and blunt, slightly hooked pharyngeal teeth with no grinding surface was collected by Michael Bell from the Truckee Formation southeast of Ferndale, Nevada, in the Hemphillian Quarry (N81) along with numerous sticklebacks (~6 Ma). A similar fish was collected nearby by J. Platt Bradbury from the Eagle-Picher Mine in the Clarendonian section (~12 Ma) of the Truckee Formation (Axelrod, 1956). The Bell specimen has dentaries like those of *Gila* or *Siphateles*, but it has extremely short articular angulars, like those of *Ptychocheilus* or *Mylopharodon*. These forms could be related to *Siphateles* from Mono Lake and could be near the stem group for *Gila*, *Ptychocheilus*, *Siphateles*, and *Mylopharodon*, judging from the shape of the angulars and the dentaries. *Siphateles*, *Mylopharodon*, *Ptychocheilus*, and most *Gila* differ from each other by an average of about 10%–12% sequence divergence.

#### *Ptychocheilus*–*Relictus*–*Eremichthys* Subgroup

This group is not monophyletic in the analysis from which Figure 2 was drawn, because *Ptychocheilus* is polyphyletic in that tree. The possibility that *Ptychocheilus* is paraphyletic is supported by the existence of fossils from 15 Ma bearing *Ptychocheilus* apomorphies (Smith et al., 2000), but the issue is in need of further study.

**30.** \**Ptychocheilus oregonensis* (Richardson) (northern pike-minnow). This Snake River–Columbia River species also lives in the Harney–Malheur Basin. *Ptychocheilus* occurred in the Pliocene Mono Basin, Alturus Basin, Madeline Plains, and Secret Valley, California (Wagner et al., 1997). It is known from Miocene (15 to ~6 Ma) and Pliocene (5.5 to 3 Ma) deposits in

the Columbia River and Snake River basins (Smith et al., 1982; Smith et al., 2000). Numerous Miocene to Pliocene sites in Carson Valley, Douglas County, Nevada (Kelly, 1994), have yielded *Ptychocheilus* dentaries, quadrates, vertebrae, a tooth, and a neurocranium. During this study a single vertebra was identified from Miocene deposits in Brady Park, Churchill County, Nevada. McClellan (1977) identified long, slender, caniniform pharyngeal teeth from the Miocene Salt Lake group in the Junction Hills, Box Elder County, Utah, as *Ptychocheilus*. Living *Ptychocheilus oregonensis* differ from their cladistic relatives by an average of 11.2% (s.d. = 2.1%) sequence divergence (Figure 14; Table 2). The oldest known fossil *Ptychocheilus* bears a well-constrained date of 15 Ma from the Columbia Basin (Smith et al., 2000).

**31. *Relictus solitarius*** Hubbs and Miller (relict dace). This small fish is endemic to Ruby and Butte Valleys (pluvial lakes Franklin and Gale) and to Goshute and Steptoe Valleys (pluvial lakes Waring and Steptoe); each of the four valleys compose parts of both Elko and White Pine Counties, Nevada (Hubbs and Miller, 1972). *Relictus* displays the western spring morphotype: small size (usually less than 10 cm SL), small rounded fins, no barbels, reduced lateral line, and scales not in orderly rows. It also has distinctive, cone-like nuptial tubercles on the head and pectoral fins (Hubbs and Miller, 1972). According to mtDNA evidence, it may be cladistically, but distantly related to *Eremichthys* (sequence divergence = ~15%), but its sequence is phenetically more similar to *Gila robusta* (sequence divergence = ~11%) (Table 2). The data indicate that it is an ancient relict (Figure 2), as concluded by Hubbs and Miller (1972).

**32. *Eremichthys acros*** Hubbs and Miller (desert dace). This is a highly localized endemic of Soldier Meadows, in the northwestern part of the Lahontan Basin. It is diagnosed by its small size (usually less than 6 cm SL), laterally broad pharyngeal arches, uniserial teeth, and specialized sheaths on the jaws (Hubbs and Miller, 1948b). According to parsimony cladistic analysis of mtDNA data, its closest relatives are *Relictus* (sequence divergence = 15%) and *Ptychocheilus* (sequence divergence = 14%), but it also shares 13% similarity with several species of *Gila*. These data indicate that it is an ancient relict, as suggested by Hubbs and Miller (1948b).

#### *Snyderichthys*–*Lepidomeda* Group

**33. *Lepidomeda albivallis*** Miller and Hubbs (White River spinedace). This species was found in springs and their effluents in the upper White River valley of White Pine and Nye Counties, Nevada (Hubbs and Miller, 1960), but it is now extinct. It differs from its sister species, *Lepidomeda altivelis* and *L. mollispinis*, from elsewhere in the Virgin–White drainage, by 0.5% sequence divergence (Table 2). It lived with *Rhinichthys osculus*, *Catostomus clarki*, and *Crenichthys baileyi*.

**34. *Lepidomeda altivelis*** Miller and Hubbs (Pahranagat spinedace). This localized species, now extinct, lived in the Ash Spring and Pahranagat Lake area of the White River val-

ley, in Lincoln County, Nevada (Hubbs and Miller, 1960). It differed from its sister species, *Lepidomeda albivallis*, by having (on average) a more oblique mouth, a sharp snout, less dark pigment, and a larger and more pointed dorsal fin with a stronger spine.

**35. *Snyderichthys copei*** (Jordan and Gilbert) (leatherside chub). This apparently paraphyletic species is endemic to the Bonneville Basin, upper Snake River, and Little Wood River drainages in Utah, Wyoming, and Idaho. Its generic affinities have been ambiguous (Miller, 1945a), but Hubbs and Miller (1960) suggested a relationship to *Lepidomeda*. *Snyderichthys* shares mtDNA similarity at the level of 5% sequence divergence with the Virgin River *Lepidomeda*, which provides an important clue to its relationships and to western biogeography. *Snyderichthys* and the Virgin River and White River *Lepidomeda* spp. differ from *Lepidomeda vittata* of the Little Colorado River and from more plesiomorphic members of the plagiopeterin clade (Simons and Mayden, 1997; Dowling et al., 2002) by 8%–9% sequence divergence (Figure 2; Table 2). This pattern of relative similarity in mtDNA indicates the relationships among the northern and southern members of this species are complex (Dowling et al., 2002). The Bear River and Snake River populations are more similar to Virgin River drainage *Lepidomeda* (5% sequence divergence) than to Sevier River and other Bonneville Basin *Snyderichthys* (11%–12% sequence divergence; Table 2), suggesting there has been independent loss of spines or introgressive transfer of mtDNA in *Snyderichthys*. This pattern of mtDNA similarity supports other evidence for a former drainage connection between the upper Snake River and the Virgin–White drainage of the Mio–Pliocene Bouse Embayment (see “Discussion”). Additional evidence of this connection is the presence of the Muddy Creek Formation from the Lake Mead area to the southwestern Escalante Desert of the Bonneville Basin, prior to 4 Ma (Spencer Reber, pers. comm. to G.R.S., 1999).

#### *Iotichthys*–*Richardsonius*–*Rhinichthys*–*Mylocheilus* Group

**36. *Iotichthys phlegethontis*** (Cope) (least chub). This small species is endemic to the Bonneville Basin. It was formerly known from eastern tributaries to the Great Salt Lake south to Snake Valley and Juab County, Utah. It shares a unique morphological character, namely retarded closure of the posterior cranial fontanel by the parietal, with *Gila atraria* (Coburn and Cavender, 1992:346), but it shares its mtDNA haplotype with *Richardsonius* (sequence divergence 9% with *R. balteatus*; 18% with *G. atraria*) (Figure 2; Table 2). Incongruent morphological and molecular characters suggest there has been introgressive transfer of either morphology or mtDNA from either *Gila atraria* or *Richardsonius* (respectively) to *Iotichthys* (Figure 2 versus Figure 3).

**37. \**Richardsonius balteatus balteatus*** (Richardson) (Columbia reddsider shiner). This subspecies is characterized by its long anal fin. It lives in the Columbia River drainage and in the Great Basin. In the latter, it inhabits the Silvies River of the

Harney–Malheur Basin (Bisson and Bond, 1971). We infer that it dispersed north from the Columbia Basin postglacially because it is not in northern refugia. Although *Richardsonius* is a solely western North American genus, it is closest to eastern North American *Clinostomus* (sequence divergence = 12%; Dowling, unpublished data). There is a fossil record of the *R. balteatus* lineage from the Pliocene (~3.5 Ma) of the Snake River Plain (Smith et al., 1982).

**38.** \**Richardsonius balteatus hydrophlox* (Cope) (Bonneville redband shiner). This subspecies differs from *R. b. balteatus* in having fewer anal-fin rays. It is found in the Bonneville Basin, in isolated creeks of the Harney–Malheur Basin, and above barrier falls in the Snake River drainage and in the South Fork of the John Day River in Oregon (Bisson and Bond, 1971). The presence of relicts of this subspecies above various barrier falls in the Columbia River drainage suggests that the plesiomorphic morphology of this subspecies represents an earlier form than its sister subspecies, *R. b. balteatus*. It presumably dispersed after connection of the Snake River to the Columbia River about 2 Ma, but before formation of the falls and other causes of isolation in the late Pleistocene. A fossil right pharyngeal arch of *R. balteatus*, presumably *R. b. hydrophlox*, was recovered by G.R.S. from Wisconsinan deposits in Homestead Cave, northern Bonneville Basin (Broughton, 2000a).

**39.** *Richardsonius egregius* (Girard) (Lahontan redband shiner). This small shiner and its cohabitant in the Lahontan Basin, *Catostomus tahoensis*, are the only widespread endemic species of the Great Basin. Their absence from surrounding basins is (weak) evidence against low-elevation drainage connections between the Lahontan Basin and other basins in the last several million years. *Richardsonius egregius* is abundant in diverse habitats, but it has not differentiated as much as *Siphates* or *Rhinichthys*. It differs from its sister species, *R. balteatus*, primarily in its smaller body size and smaller fins.

**40.** *Rhinichthys cataractae* (Valenciennes) (longnose dace). This one of the most widely distributed fishes in North America, especially in the eastern and northern parts of the continent. Within the Great Basin, it is found in the northeastern Bonneville Basin, specifically the Provo River, and northward into Utah, Idaho, Wyoming, and the Harney–Malheur Basin of Oregon.

*Rhinichthys (Apocope) osculus* (Girard) (speckled dace). This is a ubiquitous, polytypic species in the Great Basin and surrounding waters; its subspecies are summarized in the entries to follow. Geographic and ecophenotypic variation is extreme in Great Basin representatives of this species (Hubbs et al., 1974). The general pattern of variation usually trends toward one of two ecological morphotypes. The lotic morphotype has a well-developed frenum and barbels, 2,4–4,2 pharyngeal teeth, small scales, medium-sized fins, and a fusiform body shape that is adapted to rheophilic life. The lentic morphotype is a reductively evolved form; it has a reduced frenum, barbels, and lateral line; 1,4–4,1 teeth; small, rounded fins; small body size; and inhabits quiet, isolated waters

(Hubbs et al., 1974; Miller, 1984:15). The following subspecies represent only part of the variation in the group.

**41.** *Rhinichthys osculus carringtoni* (Cope) (Bonneville speckled dace). This subspecies name applies not only to Bonneville Basin, upper Snake River, and most Harney–Malheur Basin populations, but also to the lower Snake River and some Columbia Basin populations. This morphotype is probably an early form of the genus. The features of the lotic morphotype, listed above, characterize *R. o. carringtoni*; however, the Harney–Malheur Basin fish are smaller and have reduced barbels, especially in Warm Springs (Bisson and Bond, 1971). Hubbs and Miller (1948b) suggested that the Warner Basin contains three subspecies of *R. osculus*.

**42.** *Rhinichthys osculus adobe* (Jordan and Evermann) (Sevier speckled dace). This dace of the southern Bonneville Basin is distinctive in its large head, large, horizontal mouth, flat snout, and many pigment differences (Hubbs et al., 1974).

**43.** *Rhinichthys osculus velifer* Gilbert (Pahranagat terete dace). This dace inhabits the swift water outflow of Ash Springs, in Pahranagat Valley, Lincoln County, Nevada. The fish is slender, with barbels, a frenum, and large, falcate fins (Miller, 1984:15,17–18).

**44.** *Rhinichthys osculus robustus* Rutter (western speckled dace). This name was applied to the form of *Rhinichthys osculus* of the Sacramento River, Lahontan Basin, and some associated drainages by Snyder (1917a) and Hubbs et al. (1974). It is characterized by possession of barbels and usually 1,4–4,1 pharyngeal teeth. Prior to 3.2 Ma, the Sacramento and Lahontan drainages were connected by a pass at the head of San Joaquin Canyon in Mono and Madera Counties, California (G.I. Smith, pers. comm. to G.R.S.). The form in Soldier Meadows, Humboldt County, Nevada, shows possible evidence of introgression—it usually has the normal tooth formula of 1,4–4,1, but a unique specimen has 0,5–4,0, like sympatric *Eremichthys acros* (Hubbs and Miller, 1948a:17).

**45.** *Rhinichthys osculus nevadensis* (Gilbert) (Amargosa speckled dace). This fish lives in Ash Meadows, Nye County, Nevada. It is small, with barbels, large scales, an incomplete lateral line, 1,4–4,1 teeth, and no frenum. Its closest relative was *Rhinichthys osculus deaconi* (Las Vegas dace), which was endemic to Las Vegas Creek and Las Vegas Springs, which were tributary to the Colorado River (Hubbs and Miller, 1948a; Miller, 1984). The Amargosa and Las Vegas drainages are connected by the Indian Springs Basin, a large section of which was captured by, and is now a tributary to, the Amargosa River (Gilluly, 1929:682; Miller, 1946a). The similarity of the subspecies *R. o. deaconi* and *R. o. nevadensis* indicates a confluence of fish habitat and gene flow occurred between the Las Vegas and Indian Springs Valleys, probably in the pass occupied by the old railroad bed and Highway 95 east of Indian Springs.

**46.** *Rhinichthys osculus deaconi* Miller (Las Vegas speckled dace). This subspecies (now extinct) was endemic to Las Vegas Creek and Las Vegas Springs, which were tributary to the

Colorado River in pluvial times. It was characterized by a uniquely rounded anal fin, large scales, small pectoral fins, 1,4–4,1 teeth, no barbel or frenum, and an incomplete lateral line (Miller, 1984).

47. *Rhinichthys osculus reliquus* Hubbs and Miller (Grass Valley speckled dace). This form lived in the valley of pluvial Lake Gilbert, Lander County, Nevada, and is probably extinct. It lacked barbels and had a much-reduced lateral line (Miller, 1984).

48. *Rhinichthys osculus oligoporus* Hubbs and Miller (Clover Valley speckled dace). Clover Valley is in the valley of pluvial Lake Clover, Elko County, Nevada. *Rhinichthys osculus oligoporus* lacks barbels and has a reduced lateral line (Miller, 1984).

49. *Rhinichthys osculus lethoporus* Hubbs and Miller (Independence Valley speckled dace). This subspecies lives in Independence Valley, a tributary to the valley of pluvial Lake Clover, Elko County, Nevada. It was apparently derived from *R. o. robustus* of the Lahontan Basin drainage (Hubbs et al., 1974). It is small and compressed, lacks a frenum and barbels, and has a reduced lateral line.

50. *Rhinichthys osculus lariversi* Lugaski (Big Smokey speckled dace). Described as a new species by Lugaski (1972), this form was regarded as a subspecies by Hubbs et al. (1974) and Miller (1984). It lives in the valley of pluvial Lake Toiyabe in Lander and Nye Counties, Nevada. This fish has 62–70 lateral scale rows, 1,4–4,1 pharyngeal teeth, 8 dorsal-fin rays, 7 anal-fin rays, no frenum, and variable development of barbels and lateral line. The Lahontan form of *R. o. robustus* is its closest relative; Hubbs and Miller (1948b) hypothesized that *R. o. lariversi* gained access to the valley of Lake Toiyabe through a stream connection with the valley of Lake Gilbert, on its northern border. The taxon is unusual in that it coinhabits the springs on the east side of the valley with a local form of *Siphateles bicolor obesus*. In most areas of the western Great Basin only a single form of *Rhinichthys* or *Siphateles* exists in a given spring, or *Siphateles* lives in the spring and *Rhinichthys* lives below the spring outflow.

51. *Rhinichthys osculus moapae* (Williams) (Moapa dace). This subspecies was described from the Moapa River, Clark County, Nevada. It is a rheophile and has barbels, a frenum, falcate fins, and silver coloration (Williams, 1978).

52. *Rhinichthys osculus* subsp. (Meadow Valley Wash dace). This inhabitant of springs in Lincoln County, Nevada, is a large dace with small scales, a complete lateral line, a frenum, barbels, 1,4–4,1 pharyngeal teeth, and 37–39 vertebrae (Miller, 1984).

53. *Rhinichthys osculus* subsp. (Pahranagat speckled dace). The subspecies occurs in Lincoln and Clark Counties, Nevada. It has rather large scales, small fins, an incomplete lateral line, and reduced number and size of barbels, but it has 2,4–4,2 pharyngeal teeth (Miller, 1984).

54. *Rhinichthys osculus* subsp. (White River shortfin dace). The dace that lives in quiet waters of the White River

valley in White Pine County, Nevada, is an undescribed subspecies with robust body, small rounded fins, no barbels, no frenum, and 2,4–4,2 pharyngeal teeth (Miller, 1984).

55. *Rhinichthys* sp. (Deep Creek dace). This endemic species has been collected in the western Bonneville Basin, from Fish Springs to Snake Valley. It differs from other robust *Rhinichthys osculus* in color, body shape, meristics, and 2,4–4,2 pharyngeal teeth (R.R. Miller and G.R. Smith, unpublished data).

56. †*Mylocheilus inflexus* (Cope) (Chalk Hills chub). This fossil form of *Mylocheilus* from Idaho and Nevada is similar to *Mylopharodon* (Appendix, number 5) in the possession of molariform teeth. The two lineages may have hybridized in the past, according to molecular and fossil evidence (Dowling and Smith, unpublished data). Mitochondrial DNA data indicate that *Mylocheilus caurinus* (number 58 in Table 2) belongs in the shiner clade with *Richardsonius* (sequence divergence = 33%, Table 2). Miocene(?) chub pharyngeals from Brady Pocket (Churchill County, Nevada, collected by Charles Dailey) are similar to specimens of *M. inflexus* from the late Miocene (~7 Ma) Snake River Plain (Smith et al., 1982, fig. 4A). This suggests a Miocene connection existed between central Nevada and the Snake River Plain.

57. †*Mylocheilus* sp. (chub). A pharyngeal arch and teeth of a *Mylocheilus*, intermediate between *M. inflexus* and *M. robustus*, were collected from the Salt Lake group at Junction Hills, Box Elder County, Utah (McClellan, 1977). Correlation with other *Mylocheilus* suggests that the Junction Hills fauna is Hemphillian in age. The presence of this form and fossil *Ameiurus* in the fauna agrees with molluscan evidence for a Miocene connection and subsequent isolation between waters in northern Utah and the western Snake River Plain (Taylor, 1966).

58. †*Mylocheilus robustus* (Cope) (baby-jaw chub). This species was described from late Miocene and Pliocene pharyngeal arches from the Snake River Plain; the arches are large and have molar teeth. Similar arches with molariform teeth are in beds dated from the late Clarendonian to Hemphillian in the Virgin Valley Formation, Nevada. A single tooth fragment from the Barstovian to Hemphillian age in Esmeralda Formation equivalent beds of Stewart Valley, Nevada, may represent this species (but see *Mylopharodon* from the Esmeralda Formation). *Mylocheilus robustus* is replaced in the modern Snake River and Columbia River drainages by *Mylocheilus caurinus*.

#### CATOSTOMIDAE

59. †*Deltistes* sp. (Fort Rock Lake sucker). Rare maxillae and dentaries from Pliocene localities at Fossil Lake, Fort Rock Basin, Oregon, have characters that separate these fish from the abundant *Chasmistes* in the basin. The maxilla has a posteriorly directed premaxillary process and a general shape similar to *Deltistes luxatus* of Klamath Lakes basin. The ventral keel of the maxilla is prominent anteriorly; the dorsal keel is weak,

with a long convex slope anteriorly. The dentaries are shorter and more robust than those of the *Chasmistes* clade, with the gnathal ramus deflected mesially and lacking a ventral concavity. An almost complete Weberian apparatus, similar to that of the *Deltistes* clade of the Snake River Plain, was collected by Sue Ann Bilby from sediments of the Salt Lake group, near Georgetown, Idaho.

60. \**Chasmistes cujus* Cope (cui-ui). This is a large planktivore in Pyramid Lake that formerly occupied Lake Lahontan and its postpluvial remnants. It has the most specialized morphology among the Holocene species in the genus. Fossil dentaries, vomer, pterotic, and vertebrae from sediments of the Humboldt River canyon confirm the presence of *Chasmistes* in the pre-Lahontan system in the middle Pleistocene. Pleistocene fossils were collected from near Fallon, Nevada, by J.R. Alcorn. A similar form is found in Pliocene sediments at Secret Valley and Honey Lake, California (see below; Taylor and Smith, 1981). *Chasmistes cujus* is known from widespread Lahontan Basin Indian middens, such as those in Humboldt Cave, Lovelock Cave, Fishbone Cave, and Hidden Cave, Nevada, and in Karlo, California (Hubbs and Miller, 1948b:41; Follett, 1963, 1967, 1980; Miller and Smith, 1981; Smith, 1985). These specimens were probably transported by American Indians from Pyramid and Walker Lakes.

61. \**Chasmistes liorus* Jordan (June sucker). This species is now endemic to Utah Lake, but it was probably a Pleistocene inhabitant of Lake Bonneville. It is apparently not closely related to *Chasmistes muriei*, the form that survived in the upper Snake River (Miller and Smith, 1981). *Chasmistes* that were not diagnostic to species were collected from the Thatcher Basin near Preston in southeastern Idaho by R.C. Bright (1967). *Chasmistes* fossils were collected by McClellan (1977) from sediments of the Salt Lake group at Junction Hills, Box Elder County, Utah.

*Chasmistes muriei* of Jackson Hole, Wyoming, was native to the upper Snake River drainage, where one specimen was collected in the 1930s, but it is now apparently extinct. The morphology of *C. muriei* is similar to that of *C. batrachops* (extinct, Fossil Lake) or *C. brevirostris* (Klamath drainage). Pliocene fossils from the Teewinot Formation, upper Snake River drainage in Teton County, Wyoming, are similar to *C. muriei* in the Snake River and to *C. brevirostris* in the Klamath Basin (Miller and Smith, 1981).

62. †*Chasmistes batrachops* Cope (Fossil Lake sucker). This sucker was described from Pliocene or Pleistocene sediments of Fossil Lake, Fort Rock Basin, Oregon. Its dentary and maxillary osteology is generalized. The name may be applicable to similarly generalized bones from the Pliocene Glens Ferry Formation of Owyhee County, Idaho (not *Chasmistes spatulifer*); Mono Basin, Mono County, California; China Lake and White Hills, Inyo County, California; and Duck Valley, Washoe County, Nevada (Miller and Smith, 1981). *Chasmistes* bones are variable in Fossil Lake, perhaps

because Pliocene and Pleistocene remains might be mixed as lag clasts on deflation surfaces in the basin.

63. †*Chasmistes* sp. indeterminant (Mono Basin lake sucker). This lake sucker is found in Pliocene sediments of the Mono Basin, California, with *Ptychocheilus*, *Siphateles*, *Catostomus*, and Pliocene mollusks (Taylor, 1966). Skulls from Mono Basin resemble skull bones of *C. batrachops* from Fossil Lake, Oregon. Dentaries and maxillae from Mono Basin are similar to those from Secret Valley, California. Dentaries are similar to those of *C. batrachops* from Fossil Lake (UMMP 74488) in the medially flattened ridge, in the depth of the groove between the gnathal ridges, and in the anterior recess caudal to the symphysis and gnathal ridges. The position of the median mental foramen and the end of the Meckelian groove are similar to those of *C. batrachops* from the Snake River Plain (UMMP 72458). Maxillae are similar to those from Fossil Lake (UMMP 774490) in the narrow, pointed dorsal keel.

64. †*Chasmistes* sp. (Carson Valley lake sucker). An early Blancan form from Carson Valley, Douglas County, Nevada, is known from dentaries and a maxilla; late Blancan fossils include an opercle, dentaries, and a vomer; an Irvingtonian dentary extends the record into the Pleistocene. The axial ridge of the vomer is broad and flat, as in *Chasmistes* and *Xyrauchen*, but lacks the postrostral constriction of *Catostomus*. The dentaries are more slender than those of *Catostomus* but are similar to those of *Chasmistes*. The medial ridge posterior to the symphysis resembles that of *C. batrachops*, but it is less pronounced than those of the Mono and Lahontan Basins and those of *C. spatulifer* of the Snake River Plain.

65. †*Chasmistes* sp. (Honey Lake sucker). This species was collected from Pliocene sediments of "The Island" of Honey Lake by Taylor and Smith (1981) and Charles Dailey. The Honey Lake sucker is intermediate between *C. cujus* of the Lahontan Basin system and *C. spatulifer* of the Snake River Plain (Miller and Smith, 1981). It is found with *Oncorhynchus* cf. †*lacustris*, *Gila*, *Siphateles*, and *Catostomus*. Similar bones are known from Duck Valley, Washoe County, Nevada, and from the Alturus Basin, the Madeline Plains, and Secret Valley of northeastern California.

66. \**Catostomus ardens* Jordan and Gilbert (Utah sucker). This species is native to the Bonneville Basin drainage in Utah and to the upper Snake River drainage in Utah, Idaho, and Wyoming. It is an old lineage that is related to *Catostomus macrocheilus* of the lower Columbia drainage and to *Catostomus latipinnis* of the Colorado River drainage (Smith, 1992b; Figure 5). During the drought in the early 1930s, *Catostomus ardens* hybridized with *Chasmistes liorus* on spawning grounds in the Provo River, Utah, resulting in introgression that is still seen in *Chasmistes liorus* specimens (Miller and Smith, 1981). Late Pleistocene fossils were reported from the Hot Springs locality, Salt Lake County, Utah (Smith et al., 1968); from Homestead Cave, Tooele County, Utah (Broughton, 2000a), and from the Old River Bed between northern Bonneville and Sevier Basins, Millard County, Utah (Oviatt, 1984). A small,

nearly complete Weberian apparatus, similar to that of *Catostomus ardens*, was collected from sediments of the Salt Lake group near Georgetown, Idaho, by Sue Ann Bilby and has been deposited in the Idaho State Museum of Natural History.

67. \**Catostomus macrocheilus* Girard (largescale sucker). This Holocene species was a lower Columbia River (Ringold Formation) sucker in the Pliocene; fossil evidence indicates that it spread to the Snake River basin in the late Pliocene (~2.8 Ma), after capture of the Snake River at Hell's Canyon (Smith et al., 2000). It spread north of the Columbia as the glaciers receded. It persists in the Harney–Malheur Basin as a relict of the former Snake River outlet through Crane Gap or Malheur Gap. Fossil ages indicate that the colonization of the Harney–Malheur Basin could have occurred after the species immigrated south through Hell's Canyon and prior to (or even after, until about 9 Ka) occlusion of the outlet to the South Fork of the Malheur River by the Voltage lava flow (Piper et al., 1939), 0.04–1 Ma (Gehr and Newman, 1978; Luedke and Smith, 1982).

68. †*Catostomus cristatus* Cope (sucker). This fossil species is best known from the Pliocene of the Snake River Plain. A complete maxilla was collected by Charles Dailey in deformed Pliocene sediments on "The Island" of Honey Lake. The species is diagnosed by the slender anterior neck of the maxilla in the vicinity of the ventral maxillary muscle, anterior to the dorsal and ventral crests (Taylor and Smith, 1981, pl. 19: fig. 3) and the long, gently curved gnathal ramus of the dentary (Taylor and Smith, 1981, pl. 19: figs. 5, 6).

69. †*Catostomus* sp. (Secret Valley sucker). This form displays characters of *C. cristatus* (Pliocene) and *C. macrocheilus* (Holocene) of the Snake and Columbia Basins, respectively. As in *C. macrocheilus*, the dentaries are short, relatively straight, and wide anteriorly, with strong ridges for the labial cartilage (Smith, 1975, fig. 12I). The maxillae have medium-high dorsal and ventral ridges and a general shape like those of the Wall Canyon *Catostomus*; however, the ridge for insertion of the palatine ligament (the anterior edge of the bone), although mostly vertical, has a small, horizontal, J-shaped curve that resembles the condition in *C. shoshonensis* (Smith, 1975, fig. 12A and points *xpy* on fig. 12G). McClellan (1977) collected similar sucker bones from the Salt Lake group at the Junction Hills, Box Elder County, Utah. Suckers from the Alturus Formation may be correlated with the Secret Valley form (Wagner et al., 1997). Age of the Alturus beds is correlated with the Pliocene Glens Ferry Formation by a tephra at Crowder Flat Road near Alturus, California, which bears the chemical signature of a Pliocene ash of the Glens Ferry Formation (Swirydzuk et al., 1982).

70. †\**Catostomus shoshonensis* Cope (Shoshone sucker). This species (including its synonym, *C. ellipticus*) is from the Miocene and Pliocene Snake River Plain (Smith et al., 1982) and from Pliocene sediments at Honey Lake, California (Taylor and Smith, 1981). *Catostomus shoshonensis* is diagnosed by an elliptical maxilla with the attachment of the pa-

latine ligament high on the neck of the anterodorsal process (Smith, 1975, fig. 12A). This form is represented by the relict sucker of Wall Canyon, Surprise Valley, Nevada; this conclusion is based upon the shape of the maxilla.

71. *Catostomus warnerensis* Snyder (Warner sucker). This species lives in the Warner Valley in eastern Lake County, Oregon, and is similar to *Catostomus shoshonensis* of the Snake River Plain. It is also osteologically similar to the form in Wall Canyon, Surprise Valley, Nevada.

72. \**Catostomus tahoensis* Gill and Jordan (Tahoe sucker). This Holocene sucker lives only in the Lahontan Basin. Fossils have been found in Pliocene sediments at Mopung Hills, Churchill County, Nevada (Taylor and Smith, 1981), in middle Pleistocene, pre-Lahontan sediments of the Humboldt River canyon, and in Holocene Indian midden material in the western part of the Lahontan Basin (Thomas, 1985:172, and references therein). The maxilla has a thick anterior segment in the vicinity of the ventral maxillary muscle attachment, with low dorsal and ventral keels that are similar to maxillae of *Pantosteus* (mountain suckers). The dentary has a mesially inflected gnathal ramus suggestive of the plesiomorphic mountain suckers. *Catostomus tahoensis* was a basal member of the *Pantosteus* clade in the cladogram of Smith and Koehn (1971). This is supported by the maxillary shape of Holocene and fossil maxillae, which are *Pantosteus*-like (Taylor and Smith, 1981, pl. 19: 1, 2). Additional material representing *C. tahoensis* was collected by Marith Reheis (USGS) from sediments deposited ~1 Ma at Sunshine Amphitheater (northwest of Walker Lake) and Lone Tree Mine, Nevada, and by J.R. Alcorn from near Fallon, Nevada.

73. \**Catostomus fumeiventris* Miller (Owens sucker). This species is osteologically similar to *C. tahoensis*, except in details described by Miller (1973). It is less derived than the Mopung Hills form of *C. tahoensis*. Fragments of *Catostomus fumeiventris*(?) were recovered from the Pleistocene Owens Lake core (Firby et al., 1997). Holocene Indian midden materials from along the Owens River near the Alabama Hills in Inyo County, California, are rich in remains of the Owens sucker and *Siphateles bicolor snyderi*.

74. †*Catostomus* sp. (Mono Basin sucker). This Pliocene fish lived with *Chasmistes* sp., *Ptychocheilus* sp., and *Siphateles* sp. Its dentary has an abrupt anterior edge of the coronoid process, which is similar to that of *Catostomus fumeiventris* of Owens Valley (Miller, 1973) and to *C. tahoensis* (see Reheis et al., 2002). The maxilla is similar to that of *Catostomus cristatus* of the Miocene and Pliocene Snake River Plain, Idaho (Smith, 1975, fig. 12G), and Secret Valley, California.

75. †*Catostomus* sp. (Carson Valley sucker). Pliocene sediments in Carson Valley contain remains of a *Catostomus* associated with *Siphateles*, *Ptychocheilus*, *Lavinia*, *Chasmistes*, and *Oncorhynchus*. The dentary of this form is more similar to *C. occidentalis* than to *C. tahoensis* or *C. fumeiventris* in the weak peripheral labial ridge and the modest scalloping of the lateral surface of the precoronoid ramus. These characters sug-

gest a pre-Lahontan connection existed that allowed populations of *C. occidentalis* of the Sacramento River drainage to mix with the Carson Valley sucker of the pre-Lahontan drainage. According to G.I. Smith (pers. comm. to G.R.S., 1999), such a connection existed at the head of the San Joaquin Canyon prior to being blocked by volcanics 3.2 Ma.

76. \**Catostomus columbianus* (Eigenmann and Eigenmann) (bridgelip sucker). This species of mountain sucker (subgenus *Pantosteus*) is native to the Columbia Basin and further north, but within the Great Basin it is restricted to the Harney–Malheur Basin. It normally has small scales, but in the Harney–Malheur Basin it has large scales and similarities to isolated headwater populations found in the Columbia–Snake Basin (Smith, 1966; Bisson and Bond, 1971). *Catostomus columbianus* is represented in the Pliocene of the Snake River Plain. Miller and Smith (1981) described the Pliocene specimens as a new species, *C. arenatus*, but, because no evidence of lineage splitting has been found, there is no need for the fossil name.

77. *Catostomus discobolus* Cope (bluehead sucker). This species of mountain sucker (subgenus *Pantosteus*) arose in the upper Colorado River drainage, but it is also native to the Weber River, Bear River, and upper Snake River drainages (Figure 7; Smith, 1966). It is the sister species to *C. clarki* of the lower Colorado River drainage; the two species are the most morphologically apomorphic in the genus. *Catostomus discobolus* is the most widespread mountain sucker in the upper Colorado River drainage, indicating this was the area of its origination and subsequent dispersion. Populations spread from the headwaters of the Green River to the headwaters of the Bear River via stream capture at the east end of the Uinta Mountains, perhaps before the upper Bear River was diverted from the Snake River to Lake Bonneville (Bright, 1967; Bouchard et al., 1998). It is reported from Pleistocene deposits in Homestead Cave near Great Salt Lake by Broughton (2000a). Stream capture in the headwaters of Chalk Creek, Summit County, Utah (Hansen, 1969) could have transferred *C. discobolus* from the Bear River to the Weber River.

78. *Catostomus clarki* (Baird and Girard) (desert sucker). This sister species to *C. discobolus* occupies headwaters of the lower Colorado River drainage below the Grand Canyon. It inhabits Great Basin streams that were formerly connected to the Colorado River in the Pahranaagat Valley–White River drainages in eastern Nevada and co-occurs with species of clades *Lepidomeda*, *Rhinichthys*, and *Crenichthys*. It is clinally variable in the Virgin River drainage. Northern populations possess high scale counts similar to those of *C. platyrhynchus* in the adjacent southern Bonneville Basin (see “Discussion”).

79. \**Catostomus platyrhynchus* (Cope) (mountain sucker). This species of the subgenus *Pantosteus* lives in the Bonneville and Lahontan drainages, but probably early in the Pleistocene it spread north to the Snake and Columbia drainages, then east to the Colorado and Missouri drainages (Smith, 1966). Pleistocene fossils are unknown from the Great Basin,

but specimens have been collected by J.D. Stewart from the Pleistocene of northwestern Nebraska. It is the sister to the clade of three species, *C. santaanae* (of the Los Angeles Basin), *C. clarki* (lower Colorado River drainage), and *C. discobolus* (upper Colorado River drainage). Differences between the Bonneville Basin and Lahontan Basin forms are slight. The population of *C. platyrhynchus* in Shoal Creek, Washington County, Utah, shows introgressed characters from *C. clarki* of the Virgin River drainage, possibly as a result of genetic contact at the time of the outlet of Lake Bonneville to Meadow Valley Wash in the middle Pleistocene (Ives, 1948).

#### ICTALURIDAE

80. †*Ameiurus hazenensis* Baumgartner (Truckee bullhead). This is one of only two Late Cenozoic catfishes of the Great Basin. It is known only from late Miocene sediments of the Truckee Formation, near Hazen, Nevada (Baumgartner, 1982). *Ameiurus hazenensis* is related to *A. peregrinus* of the Chalk Hills Formation, Oregon, to *A. vespertinus* of the Glens Ferry Formation, Idaho (Lundberg, 1992), to *Ameiurus* sp. from the Junction Hills, Box Elder County, Utah (see number 81, below), and to *Ameiurus reticulatus* from the Ringold Formation of Washington (Smith et al., 2000).

81. †*Ameiurus* sp. (Junction Hills bullhead). McClellan (1977) collected spines of a small bullhead, possibly of Hemphillian age, from the Junction Hills, Box Elder County, Utah.

#### SALMONIDAE

##### COREGONINAE

82. \**Prosopium williamsoni* (Girard) (mountain whitefish). This widespread western North American mountain species lives in the Bonneville, Harney, Lahontan, and surrounding basins (Figure 8). Fossil scales of *Prosopium* (not necessarily *williamsoni*) were taken from the Old River Bed units of Lake Bonneville (Oviatt, 1984) and the Pleistocene part of the Owens Lake core (Firby et al., 1997). The earliest known form of *Prosopium*, i.e., *P. prolixus*, occupied Lake Idaho on the Snake River Plain throughout much of the Pliocene (Smith, 1975). Cold adaptations, cladistic relationships, and paleogeography indicate that the genus *Prosopium* is northern in origin.

83. *Prosopium abyssicola* (Snyder) (Bear Lake whitefish). This whitefish is now endemic to Bear Lake, a part of the Bear River drainage, which is a tributary to Lake Bonneville. It is not represented among the abundant Lake Bonneville fish bones examined by Smith et al. (1968) or Broughton (2000a, 2000b).

84. \**Prosopium spilonotus* (Snyder) (Bonneville whitefish). This species is now a Bear Lake endemic. *Prosopium spilonotus* existed in late Lake Bonneville (Smith et al., 1968; Broughton, 2000a, 2000b).

85. \**Prosopium gemmifer* (Snyder) (Bonneville cisco). *Prosopium gemmifer* is a specialized planktivore that is now endemic to Bear Lake, but a similar form also occurred in Lake Bonneville (Smith et al., 1968; Broughton, 2000a, 2000b). The two forms of *P. gemmifer* differ significantly in bones that reflect the shape of the head and jaws. The Bear River was a tributary to the Snake River prior to the late Pleistocene diversion of the Bear River into the Bonneville Basin at Soda Springs (Bright, 1967; Bouchard et al., 1998).

#### THYMALLINAE

86. *Thymallus arcticus* (Pallas) (Arctic grayling). Grayling have not been previously acknowledged as native to the Great Basin fauna, but they were recognized among fishes collected in 1834 from the Bear River near Georgetown, Idaho, by John Kirk Townsend (1978:89). Townsend was a physician and zoologist working with Thomas Nuttall, a British botanist from Harvard University who was en route to the Columbia River. Nuttall was familiar with Great Lakes fauna, which includes grayling and char. Townsend was the first trained zoologist to cross the American continent, collecting specimens and recording observations of natural history. Townsend recorded grayling with trout and whitefish in the headwaters of the Green River (1978:84 (June 30)) and contrasted them in a way that implies that he and Nuttall knew the difference between grayling and whitefish: "The river, here, contains a great number of large trout, some grayling, and a small, narrow-mouthed whitefish, resembling a herring. They are all frequently taken with the hook." On the Bear River, about 12 miles south (upstream) of Soda Springs, Idaho, on 6 July 1834, Townsend (1978:89) wrote: "Trout, grayling, and a kind of char are very abundant here—the first very large." On the previous day, he recorded: "This is a fine stream of about 150 feet in width, with a moveable sandy bottom." (This was prior to the overgrazing, erosion, and destruction of these aquatic habitats that commenced three to four decades later.) Grayling are now native, nearby, to the upper Missouri River in Montana, in streams that were tributaries to the Hudson Bay during preglacial and early glacial times (Menely et al., 1957; Howard, 1960; Lemke et al., 1965:15). Grayling had access from the upper Missouri River to the North Platte River, the upper Green River basin (Sears, 1924; Bradley, 1936), the upper Snake River, the Bear River, and the Bonneville Basin through headwater-stream captures northeast of the Uinta Mountains (Hansen, 1969; see "Discussion"). There are no Holocene or fossil specimens from the Great Basin in the collections we examined.

#### SALMONINAE

87. \**Salvelinus confluentus* (Suckley) (bull trout). Townsend (1978), in the account of his (1834) westward journeys, reported "charr" from the Bear River, as pointed out by Roslund (1951). That the upper Bear River was sufficiently cold

and stable in 1834 to support grayling, char, and large trout (Townsend, 1978:88; see *Thymallus arcticus*, above) has rarely been considered. In 1934, Steven D. Durrant, of the University of Utah, discovered a population of *S. confluentus* in the Jarbidge drainage, a tributary to the Snake River drainage, north of the edge of the Great Basin (Miller and Morton, 1952; Cavender, 1978). Hubbs and Miller (1948b) captured specimens in the Lost River system on the eastern Snake River Plain, an area that shares most of the Bonneville Basin fauna. Bull trout could have colonized the Bonneville Basin from the Snake River while Lake Bonneville was a tributary to the Snake River (Bright, 1967). *Salvelinus confluentus* might have gained access to the Snake River via headwater transfer from the Salmon River (Behnke in Cavender, 1978) and then to the Bear River when it was a tributary to the Snake River. Char also could have occupied the Great Basin throughout the late Cenozoic. One premaxilla with diagnostic characteristics of *S. confluentus* was identified by Jack Broughton from abundant fossils in Homestead Cave (Broughton, 2000a, 2000b). We (GRS and KWG) have examined the maxilla and concur in the identification; we are searching for additional bones to confirm the record. In the middle Miocene, about 14 Ma, *Salvelinus* was in central Nevada (Churchill County, collected by J.R. Alcorn and Ted Cavender; UMMP57107) and in the Columbia River drainage of Idaho (Smiley and Rember, 1985) as *Hucho* sp. (Smith and Miller, 1985). It lived in the Snake River Plain in the late Miocene (referred to as †*Hucho larsoni*) (Kimmel, 1975; Smith et al., 1982). Native *Salvelinus* are now extinct in the Great Basin.

88. †*Oncorhynchus cynoclope* (LaRivers) (Rabbit Hole trout). This trout was named for Rabbit Hole, Pershing County, Nevada, by LaRivers in 1964. "*Salmo esmeralda*" was named by LaRivers in 1966; the description was based upon fragmentary material from the late Miocene Alum Mine, Nye County, Nevada, in the upper portion of the Esmeralda Formation. It is not clear how these trouts are related to each other or to a trout from the Miocene Truckee Formation of western Nevada. The oldest name is used until more material enables more detailed comparisons. Salmonid bones from Stewart Valley, Mineral County, Nevada, are slightly older than the specimens from the Esmeralda Formation (15–12 Ma, radiometric date); they were found with plants, insects, mammals, and other fishes. A late Hemphillian salmonid dentary was collected by Tom Kelley with mammals from the Coal Valley Formation, Mineral County, Nevada. A trout from Carson Valley, Nevada, is known from vertebrae of individuals about 45 and 54 cm in standard length. The perforated pattern on the centra of the vertebrae and the smooth connections of the arches to the centra indicate the vertebrae are different from recent salmon and trout. A dentary of a similar salmonid was collected by Lily Lugaski with cyprinid bones and fossil plants from the Buffalo Canyon Formation (~15 Ma), Churchill County, Nevada.

89. †*Oncorhynchus* sp. (Truckee trout). The Truckee Formation produced a small, nearly complete trout collected by

Michael Bell from a diatomite mine near Hazen, Nevada. The late Miocene diatomite deposit also produced *Fundulus*, *Gila*, *Ameiurus* (Baumgartner, 1982), and a rich record of *Gasterosteus* evolution described by Bell (1994) (see number 128, below).

**90.** \**Oncorhynchus mykiss gairdneri* Richardson (redband trout of the inland Columbia River and Oregon Lakes basins). The redband trout of the Columbia Basin between the Cascade Range and upstream barrier falls are closely related to the redband trout of the Oregon Lakes division of the Great Basin and those of Goose Lake in Oregon and California (Figure 9; Behnke, 1992, map). Unusual variation exists within and among the many populations of the redband subspecies *O. m. gairdneri*. The fish typically have 130–170 large scales in the lateral line (mean = 135–160), 63–66 vertebrae, zero to many basibranchial teeth, 18–24 (mean = 20) gill rakers, 30–50 pyloric caeca, 58 chromosomes, intermediate-sized spots and parr marks, variable cutthroat marks, and light-colored tips on the dorsal, anal, and pelvic fins (Behnke, 1992). Some of this variation (especially in basibranchial teeth and cutthroat marks) is shared with cutthroat trout, *O. clarki*. Many populations of redbands were originally regarded as *O. clarki* (Cope, 1889; Snyder, 1908; Hubbs and Miller, 1948b). In particular, the trout of the Fort Rock Basin frequently have a high basibranchial tooth count (Behnke, 1992) and are more like *O. clarki* than *O. mykiss*, as were their Pliocene and Pleistocene ancestors in the basin (see below). The general trend of redband characters is, however, less like *O. clarki* and more like *O. mykiss*. Cope (1879) and Behnke (1992) identified redband trout populations as *O. mykiss*.

All authors have agreed that the populations in question show composites of cutthroat trout and rainbow trout characters, but each has offered different ideas about whether the mixture was plesiomorphic or the product of ancient or post-introduction introgression. Gilbert and Evermann (1894) and Needham and Behnke (1962) regarded redband trout to be the product of introgression. Redband trout have been reported (Behnke, 1992) from the McCloud drainage (northern California home of hatchery rainbows), from the Goose Lake drainage of the Sacramento system, and from five desert basins of the "Oregon Lakes system" (Snyder, 1908; Allison, 1940; Hubbs and Miller, 1948:67), namely, the Harney–Malheur, Fort Rock Valley, Catlow Valley, Lake Chewaucan, and Warner Lakes. These are west and north of the basins containing *O. clarki*, namely, Alvord and Whitehorse Basins (Legendre et al., 1972; Legendre, 1976; Smith, 1978; Behnke, 1992). Hubbs and Miller (1948b) described the close relationships of trouts, minnows, and suckers to the pluvial lakes in these basins.

The Harney–Malheur and Catlow Valley basins (central Harney County, Oregon) were occupied by Malheur and Catlow Lakes, respectively, in the late Pleistocene and possibly many times earlier. The Harney–Malheur Basin fishes are derived from two different colonizations, as documented by Bisson and Bond (1971): (1) the John Day River connection with the Co-

lumbia River to the north; and (2) the Malheur River connection east to the Snake River, dated to have occurred less than 1 Ma (Luedke and Smith, 1982). The Harney–Malheur Basin possibly received drainage from Catlow Valley in pluvial times, but this neighbor to the south is now isolated (Allison, 1982) and nearly fishless. Catlow Valley lost the heads of its eastern tributaries to capture by Donner and Blitzen Creeks of the Malheur Lake basin on the west side of Steens Mountain in southeast Harney County. The trouts in these two drainage basins are similar, but those from Catlow Valley have larger scales, as expected for the more southern fish in a cline. Behnke (1992) regarded the native inhabitants of these basins to be redband trouts. This conclusion is supported by testimony from older inhabitants of Steens Mountain, indicating that native redband trout were in Home, Three-Mile, and Skull Creeks in the Catlow Basin (west of Steens Mountain) as early as 1917. By contrast, these residents noted, cutthroat trout were native on the east side of Steens Mountain (letter from Stanley Jewett to Carl Hubbs, 13 Jan 1937). The Catlow Valley redband trout in the UMMZ (collected by S. Jewett in 1936–1937) have 20–22 gill rakers, large, posteriorly concentrated spots, and no basibranchial teeth.

Holocene redband trout examined by Behnke from the Fort Rock drainage were variable, with an intermediate frequency of basibranchial teeth that is expected in products of introgression or plesiomorphic character retention. As a consequence of this mixture of characters, we conclude that the Fort Rock trout (ancient and modern) are not cladistically diagnosable as *O. clarki* or *O. mykiss*. They possess a mixture of the characters of *O. mykiss* and *O. clarki* from the various Oregon lakes. Apparently, as *O. clarki* and *O. mykiss* were diverging elsewhere in the Pliocene and Pleistocene, a mixture of ancestral characters were only partially sorted out in the Oregon Lakes system, possibly under the influence of gene flow from the north and south. The population remained mixed in the Fort Rock Basin. A relative of †*O. lacustris* also apparently inhabited the Fort Rock Basin in the Pliocene. The reports of Pacific salmon in the Fort Rock Basin (Hubbs and Miller, 1948b) are based upon bones of redband trout (Allison and Bond, 1983).

The redband trouts of the Warner Lakes (pluvial Lake Coleman; Allison, 1982) and nearby Chewaucan Basin in southern Lake County, Oregon, tend to have slightly fewer vertebrae and more gill rakers, indicating closer relationships to the Goose Lake (Sacramento drainage) redband trout (Behnke, 1992).

**91.** *Oncorhynchus mykiss aquilarum* Snyder (Eagle Lake trout). These fish were recognized by Snyder (1917a) and Behnke (1972, 1992) as a population of rainbow trout, *Oncorhynchus mykiss*, that possibly transferred from the Pit River drainage to Eagle Lake by a stream capture in Lassen County, California. Hubbs and Miller (1948b) identified *O. m. aquilarum* as a hybrid between native *O. clarki* and introduced *O. mykiss gairdneri*, redband trout.

Fossils resembling Pliocene *Oncorhynchus lacustris* of the Snake River Plain were collected by Taylor and Smith (1981)

and by Charles Dailey of Sierra College in deformed Pliocene sediments at "The Island" of Honey Lake, south of Eagle Lake in the northwestern part of what is now the Lahontan drainage. Although the Honey Lake fossils are not necessarily directly related to the Eagle Lake trout, both *O. m. aquilarum* and *O. lacustris* have mixtures of *O. clarki* and *O. mykiss* characters. The morphological and geographical circumstances are important because the diagnostic fossil maxillae (round in cross section) indicate the Pliocene presence of *O. lacustris* or *O. mykiss* characters in the area. The Honey Lake sediments also contain two species of *Catostomus* and one species each of *Chasmistes*, *Mylopharodon*, *Klamathella* (with two rows of pharyngeal teeth), and *Siphateles* (with a single row of teeth). The exact hydrographic relationship of the highest stages of Eagle Lake to the Lahontan Basin is hidden in several possible shorelines above and below the rim of Eagle Lake basin, which have been summarized by Hubbs and Miller (1948b:37–38). Observations on recent shorelines and connections are not necessarily relevant to the history of these fishes, however. It is possible that the rainbow trouts called *O. m. aquilarum* are relicts of the ancient redband trout of the Snake River–Sacramento River drainage of the early Pliocene and are part of the series of redband trouts of the Oregon Lakes System, described above. Two *Oncorhynchus* maxillae from Secret Valley (Madeline Plains, Modoc County, California) sediments (Wagner et al., 1997) establish the presence of a trout similar to the *O. clarki*–*O. mykiss* series north of Eagle and Honey Lakes in the Pliocene. A left dentary from Savage Canyon in the Mineral Mountains, Mineral County, Nevada (MVP 58685), most closely resembles *O. lacustris*.

**92.** \**Oncorhynchus clarki* (Richardson) (cutthroat trout). These are inland trout of the Rocky Mountains (Figure 9). They are the only native trout of the Bonneville and Lahontan Basins, as well as of the Alvord and Whitehorse Basins located east of Steens Mountain, Oregon (Figure 9). But as noted above, redband populations west of Steens Mountain and in parts of the lower Columbia River basin possess *O. clarki* characters in varying amounts. Cutthroat trouts possess more primitive character states than other *Oncorhynchus*, and their morphological characters are predominant in the older (ancestral) fossil record. This assessment was based upon a cladistic analysis (Stearley and Smith, 1993), which included a trout specimen collected by Michael Bell from the late Miocene–Pliocene Truckee Formation (see number 89, above) and other trouts from this portion of western Nevada (LaRivers, 1964, 1966). *Oncorhynchus clarki* fossils occur in Pliocene strata in the Carson Sink, Churchill County, Nevada, portion of the Lake Lahontan area. Fossil bones of *O. clarki* were found in Pliocene sediments in the Mopung Hills, in the central part of the Lahontan Basin drainage (associated with Pliocene mollusks, Taylor and Smith, 1981); in Savage Canyon, Cedar Mountains, Mineral County, Nevada (UCMP 58685); and in pre-Lahontan sediments in Sunshine Amphitheater northwest of Walker Lake, Nevada, by Marith Reheis (USGS). A large

sample of cutthroat trout bones from the Humboldt River canyon, in sediments below the Lava Creek tephra (665 Ka), is herein diagnosed as *O. clarki* by the following characters: the anterodorsal strut of the posttemporal is tapered, not spatulate; the median shelf of the anterior portion of the dentary approaches horizontal; and the ascending wing of the premaxilla is high anteriorly. Trout scales were recovered from the Owens Lake core at levels dated at 730 and 695 Ka (Firby et al., 1997). Molecular relationships of *O. clarki* are discussed below (numbers 93–99) and are shown in Figures 10 and 14; interpopulation genetic distances are shown in Tables 2 and 3.

**93.** \**Oncorhynchus clarki henshawi* Gill and Jordan (Lahontan cutthroat trout). The Lahontan cutthroat trout inhabits Pyramid Lake and its tributaries, except the Humboldt River (inhabited by an unnamed subspecies) and Silver King Creek of the East Fork of the Carson River (*O. c. seliniris*, Paiute trout) (Behnke, 1992:111). These several populations form a group of three subspecies that are related to the (unnamed) Alvord Basin and Whitehorse Basin subspecies (see numbers 96, 97, below), according to Behnke (1992) and our molecular data (Figure 10; Table 3).

*Oncorhynchus clarki henshawi* differs from its closest relatives in the Lahontan Basin in having large spots over most of the body compared with the Paiute trout, *O. c. seliniris*, which lacks spots, and it has more gill rakers and smaller scales than the Humboldt River subspecies. The other characters of this trio are similar to those of the Whitehorse Basin and Alvord Basin trouts (Figure 10; Behnke, 1992). The five forms differ among themselves by only 0.1% sequence divergence, according to our analysis of their mtDNA restriction sites (Table 3).

Originally, different spawning runs separated stocks in Pyramid Lake (Snyder, 1917a); an additional name, *O. c. tahoensis* (Jordan and Evermann (1896)), was applied to the "great trout" or "silver trout" from deep waters of Pyramid Lake, but Behnke (1981, 1992) found no morphological differences. Different size and color, if genetic and if characteristic of different spawning runs, would be evidence of significant (probably intralacustrine) differentiation.

*Oncorhynchus clarki henshawi* is among Holocene fossils from shore-face sediments around Pyramid and Winnemucca Lakes and from various Indian midden sites reported in the archaeological literature. These records provide documentary evidence and osteological material of the Holocene form for study; otherwise, museums lack adequate specimens from the period before the nineteenth century introductions, hybridization, and destruction.

**94.** *Oncorhynchus clarki seliniris* (Snyder) (Paiute cutthroat trout). This trout is limited to a few headwaters in Silver King Creek of the East Carson drainage in Alpine County, California. It differs from *O. c. henshawi* only in the absence of spots. There is no evidence pertaining to the time of its isolation, except for the 0.1% sequence divergence (Table 3) from the other Lahontan Basin trouts. We assume that cutthroat trout inhabited the stable environments of the East Carson

drainage and other mountain streams in the Lahontan Basin throughout the Miocene to Pleistocene because of the fossil record of *O. clarki* and its ancestors in the basin, extending back to the Miocene.

95. *Oncorhynchus clarki* subsp. (Humboldt cutthroat trout). Behnke (1992) pointed out the distinctiveness of cutthroat trout of the Humboldt River, relative to those of the Walker Lake, Truckee River, and Carson Valley drainages. The Humboldt cutthroat trout tends to have larger scales and fewer gill rakers, as expected for fish inhabiting warm, fluvial waters. It also has distinctive mtDNA (Williams, 1990, cited in Behnke, 1992), except in the Quinn River, where trout with Humboldt morphology have mtDNA characteristic of trout of the Lahontan Basin drainage. Behnke (1992:119) analyzed possible isolation dates in the context of the main dates of drainage separations, 13–10 Ka (Benson and Thompson, 1987), and he concluded that the divergence of the Humboldt form from *O. c. henshawi* dates from an earlier time, which is consistent with the 0.1% sequence divergence. The type specimen of the Pliocene *O. cynoclope* (LaRivers) is from the range of this subspecies, indicating an ancient local ancestry for the clade, but it lacks sufficient characters to clarify the ancestry of this subspecies.

96. *Oncorhynchus clarki* subsp. (Alvord cutthroat trout). These trout were collected by Hubbs from Virgin Creek in 1933 and Trout Creek in 1934, in southeastern Harney County, Oregon. Hubbs' field notes indicate that hatchery-raised rainbow trout were introduced into Virgin Creek as early as fall, 1933. Behnke (1992) indicated that Alvord cutthroat trout were similar to Lahontan cutthroat trout (*O. c. henshawi*) but had fewer spots, rosier sides and opercles, larger scales, fewer pyloric caecae, and fewer basibranchial teeth (Behnke, 1981, 1992). The rosy color is reminiscent of red-band trout (*O. m. gairdneri*) (Tol and French, 1988). Mitochondrial DNA restriction sites indicate that the Alvord trout is the sister subspecies to the Whitehorse trout (*O. clarki* subsp.) (Figure 10). Protein allele frequencies of Alvord trout (Tol and French, 1988) did not differ from frequencies of *O. c. henshawi* at five diagnostic loci, but all of the specimens showed introgressive influence from *Oncorhynchus mykiss*.

Tol and French (1988) suggested that Alvord trout were derived from the Lahontan (Quinn) drainage to the south, via Summit Lake, or were introduced. Behnke (1992:123) concluded that the Alvord trout was derived from Lahontan cutthroat trout in the late Pleistocene, assuming that a Wisconsinan connection was the first to provide access. This is consistent with mtDNA divergence of 0.1% (Table 3). The other fish lineage in the Alvord Basin, *Siphateles alvordensis*, may have been derived from the Lahontan *Siphateles* in the Pliocene. It is probable that both species would have used an existing connection; if one colonized earlier, it would probably have been the trout. Older Alvord "Trout Creek" sediments (now elevated) contain Miocene sunfish (Smith and Miller,

1985), but these were deposited in an earlier basin and are unrelated to the trout problem.

97. *Oncorhynchus clarki* subsp. (Whitehorse cutthroat trout). This form lives in the Coyote Lake drainage in southern Harney County, Oregon. It bears polymorphic mtDNA haplotypes, namely the Lahontan and Quinn (not Humboldt) haplotype and a unique haplotype (Williams, 1990, in Behnke, 1992). Its mtDNA is similar to that of Alvord trout. Whitehorse trout share most morphological characters (except fewer pyloric caeca) with Humboldt cutthroat trout and (except for fewer gill rakers) Lahontan trout (Behnke, 1992). Behnke (1992) contrasted the Whitehorse trout with the morphologically dissimilar Alvord trout and determined that the Whitehorse trout has fewer gill rakers, smaller scales, more pyloric caeca, more basibranchial teeth, and more spots than the Alvord trout. The two are similar in their mtDNA, however. The distribution of morphological characters, as well as the isolated position of the Whitehorse Basin, suggests that the Whitehorse trout could represent the most plesiomorphic form in the Lahontan–Humboldt–Alvord series.

The Whitehorse trout and Alvord trout characters require a connection to *O. clarki* of the Humboldt River drainage. According to sedimentary data (see Minckley et al., 1986:562; Reheis and Morrison, 1997), the lake beds of Alvord and Whitehorse Lakes (1231 m; 4040 ft) would have been inundated by one of two middle Pleistocene Eetza highstands of Lake Lahontan (with shoreline altitudes more than 1400 m (4600 ft)). The mtDNA molecules of the five subspecies of *O. clarki* from the Lahontan Basin and Whitehorse/Willow Creek drainages are similar to each other at the 0.1% level. The estimated rate of divergence (0.5% per 1 My; Figure 14) suggests that these populations were connected 200 Ka. (The most recent Eetza highstand is dated as just prior to the 150 Ka Wadsworth tephra (Reheis and Morrison, 1997).) Subsequent character sorting is responsible for the similarities and differences between Alvord trout and Whitehorse trout. Headwater capture has been important to the distribution of this form (Behnke, 1979). Lower Whitehorse Creek and its tributary, Willow Creek, flow north out of the Trout Creek Mountains to the dry lake floor 12 miles east of the Alvord desert. The drainage pattern (USGS 1:250,000 series, Adel Sheet, 1955) indicates two captures: (1) the headwaters of Whitehorse Creek were captured by McDermitt Creek (T. 40 S., R. 39. E.), a tributary to the Quinn River (Humboldt River drainage); and (2) the headwaters of Trout Creek (T. 39 E., R. 37 W.) were apparently headwaters of Willow Creek (T. 39 S., R. 37 E.) prior to their capture at Flagstaff Butte by Trout Creek, a tributary to Alvord Lake.

The Lahontan–Alvord–Whitehorse clade (Figures 9, 10) is the sister group to the Westslope cutthroat trout, *Salmo clarki lewisi*, from the Columbia Basin (e.g., Fish Lake, Wing Creek, and Cougar Creek, Idaho), from which they differ by 0.7%–0.9% sequence divergence (implying they were hydrographically connected 1.6 Ma). *Oncorhynchus c. lewisi* is

represented by relict populations throughout the Columbia River drainage, including as far south as the Boise River drainage near Atlanta, Idaho (UMMZ 234336 with cutthroat trout marks and *O. clarki* osteology). The distribution and mtDNA of Lahontan Basin and Columbia Basin trouts support an early Pleistocene connection between the Lahontan Basin and Columbia River drainages, as hypothesized by Reheis and Morrison (1997), but the other species in the two faunas are too different to support a direct spillover from Lake Lahontan to the Snake River drainage. Together, *O. c. lewisi* and *O. c. henshawi* and their relatives are the sister group to *Oncorhynchus clarki clarki*, from which they differ by 1.3%–1.8% sequence divergence, implying separation occurred about 3 Ma (Figure 10; Table 3).

**98.** \**Oncorhynchus clarki utah* Suckley (Bonneville cutthroat trout). The Bonneville Basin contains 41 populations of cutthroat trout (Duff, 1988) differentiated into three kinds: Bonneville, Snake Valley, and Bear River (Loudenslager and Gall, 1980; Martin et al., 1985; Behnke, 1992). They were characterized by Behnke (1992) as subdued in coloration, 133–183 (160) lateral scale rows, 33–46 (38) scales above the lateral line, 16–24 (19) gill rakers, 25–54 (35) pyloric caeca, and 1–50 basibranchial teeth in at least half the population (Hickman, 1978; Duff, 1988). The counts are basically those of the Yellowstone cutthroat trout, *O. c. bouvieri*. Mitochondrial DNA restriction-site analysis indicates that the Bonneville trouts, exclusive of the Bear River forms, are the plesiomorphic sister group to all other *O. clarki* (Figure 10), differing from them by 1%–4% sequence divergence (Table 3). The Deaf Smith Creek (Salt Lake County, Utah) population differs from other Bonneville cutthroat trouts in its mtDNA (sequence divergence >2% from other Bonneville cutthroat trouts and 3%–4% from all other cutthroat trouts; Table 3). The Bonneville cutthroat form shares a protein allele with the Colorado River subspecies (Martin et al., 1985; Shiozawa and Evans, unpublished data) and has representatives in Santa Clara River headwaters in Pine Valley in southwestern Utah (see “Discussion”). Fossil cutthroat trout are known from the late Pleistocene Black Rock Canyon locality (shoreline dated at 11,000–13,000 years B.P.) in northeastern Bonneville Basin (Smith et al., 1968); from Homestead Cave, 10,160–11,170 years B.P. (Broughton, 2000a, 2000b); and from the late Pleistocene Old River Bed between the northern Bonneville and Sevier Basins (Oviatt, 1984).

**99.** \**Oncorhynchus clarki* subsp. (Snake Valley cutthroat trout). The Snake Valley cutthroat trout forms tend to have more spots than other Bonneville cutthroat trouts. Behnke (1992) suggested that trouts were possibly absent from the Bonneville Basin until the late Pleistocene, and Duff (1988) postulated they had an insufficient time of isolation to become a distinct species. We interpret the cladistic primitiveness of the diversity in the Bonneville Basin and the level of divergence of the Bonneville cutthroat trout forms to indicate an ancient, possibly Miocene, presence of cutthroat trout in what

became the Bonneville Basin. Fossils from 12 Ka or older have been reported from Smith Creek Canyon in Snake Valley (Mead et al., 1982).

**100.** *Oncorhynchus clarki* subsp. (Bear River cutthroat trout). The Bear River form shares proteins and mtDNA with the Yellowstone cutthroat trout, which is consistent with its former connections to the Snake River, between 140 Ka and 80 Ka (Bouchard et al., 1998). The Bear River and Thatcher Basin were most recently diverted to the Bonneville Basin system about 20 Ka (Bright, 1966, 1967; Bouchard et al., 1998). The Bear Lake relative of the Bear River form has more pyloric caecae, an azure blue color that is dense on the snout but diminishes posteriorly, and yellowish fins (Nielson and Lentsch, 1988). The Bear Lake form is distinct in its life history, reproductive separation, and coloration (Nielson and Lentsch, 1988; Behnke, 1992). The Bear River form is the sister group to the Yellowstone River and Snake River populations (Figure 10), differing from them at the 0.3%–0.4% level in its mtDNA restriction sites (Table 3). These populations differ from *O. clarki utah* of the main Bonneville Basin system at the 1.4%–3.5% level, indicating their separate evolution through most of the Pleistocene.

#### CYPRINODONTIDAE

**101.** *Cyprinodon radiosus* Miller (Owens pupfish). This species inhabits the Owens River valley, which is a tributary to Owens Lake, Mono County, California. It is the sister species to *C. macularius* of the lower Colorado River drainage (Echelle and Dowling, 1992; Echelle and Echelle, 1993; Figure 11); it differs from that species by 2.8% sequence divergence of mtDNA (Table 4). *Cyprinodon macularius* and *C. radiosus* are related to various species of pupfishes from the Death Valley system (Miller, 1946a, 1948) and northern Mexico (Figure 11). *Cyprinodon radiosus* is similar to *C. macularius* in having seven pelvic-fin rays, dorsal origin at the midbody, and disrupted vertical bars in females, but it shares an apomorphic scale structure with the Death Valley species (Miller, 1943b, 1948). It is additionally characterized by having large scales and a large, deep body, like *C. nevadensis*; its long dorsal and anal fins and long prehumeral length resemble those of *C. diabolis*. Male coloration is unique, with amber-colored margins on the dorsal and anal fins and a pale or amber-colored (not black) terminal band on the caudal fin.

*Cyprinodon nevadensis* Eigenmann and Eigenmann (Amargosa pupfish). This is a geographically variable and widespread pupfish in the Death Valley system. It is found in numerous springs from Ash Meadows in Nye County, Nevada, to Shoshone, Tecopa, and Saratoga Springs and other localities along the Amargosa River near the boundary of Inyo and San Bernardino Counties, California (Miller, 1948). The species is large and deep, with large scales, preorbital scales; broad, rounded, incised outer tooth-cusps; six pelvic-fin rays; and the dorsal-fin origin usually behind the midbody. Males are deep

blue with a dark terminal border on the pale caudal fin; females have continuous vertical bars. Protein and mtDNA evidence shows the *C. nevadensis* group (Figure 11) to be related to *C. salinus*, *C. diabolis*, and *C. milleri*, with evidence of possible introgressive homoplasy (Echelle and Dowling, 1992; Echelle and Echelle, 1993).

**102.** *Cyprinodon nevadensis nevadensis* Eigenmann and Eigenmann (pupfish). This subspecies, from Saratoga Springs in southern Death Valley, California, is characterized by its robust body shape; high, narrow scales; numerous radii; and dense reticulations (Miller, 1948).

**103.** *Cyprinodon nevadensis amargosae* Miller (pupfish). This subspecies is from the Amargosa River in San Bernardino County, California, including Death Valley. Small scales with few radii characterize it. Miller (1948) recognized several isolated populations as different races.

**104.** *Cyprinodon nevadensis callidae* Miller (pupfish). This subspecies, from Tecopa Hot Springs along the Amargosa River in Inyo County, California, is diagnosed by large scales, narrow interorbital distance, and a short caudal peduncle (Miller, 1948).

**105.** *Cyprinodon nevadensis shoshone* Miller (pupfish). This subspecies is from Shoshone Springs, Inyo County, California. It is characterized by a narrow, slender body and relatively straight ventral profile (Miller, 1948).

**106.** *Cyprinodon nevadensis mionectes* Miller (pupfish). This subspecies is from Big Spring, Ash Meadows, Nye County, Nevada. Miller (1948) diagnosed it by its small size, few scales and fin rays, narrow body, posterior dorsal fin, long head, and arched predorsal profile. There are several distinct races.

**107.** *Cyprinodon nevadensis pectoralis* Miller (pupfish). This subspecies is from near Lovell's Spring, Ash Meadows, Nye County, Nevada. Small scales, large number of pectoral-fin rays, and robust body shape characterize it (Miller, 1948).

**108.** *Cyprinodon salinus* Miller (Salt Creek pupfish). This isolated species inhabits Salt Creek canyon, northern Death Valley, Inyo County, California (Miller, 1943a). A median ridge on the teeth, slender body, small scales, and scaleless preorbital region characterize it. It is similar to *C. nevadensis* and *C. milleri*, with which it shares small fins, especially the pelvics, posterior position of the dorsal fin, small head and eyes, and dark blue color. Miller (1946a) outlined geological evidence that the divergence of *C. salinus* and *C. nevadensis* occurred in the interval since isolation of the Salt River by the desiccation of Lake Manly, which was estimated at that time to be about 20 Ky (but see *C. milleri*, below). It is related to *C. nevadensis* and is the sister group to *C. milleri*, according to protein evidence (Echelle and Echelle, 1993). Molecular data indicate that *C. salinus* is the sister group to the other Death Valley and Ash Meadows species (Echelle and Dowling, 1992; Figure 11). *Cyprinodon salinus* does not differ from *C. milleri* in its mtDNA, but these two differ from *diabolis* + *nevadensis*

by 0.13% sequence divergence, indicating more than 10 Ky of divergence.

**109.** *Cyprinodon milleri* LaBounty and Deacon (Cottonball Marsh pupfish). This distinctive species was discovered living under most severe conditions in a marsh near Salt Creek, several miles southeast of the type locality of *C. salinus* in Death Valley, Inyo County, California (LaBounty and Deacon, 1972). The population lives below sea level in waters that experience a temperature range of 0°–40° C. The fish can survive a salinity range of 0–78 g/L. Large teeth, reduced or absent pelvic fins, reduced lacrimal pores, short, slender caudal peduncle, small fins, and small scales diagnose the species. The large, tricuspid teeth have a broad, spatulate central cusp with no ridge on the outer face and a slim central shaft, like that of *C. macularius* Baird and Girard but with deeper incisions separating the outer cusps. It shares the absence of preorbital scales with *C. salinus* and *C. diabolis*; it shares small scales and a slender body with *C. salinus*. *Cyprinodon milleri* and *C. salinus* differ at 4 of 31 protein loci (Rogers genetic distance <0.06) according to Echelle and Echelle (1993), but the mtDNA of *C. salinus* and *C. milleri* do not differ. The documentation of morphological differences by LaBounty and Deacon (1972) showed *C. milleri* to be the most phylogenetically derived species in Death Valley. LaBounty and Deacon (1972) and Minckley et al. (1986) hypothesized an isolation interval of only a few hundred years, assuming no heterogeneity at the time of the most recent hydrological connections documented by the geological studies of Hunt and Mabey (1966) and Hunt et al. (1966). This is consistent with the 0% sequence divergence and with geography, but it is in conflict with protein and morphological differences. Introgressive homoplasy of mtDNA is possible, in light of this inconsistency. The time of divergence is therefore ambiguous, but this is a possible example of rapid evolution.

**110.** *Cyprinodon diabolis* Wales (Devils Hole pupfish). Devils Hole is a small cave fault that opens at an elevation of 2488 ft, in Ash Meadows, Nye County, Nevada. Its pool is the sole range of the 200–400 individuals of *Cyprinodon diabolis*. This small species has no pelvic fins, long dorsal and anal fins, a posterior dorsal fin, a convex caudal fin, and no preorbital scales. Mature males have a black terminal band on the caudal fin; mature females lack vertical cross bars and show reversal of some sexually dimorphic characters (Miller, 1948). The population has lost individual territorial behavior (Liu in Turner, 1974). Mitochondrial DNA data (Figure 11) indicate that *Cyprinodon diabolis* is related to the *C. nevadensis* clade, and it shares most of its characters (e.g., large scales) with *C. nevadensis*; however, it shares two strikingly nonreductive characters, increased dorsal- and anal-fin rays, with *C. radiosus*. Turner (1974) electrophoretically analyzed 31 presumptive loci and found *C. diabolis* to be similar to *C. nevadensis* and *C. radiosus* at the 0.968 and 0.936 levels of similarity, respectively. Morphological and mtDNA

homoplasies in combination suggest reticulate evolution in the history of *C. diabolis* (Echelle and Dowling, 1992).

**111.** †*Cyprinodon breviradius* Miller (pupfish). This fossil form was found with *Fundulus curryi* in Titus Canyon on the east side of Death Valley, Inyo County, California (Miller, 1945b). The age was estimated by McAllister to be Miocene (Miller, 1981), but it could be Pliocene (see number 117, below). It is similar to *C. macularius*, but it has a slender body, like *C. salinus*, and 20 caudal vertebrae, which is several more than normal for the Death Valley group. On the basis of these apomorphies, the fossil is assumed to be ancestral to the ancestor of the *C. fontinalis*–*salinus*–*diabolis*–*nevadensis* clade in Figure 11. This clade differs from its sister species by an average of 2.9% sequence divergence.

#### GOODEIDAE

**112.** \**Empetrichthys merriami* Gilbert (Ash Meadows poolfish). This species, now extinct, was taken in five separated springs in Ash Meadows, Nevada. It was a small, robust fish with a deep body, large head, narrow mouth, and molariform pharyngeal teeth (Miller, 1948; Uyeno and Miller, 1962). Apparently always rare, it was possibly eliminated by scientific collecting (Miller, 1948:101).

**113.** \**Empetrichthys latos* Miller (Pahrump poolfish). This species lived in three springs in Pahrump Valley, Nye County, Nevada. Each spring had a distinct subspecies. Miller (1948) and Uyeno and Miller (1962) distinguished it from *C. merriami* by its slender body, broad and weak mouth, pointed teeth, and smaller scales. Springs that were inhabited by the three subspecies are geographically close to each other, and the taxa are morphologically similar. They differ from each other in body and fin shapes. A fossil relative, †*Empetrichthys erdisi* (Jordan), from Pliocene sediments in the Ridge Basin, Los Angeles County, California, had conical teeth, smaller scales, and more vertebrae (Uyeno and Miller, 1962). *Empetrichthys* pharyngeals were identified by W.L. Minckley from the Glendale Formation (locality in Van Devender and Tessman, 1975) in southern Nevada (Minckley et al., 1986:582).

**114.** *Crenichthys baileyi* (Gilbert) (White River springfish). This species inhabits springs in the Pahranaagat Valley and tributaries to the White River, in Clark, White Pine, Nye, and Lincoln Counties, Nevada. Geographic variation was recognized, and four subspecies were named by Williams and Wilde (1981).

**115.** *Crenichthys nevadae* Hubbs (Railroad Valley springfish). This species differs from *C. baileyi* primarily in coloration. It lives in Hot Springs in Railroad Valley and tributary Duckwater Valley, Nye County, Nevada. This drainage was probably connected to the Pahranaagat Valley and the White River system through the Penoyer and Desert Valleys (Hubbs and Miller, 1948b).

#### FUNDULIDAE

**116.** †*Fundulus nevadensis* (Eastman) (killifish). This is a late Miocene species (from at least 6 Ma) from the Truckee Formation in the Lahontan Basin near Hazen, Nevada. It is a long, slender fish with 11 or 12 dorsal-fin rays, the dorsal fin well in advance of the anal fin, 10–13 anal-fin rays, and small, circular scales in more than 65 lateral rows (Eastman, 1917; Miller, 1945b). LaRivers (1964) reported it in correlated beds in the Sahwave Mountains, Pershing County, Nevada.

**117.** †*Fundulus curryi* Miller (killifish). This species, from the east side of Death Valley, was similar in some ways to *Empetrichthys* (Miller, 1948:100). It is a short (44–66 mm SL), deep fish with 14 or 15 dorsal-fin rays, the dorsal fin much closer to the anal fin than to the pelvic fins, 15 or 16 anal-fin rays, a broadly rounded anal fin, and scales like those of *F. eulepis* (Miller, 1945b). Numerous specimens of *Fundulus* have been collected from Titus Canyon, Death Valley, California. Their ages are uncertain. The lower part of the Titus Canyon Formation has been dated as early Oligocene; the date was based upon the presence of *Mesohippus*, titanotheres, hydracodont rhinoceros, artiodactyls, and rodents, as well as on radiogenic dates (Saylor, 1994). But if *F. curryi* was collected near *Cyprinodon breviradius* Miller, it could be Miocene or Pliocene (Miller, 1945b). An old specimen of *Fundulus* was recently collected at the Bullfrog Mine, southeast of Beatty, Nevada. It was found in a dark gray to black shale beneath a late Oligocene to early Miocene volcanic unit dated at 23 Ma.

**118.** †*Fundulus eulepis* Miller (killifish). This species is from beds of Pliocene age in Death Valley near Furnace Creek. The specimens are relatively long (~9 cm SL), with 13 or 14 dorsal- and anal-fin rays, the dorsal fin in advance of the anal fin by about one-third of the distance from the anal fin to the pelvic-fin origins, and about 45–50 lateral scale rows (Miller, 1945b).

**119.** †*Fundulus* spp. (killifishes). Undescribed samples of *Fundulus* have been collected from three localities on the Nevada Test Site by Richard V. Wyman (of the University of Nevada, Las Vegas) and others. Specimens studied so far are large (up to 9 cm SL), with conical teeth, 13 rays in the dorsal and anal fins, the dorsal fin slightly in advance of the anal fin, 6 pelvic-fin rays, moderately small scales on the body, scaled cheeks, and 20 caudal vertebrae. The caudal peduncle is moderately long, like that of *F. eulepis*. They lack evidence for modification of the anal fin, as seen in Goodeidae. *Cyprinodon* and *Fundulus* in the Miocene and Pliocene of the Great Basin are similar in morphology and diversity to modern cyprinodontoids (Empetrichthyines, *Cyprinodon*, *Fundulus*) in the southwestern United States. The fossil *Fundulus* add to the evidence of widespread, warm, low-gradient habitats during the Miocene.

**120.** †*Fundulus* spp. (killifishes). *Fundulus* have been collected from two localities in the Esmeralda Formation, or beds reported to be Esmeralda Formation northwest of Death Val-

ley. These locations are in different and younger rocks than the Siebert tuff in which *Fundulus lariversi* was found.

**121.** †*Fundulus davidae* Miller (killifish). A single specimen (Cal. Tech. 10276) of this species was obtained through Lore David from an oil driller. The specimen is from the Mohave Desert in northwestern San Bernardino County, California, but the formation of origin was not known. Miller (1945b) judged that the fossil was of Pliocene or early Pleistocene age. The specimen is short and moderately deep, with 11 or 12 dorsal and anal-fin rays, 6 pelvic-fin rays, a large head, 40–45 lateral scale rows, and scale features like those of *F. eulepis*. Some of the characters are similar to those of *Empetrichthys erdisi* (Miller, 1945a). Specimens figured by Pierce (1959) from the Miocene Barstow Formation near Yermo in the Mohave Desert, might be *Fundulus* (Uyeno and Miller, 1962); the supposed fossil fish eggs reported from this locality were shown to be ostracods (Hubbs and Miller, 1962).

**122.** †*Fundulus lariversi* Lugaski (killifish). This species was described from the Siebert tuff (which formed 17 Ma), from Tonopah, Nye County, Nevada. It is characterized by a slender body, conical teeth, dorsal fin over anal fin and half way between snout and caudal tip, 11 dorsal-fin rays, 13 anal-fin rays, 12 pectoral-fin rays, pelvic fin reduced to seven rays, 17 caudal-fin rays, and 31 vertebrae. This species is similar to *Empetrichthys* (Lugaski, 1978), but it possesses a pelvic fin.

**123.** †*Fundulus* sp. (killifish). *Fundulus* was collected from the middle Miocene Humboldt Formation north of Wells, Nevada. The specimen is deposited at the Mackay School of Mines, University of Nevada, Reno.

#### COTTIDAE

**124.** \**Cottus beldingi* Eigenmann and Eigenmann (Paiute sculpin). This sculpin occupies the Lahontan, northern Bonneville, and Columbia–Snake drainages. Jordan (1924) reported fossils from Pleistocene cave deposits in the Lahontan Basin. Taylor and Smith (1981) reported the species from Pliocene rocks at Mopung Hills. A basioccipital diagnosed only as *Cottus* has been identified (by K.W.G.) from Pliocene sediments in Secret Valley, California, and a cottid parasphenoid was collected by Julian Humphries from Virgin Valley, Nevada. An angular–articular from middle Pleistocene sediments of the Humboldt River gorge unquestionably represents *Cottus beldingi*. R.R. Miller collected specimens from Pliocene diatomites at Fish Cave, Churchill County, Nevada. This has apparently been a Lahontan Basin cool-water species since a time when the Snake River Plain had a strikingly different sculpin fauna (Smith, 1987) and the central Columbia Basin had a warm, lowland fauna lacking sculpins (G.R. Smith et al., 2000).

**125.** \**Cottus bairdi* Girard (mottled sculpin). This is the abundant, widespread sculpin of the Snake–Columbia and Bonneville drainages (as well as of eastern North America). Two different forms are found in the Harney–Malheur drainage (Bisson and Bond, 1971). The two morphs possibly colonized

from the Columbia River drainage (by stream capture from the John Day River) and from the upper Snake River drainage (prior to separation of the Harney–Malheur drainage from the Snake River drainage). Pleistocene fossils were reported from the Black Rock and Hot Springs localities of Lake Bonneville (Smith et al., 1968). A Pliocene or Pleistocene *Cottus* was collected from Park Valley, Box Elder County, Utah (Felix, 1956), by Ted Cavender.

**126.** \**Cottus extensus* Bailey and Bond (Bear Lake sculpin). The Bear Lake sculpin is now endemic to that lake, which is on the Utah–Idaho border, but it was common in Lake Bonneville in the late Pleistocene (Smith et al., 1968; Broughton, 2000a, 2000b).

**127.** *Cottus echinatus* Bailey and Bond (Utah Lake sculpin). This extinct species is known only from Utah Lake, Utah. It has not been found among Lake Bonneville fossils, but it probably shared a common ancestor with *Cottus extensus* (Bailey and Bond, 1963).

#### GASTEROSTEIDAE

**128.** †*Gasterosteus doryssus* (Jordan) (Truckee stickleback). The fossil three-spined stickleback (*Gasterosteus doryssus*) occurs in the Great Basin in the Miocene Truckee Formation in west-central Nevada from Hazen (Bell, 1974) to the Sahwave Mountains (LaRivers, 1964). It represents a lowland fauna from the late Miocene (Bell et al., 1985) of Nevada when the drainage was west to the Pacific Ocean. Thousands of specimens have been collected and analyzed as a premier example of rates of evolution; this data has been summarized by Bell (1994, and references therein; Figure 12).

**129.** \**Gasterosteus aculeatus* Linnaeus (threespine stickleback). Threespine sticklebacks are recorded from late Pleistocene sediments in the Mohave Basin in association with ancient Lakes Manix and Thomson and Mohave River sediments (Roeder, 1985; Jefferson, 1991; Reynolds and Reynolds, 1991; Bell, 1994). Recently collected, living specimens of *Gasterosteus aculeatus williamsoni* from high elevation in the Mohave Basin have some males with a unique melanistic nuptial pattern, suggesting that they are native (Bell, 1982). But trout (with stray sticklebacks) were transplanted by fisheries biologists in that region in the 1930s or earlier, raising the possibility that the modern population is introduced (Leo Shapovilov, California Department of Fish and Game, in litt. to R.R. Miller, University of Michigan, Museum of Zoology; Miller and Hubbs, 1969).

#### CENTRARCHIDAE

**130.** †*Archoplites* sp. (perch). Late Miocene sunfish occur in or near the Great Basin at several localities. These include Park Valley, Box Elder County, Utah (Felix, 1956); the Salt Lake group, (MVP 117073, collected by Patrick McClellan); Windermere Hills near Elko, Nevada; the Snake River Plain in Idaho

and Oregon; and Trout Creek, Harney County, Oregon (Smith and Miller, 1985). Trout Creek specimens have been referred to the genus *Plioplarchus* Cope. Two partial dentaries of large sunfish were collected by J.A. Shotwell from the Juntura For-

mation, outside the edge of the Great Basin in Malheur County, Oregon. Other specimens are from Miocene sediments in Klamath Lake, Harney and Malheur Counties. These centrarchids are diverse and under study.

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# Basins and Ranges: The Biogeography of Aquatic True Bugs (Insecta: Heteroptera) in the Great Basin

*Dan A. Polhemus and John T. Polhemus*

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## ABSTRACT

The endorheic drainage catchments of the Great Basin form an obvious, topographically defined biogeographic region for the aquatic true bugs (Heteroptera) of North America. The Great Basin, however, does not have a homogenous regional fauna, because of its broad north-to-south extent and the consequent variation of both present day climate zones and past limnological regimes. An east–west drainage divide, apparently linked to a transverse geological accommodation zone, separates the northern basins, including the Bonneville and Lahontan Basins and those of southeastern Oregon, from the southern basins lying in southeastern California and southern Nevada. The northern basins have depauperate water bug faunas characterized by a widespread suite of north temperate generalist species, and by the absence or near-absence of many families found at similar latitudes outside the Great Basin. We hypothesize that this pattern resulted from the presence of cold-water lakes in these northern basins at various times during the Pliocene and Pleistocene, which represented hostile habitats for many aquatic Heteroptera and which did not permit southerly escape along river corridors in response to periods of increased climatic stress. The southern basins have had a much different faunal history. One of the most remarkable concentrations of disjunct and endemic aquatic Heteroptera in North America occurs in three of these isolated, endorheic drainages: Railroad Valley and the White River, in southern Nevada, and the Amargosa River drainage, straddling the adjacent California–Nevada border. As with other isolated aquatic elements, including spring

fishes, the nearest conspecific or congeneric populations of many of these isolates occur in northern Mexico or central Texas rather than in the more geographically proximal Colorado River basin. This indicates that these southern basins may have had an historical connection to the Rio Grande system before the formation of the Colorado River in its current configuration. In addition, the southern basins also contain highly isolated populations of species adapted to cold-water regimes. Unlike the isolates associated with thermal waters, these cold-water species have their nearest associated populations in sections of the upper Virgin and Colorado River systems immediately to the south. We suggest that this cold-water pattern is of more recent origin, and it has resulted from dispersal through post-Pliocene cold-water drainages that once existed in the region.

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## Introduction

The endorheic drainage catchments of the Great Basin, as defined in the broad sense, form a topographically delimited biogeographic subregion for the aquatic true bugs (Heteroptera) of North America. The basin as a whole, however, does not have a homogenous regional fauna, because of its broad north-to-south extent and the consequent variation of both current-day climate zones and past limnological regimes. Despite the obvious north-to-south expression of the surface topography, the Great Basin also contains a marked west-to-east drainage divide, cutting roughly across the middle of Nevada, then jogging southeastward along the Utah border (Figure 1). This drainage divide is roughly correspondent to the Caliente–Enterprise accommodation zone, an east–west band of structural discontinuity and magmatic intrusion that has persisted transverse to regional extensional structures for nearly 30 My, from the Early Oligocene to the Holocene (Axen, 1998). This zone also appears to correspond to the Blue Ribbon–Warm Springs lineament, noted by various authors as a zone of volcanism and caldera formation from 30 to 20 million years ago (Ma) (Rowley et al., 1978; Mutschler et al., 1998; Rowley et al., 1998). As pointed out by Rowley et al. (1998), such transverse structures are analogous to the transform faults seen in oceanic basins running perpendicular

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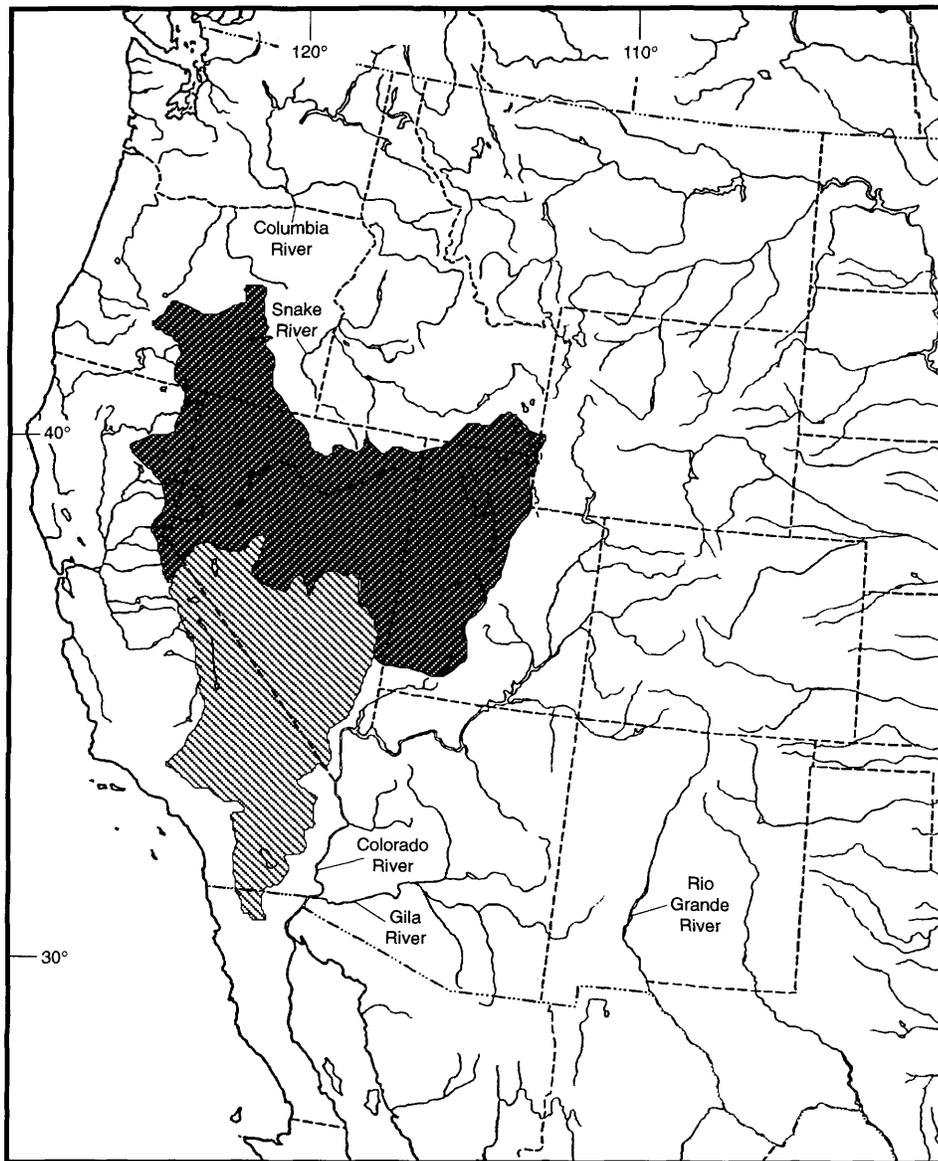


FIGURE 1.—The Great Basin within the context of western North America. The cold, northern basins, as defined herein, lie within the dark hatched area, and the warm, southern basins lie within the area indicated by lighter hatch markings.

to plate boundary spreading centers. In each case, they allow the crust to accommodate different amounts of spreading on either side of the structure, be this spreading because of magmatism (as at mid-oceanic ridges) or extensional faulting (as in the Great Basin).

Many of the basins north of the divide formed by the Caliente–Enterprise accommodation zone, which we term the northern basins, contained large cold-water lakes during the Pliocene and Pleistocene and had periodic drainage connections to the Snake and Columbia Rivers. The basins south of the divide, which we term the southern basins, contained fewer and smaller lakes, had warmer Pliocene and Pleistocene

climates, and had previous drainage connections that led southward toward the modern day Colorado River (Hubbs and Miller, 1948). Along the transverse divide itself are several basins of ambiguous affinity that appear to have been strictly endorheic throughout their histories; these include Dixie, Toiyabe, and Steptoe, plus the series of endorheic catchments devoid of native fishes that Hubbs and Miller (1948) referred to as the “area of sterile basins” (see Figure 2). For the purposes of the current report the first three basins have been grouped with the northern basins, whereas the latter group has been included in the southern basins (although it is treated as a separate faunal unit in Table 1).

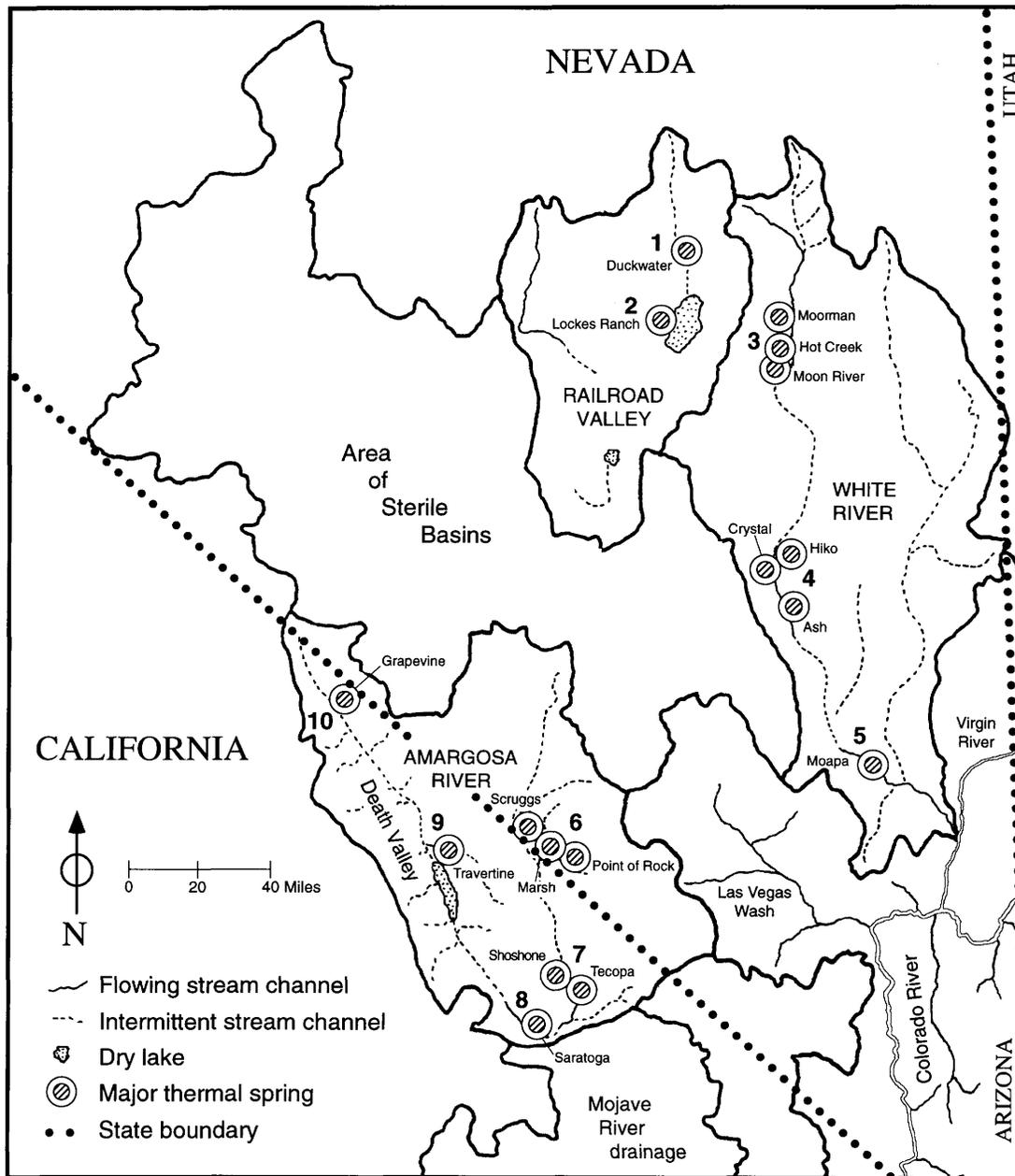


FIGURE 2.—Map of the southern Great Basin, showing locations of thermal springs (hatch-filled spots) within the principal drainage basins discussed in the text. Localities: 1 = Duckwater, 2 = Lockes Ranch, 3 = upper White River, 4 = Pahranagat Valley, 5 = Moapa Warm Springs, 6 = Ash Meadows, 7 = middle Amargosa River basin, 8 = Saratoga Spring, 9 = Furnace Creek, 10 = Grapevine Springs.

The divide separating the northern and southern basins has been a distinctive biological barrier as well as a topographic one, and this is reflected in the distributions of aquatic Heteroptera and other aquatic insects. The northern basins, including the Bonneville Basin, the Lahontan Basin, and those of southeastern Oregon, have depauperate water bug faunas characterized by the absence or near-absence of many groups, such as Hebridae, Hydrometridae, most Nepidae and Veliidae, and

the genus *Buena* in the Notonectidae, which are found at similar latitudes outside the northern Great Basin (Table 1). We hypothesize that this pattern resulted from the former presence of cold-water lakes in these northern basins at various times during the Pleistocene, which represented hostile habitats for many aquatic Heteroptera, precluding the possibility of escape along southward-leading river corridors in response to periods of increased climatic stress. Even among cold-tolerant families

TABLE 1.—Geographic distribution of aquatic heteroptera within the Great Basin, by drainage basin: BV, Bonneville Basin; LH, Lahontan Basin; SO, southeastern Oregon closed basins; SB, area of sterile basins; RR, Railroad Valley and tributaries; WR, White River basin; AR, Amargosa River basin. X, species found in basin; —, species not found.

Species, by family	Northern basins			Southern basins				Colorado River	Snake River	Mexico
	BV	LH	SO	SB	RR	WR	AR			
<b>Belostomatidae</b>										
<i>Belostoma bakeri</i> Montandon	X	X	—	X	X	X	X	X	X	X
<i>Belostoma flumineum</i> (Say)	—	—	—	—	—	X	—	X	—	X
<i>Lethocerus americanus</i> (Leidy)	X	X	X	—	—	—	—	—	X	—
<i>Lethocerus angustipes</i> (Mayr)	—	—	—	—	—	—	X	—	—	X
<b>Corixidae</b>										
<i>Callicorixa audeni</i> Hungerford	X	X	X	—	—	—	—	—	—	—
<i>Callicorixa scudderi</i> Jansson	—	—	X	—	—	—	—	X	X	—
<i>Callicorixa vulnerata</i> (Uhler)	X	—	—	—	—	—	—	—	—	—
<i>Cenocorixa bifida bifida</i> Hungerford	X	—	—	—	—	—	—	—	X	—
<i>Cenocorixa utahensis</i> (Hungerford)	X	—	—	—	—	—	—	—	X	—
<i>Cenocorixa wileyae</i> (Hungerford)	—	X	X	X	X	X	—	X	X	—
<i>Corisella decolor</i> (Uhler)	X	X	X	—	X	X	—	—	X	—
<i>Corisella edulis</i> (Champion)	X	X	—	—	X	—	—	X	—	X
<i>Corisella inscripta</i> (Uhler)	X	—	X	—	—	X	—	X	X	X
<i>Corisella tarsalis</i> (Fieber)	X	—	X	—	—	—	—	X	X	X
<i>Graptocorixa abdominalis</i> (Say)	—	X	—	—	—	—	—	X	—	X
<i>Graptocorixa serrulata</i> (Uhler)	—	—	X	—	—	X	—	X	—	X
<i>Hesperocorixa laevigata</i> (Uhler)	X	X	X	X	X	X	—	X	X	X
<i>Hesperocorixa vulgaris</i> (Hungerford)	—	—	X	—	—	—	—	—	X	—
<i>Sigara alternata</i> (Say)	—	X	—	X	—	—	—	—	—	—
<i>Sigara grossolineata</i> Hungerford	X	—	X	—	—	—	—	—	X	—
<i>Sigara mckinstrii</i> Hungerford	—	X	—	—	—	—	—	—	—	—
<i>Sigara nevadensis</i> Walley	X	X	—	—	—	—	—	X	—	—
<i>Sigara omani</i> (Hungerford)	—	X	X	X	X	—	—	—	X	—
<i>Sigara washingtonensis</i> Hungerford	X	X	X	—	—	—	—	X	X	—
<i>Trichocorixa calva</i> (Say)	—	—	—	—	—	X	—	X	—	—
<i>Trichocorixa reticulata</i> (Guérin-Ménéville)	—	—	—	X	—	—	—	X	X	X
<i>Trichocorixa uhleri</i> Sailer	—	—	—	—	—	X	—	X	—	—
<i>Trichocorixa verticalis interiores</i> Sailer	X	—	—	—	—	—	—	X	—	—
<i>Trichocorixa verticalis saltoni</i> Sailer	—	—	—	—	X	X	—	—	—	—
<b>Gelastocoridae</b>										
<i>Gelastocoris oculatus oculatus</i> (Fabricius)	X	X	X	—	—	—	—	X	X	X
<i>Nerthra martini</i> Todd	—	—	—	—	X	X	X	X	—	X
<b>Gerridae</b>										
<i>Aquarius remigis</i> (Say)	X	X	X	—	X	X	—	X	X	X
<i>Gerris buenoi</i> Kirkaldy	X	—	X	—	—	—	—	X	X	—
<i>Gerris gillettei</i> Lethierry & Severin	X	X	X	X	X	—	—	X	X	—
<i>Gerris incognitus</i> Drake & Hottes	—	—	X	—	—	—	—	—	X	—
<i>Gerris incurvatus</i> Drake & Hottes	—	X	X	—	—	—	—	—	X	—
<i>Limnopus notabilis</i> (Drake & Hottes)	X	—	—	—	—	—	—	X	X	—
<b>Hebridae</b>										
<i>Hebrus hubbardi</i> Porter	—	—	—	—	X	X	—	X	—	—
<i>Merragata hebroides</i> White	—	—	—	—	X	X	X	X	—	X
<b>Hydrometridae</b>										
<i>Hydrometra australis</i> Say	—	—	—	—	—	X	X	X	—	X
<b>Mesoveliidae</b>										
<i>Mesovelia amoena</i> Uhler	—	—	—	—	—	—	X	X	—	X
<i>Mesovelia mulsanti</i> White	—	X	—	—	—	X	X	X	—	X
<b>Naucoridae</b>										
<i>Ambrysus amargosus</i> La Rivers	—	—	—	—	—	—	X	—	—	—
<i>Ambrysus funebris</i> La Rivers	—	—	—	—	—	—	X	—	—	—
<i>Ambrysus mormon</i> Montandon	X	X	—	—	—	X	X	X	X	X
<i>Ambrysus relictus</i> J. & D. Polhemus	—	—	—	—	—	—	X	—	—	—
<i>Ambrysus woodburyi</i> Usinger	X	—	—	—	X	X	—	X	—	—
<i>Limnocoris moapensis</i> (La Rivers)	—	—	—	—	—	X	—	—	—	—
<i>Pelocoris biimpressus biimpressus</i> Montandon	—	—	—	—	—	—	X	—	—	X
<i>Pelocoris biimpressus shoshone</i> La Rivers	—	—	—	—	X	X	X	—	—	—

TABLE 1.—Continued.

Species, by family	Northern basins			Southern basins				Colorado River	Snake River	Mexico
	BV	LH	SO	SB	RR	WR	AR			
Nepidae										
<i>Ranatra fusca</i> Palisot Beauvior	X	—	X	—	—	—	—	—	X	—
Notonectidae										
<i>Buenoa margaritacea</i> Bueno	—	—	—	X	—	—	—	X	—	X
<i>Buenoa omani</i> Truxal	—	—	—	—	—	X	—	—	—	X
<i>Buenoa scimitra</i> Bare	—	—	—	—	—	—	X	X	—	X
<i>Notonecta kirbyi</i> Hungerford	X	X	X	X	X	X	—	X	X	—
<i>Notonecta spinosa</i> Hungerford	X	X	—	—	—	—	—	—	—	—
<i>Notonecta undulata</i> Say	X	X	—	—	—	X	X	X	X	X
<i>Notonecta unifasciata</i> Guérin-Méneville	X	X	X	X	X	X	X	X	X	X
Ochteridae										
<i>Ochterus barberi</i> Schell	—	—	—	—	—	X	—	X	—	X
Veliidae										
<i>Microvelia beameri</i> McKinsty	—	—	—	X	X	X	X	X	—	X
<i>Microvelia buenoi</i> Drake	X	X	X	—	—	—	—	—	—	—
<i>Microvelia cerifera</i> McKinsty	—	X	—	—	—	X	—	—	—	—
<i>Microvelia gerhardi</i> Hussey	—	—	—	—	—	X	—	X	—	X
<i>Microvelia hinei</i> Drake	—	X	—	—	X	X	X	X	—	X
<i>Microvelia signata</i> Uhler	X	X	—	—	—	—	—	—	—	X
<i>Microvelia torquata</i> Champion	—	—	—	—	—	X	—	X	—	X
<i>Rhagovelia becki</i> Drake & Harris	—	—	—	—	—	X	—	—	—	X
<i>Rhagovelia distincta</i> Champion	X	—	—	—	—	X	X	X	X	X

such as the Gerridae and Corixidae, the present-day fauna of these basins is composed primarily of widespread generalist species also seen in the Snake and Columbia River systems (Table 1). The absence of interbasin or intrabasin endemism also indicates that the former lake systems of the northern basins presented relatively homogenous habitats to those species capable of inhabiting them, and these systems were sufficiently interconnected to preclude allopatric speciation.

The southern basins, particularly those lying in southern Nevada and the adjacent southeastern California–Nevada border area, have had a much different faunal history. One of the most remarkable concentrations of disjunct and endemic aquatic Heteroptera species in North America is found in the thermal springs of three of these catchments: Railroad Valley, White River, and Amargosa River (see Figure 2). The nearest conspecific or congeneric populations of many of these Heteroptera isolates are frequently found in central Texas or northern Mexico, rather than in the more geographically proximal drainages of the modern Colorado River basin and the Sierra Madre Occidental of western Mexico, a pattern also seen in other similarly relictual aquatic elements, such as spring fishes. We hypothesize that these drainages were continuous and probably integrated in the Miocene, connecting to a drainage network that flowed southeast toward the modern Rio Grande and the Gulf of Mexico, as suggested by McKee et al. (1967). After the late Miocene to early Pliocene extension in the southern Great Basin (Stewart, 1998), these drainages then became endorheic and underwent desiccation, becoming reduced to sets of discontinuous spring-fed oases.

In addition to these thermal isolates, the southern basins also contain highly disjunct populations of certain species, such as

creeping water bugs, adapted to cold-water regimes. These cold-water isolates have their nearest associated populations in sections of the upper Virgin and Colorado River systems lying immediately to the east. It is suggested that this pattern is of much more recent origin and has resulted from dispersal through Pleistocene or post-Pleistocene cold-water drainages that formed in the region, followed once again by subsequent desiccation and fragmentation.

We review herein the evidence for the above patterns supplied by various families of aquatic Heteroptera. We detail the distributions of selected genera and species, address taxonomic problems relating to these, and discuss the biogeographic significance of the thermally associated fauna in the White River, Railroad Valley, and the Amargosa River basins.

#### Distribution of Aquatic Heteroptera Species in the Great Basin

The Great Basin distributions of aquatic Heteroptera species in the infraorders Gerromorpha and Nepomorpha are detailed in Table 1. The data for this table were obtained both from examination of major museum collections and from existing taxonomic literature (Drake and Harris, 1934; Hungerford, 1934, 1948; Harris and Shull, 1944; Truxal, 1953, 1979; Knowlton, 1956; Lauck, 1979; Menke, 1979a, 1979b, 1979c; Polhemus, J.T., 1979; Polhemus and Chapman, 1979a, 1979b, 1979c, 1979d, 1979e; Smith, 1980; Stonedahl and Lattin, 1982, 1986; Henry and Froeschner, 1988; Sites and Polhemus, 1994). Three sets of collection data were of particular importance in regard to this analysis: (1) general collections from throughout the Great Basin by the authors from 1964 to the present; (2)

collections in southern Nevada and Death Valley, California, from 1992 to 1997, by the authors specifically in support of this study; and (3) results from a year-long entomological survey (1996–1997) by Richard W. Baumann and colleagues in the Muddy River basin of the lower White River system, southern Nevada.

In the following discussion, we use the terms “thermal endemic” and “thermal disjunct” in reference to species confined to thermal spring waters and incapable of tolerating the ambient water temperatures currently prevailing in the Great Basin. In cases where such taxa are endemic to single springs, we refer to them as thermal endemics. Alternately, when such taxa are distributed among several thermal springs in different drainage basins (Figure 3) or when they represent isolated populations having broader distributions independent of thermal

springs in areas further to the south (Figures 4, 5), we refer to them as thermal disjuncts.

### Taxonomic Considerations

Taxonomic interpretations given in Table 1 are valid under existing nomenclature and, for the most part, are stable. In a few groups, however, the taxonomy is undergoing renewed scrutiny, and species concepts are likely to be revised in the next several years. This section reviews several biogeographically informative genera, in three families, that are under study by specialists. The problems involved are illustrative of the difficulties encountered when dealing with the taxonomy of incipiently speciating populations fragmented by recent tectonic and climatological events.

### BELOSTOMATIDAE

*Belostoma saratogae* was described by Menke (1958), who examined a series of specimens from Saratoga Spring, in southern Death Valley. Subsequent workers considered this a valid species endemic to the type locality. Data obtained from our recent collections of *Belostoma* from across the American Southwest, however, reveal that the characters used to separate *B. saratogae* from the more widespread and closely related *B. bakeri* (Figure 6) exhibit variation and that the two species in

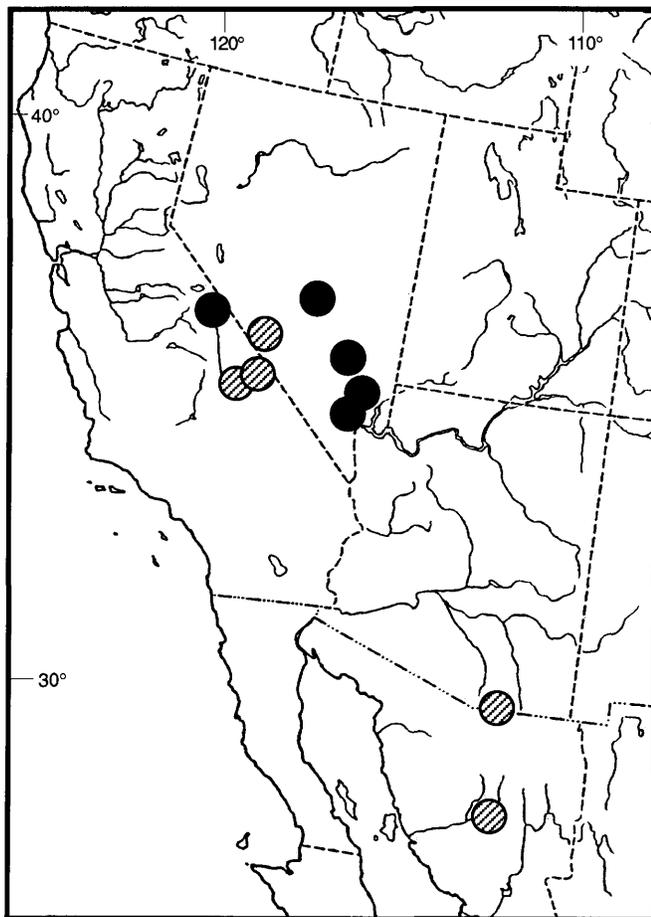


FIGURE 3.—Distribution of the subspecies of *Pelocoris biimpressus* in the southwestern United States and northern Mexico. Hatch-filled spots = *Pelocoris biimpressus biimpressus*. Solid black spots = *Pelocoris biimpressus shoshone*. In addition to the localities shown here, *P. biimpressus biimpressus* is also recorded from eastern Texas, the Mexican states of Veracruz and Jalisco, and Guatemala; *P. biimpressus shoshone* is endemic to the southern Great Basin. *Pelocoris* is absent in the Colorado River basin—the locality shown in southern Arizona lies on a tributary of the Río Concepción flowing southward into Mexico.

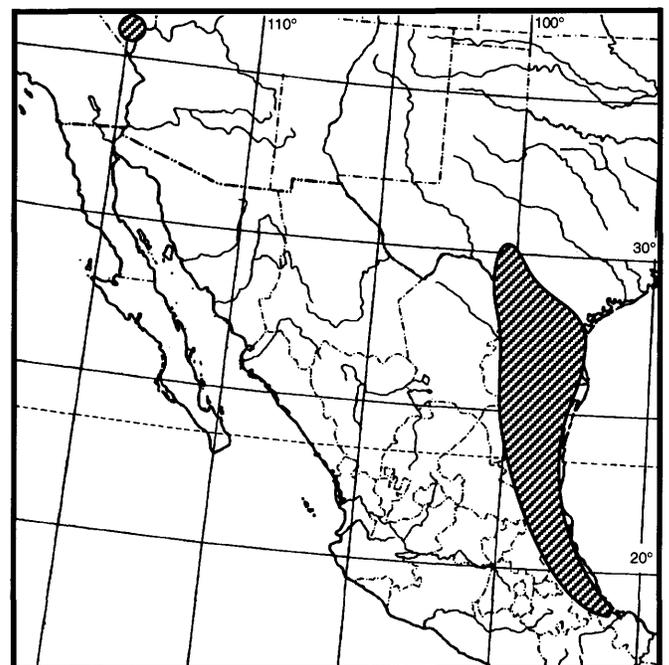


FIGURE 4.—Distribution of *Rhagovelia becki* (hatched areas). This species is an example of a thermal disjunct, as discussed in the text. Its primary distribution is in southern Texas and northeastern Mexico, but a single, highly isolated population exists at Moapa Warm Springs in the White River basin of southern Nevada.

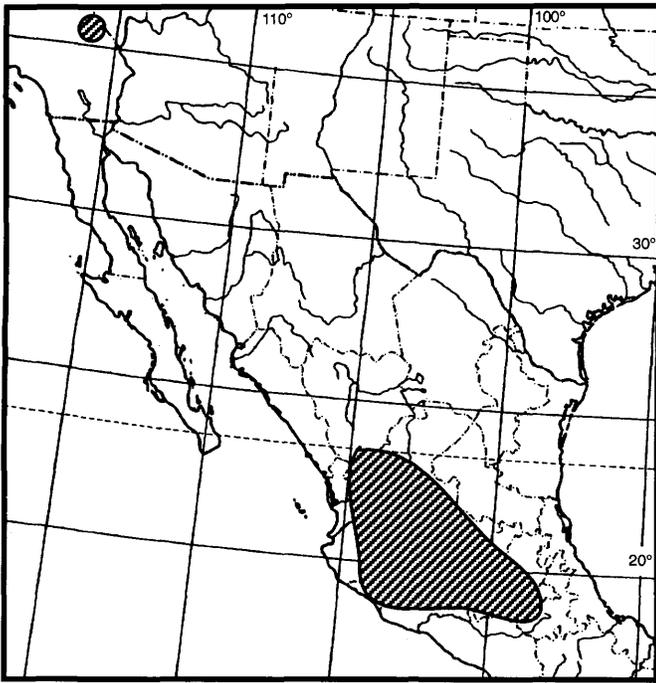


FIGURE 5.—Distribution of *Lethocerus angustipes* (hatched areas). This species is another example of a thermal disjunct (discussed in the text), having its primary distribution in central Mexico with a single, highly isolated population in the Amargosa River basin of southern Nevada and California.

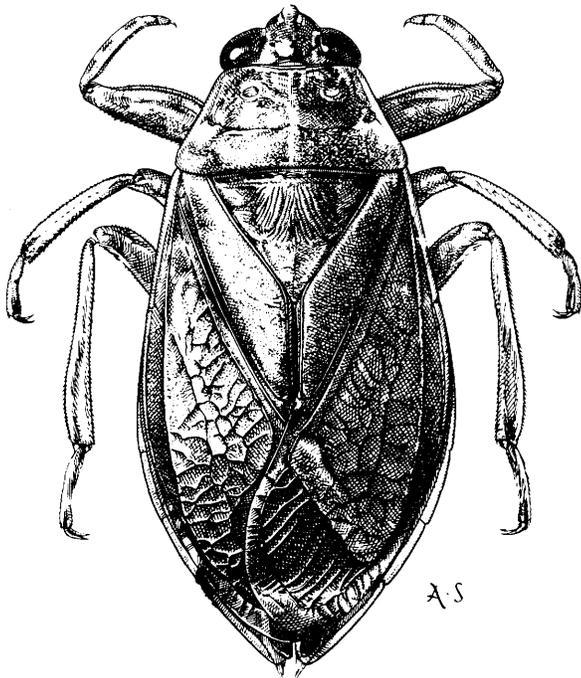


FIGURE 6.—*Belostoma bakeri* Montandon. This giant water bug occurs throughout the Great Basin. In the southern basins it intergrades with *Belostoma saratogae* Menke, a species found in the thermal springs of the Railroad Valley, White River, and Amargosa River basins.

fact appear to intergrade. Character sets examined provide conflicting diagnoses; these include male phallic features, airstrap measurements, and head structure.

Two species, however, still may be involved, and they may segregate on the basis of thermal-spring versus cold-spring habitats. For instance, at Moorman Hot Spring (along the upper White River) we can distinguish a single male taken in the cold marsh from a long series of males taken in the warm waters of the outflow creek. If one bases the diagnosis solely on the ventral diverticulum of the phallus and ignores all other characters, then the "warm" specimens from Moorman Hot Spring are *B. bakeri*, and the "cold" specimen is *B. saratogae*.

The situation at other spring-fed habitats around the region is less clear and provides no obvious geographic or ecological pattern. Populations inhabiting thermal springs at Duckwater and Lockes Ranch in Railroad Valley (see Figure 2) are *B. bakeri*, whereas specimens from thermal waters at Hot Creek along the upper White River are *B. saratogae*. Most of the specimens from thermal springs in Ash Meadows conform to a broad interpretation of *B. saratogae* except for a few indeterminate specimens from a cool-water marsh. The population at the type locality conforms to the original description, but the airstrap measurements are variable even within this population, and this character is not as definitive as stated by Menke (1958).

Given the above observations, it is reasonable to propose that *B. saratogae* is simply a synonym of *B. bakeri*. At the same time, the *Belostoma* populations in the Railroad Valley, White River, and Amargosa River drainages clearly represent a variable but related complex, which can in turn be separated consistently from populations of *B. bakeri* inhabiting surrounding regions. It may be necessary, therefore, to redefine the entire insular complex as *B. saratogae* and to interpret this species as more widespread and variable than was previously believed. All related populations outside the three basins noted above then would be considered *B. bakeri*. The only specimens failing to conform to this arrangement are a series from San Diego, California, that falls within the new "broad" concept of *B. saratogae*. This record is of interest biogeographically in light of hypotheses that the Mojave River once had a connection to the Pacific Ocean via the Los Angeles Basin (Hershler and Pratt, 1990). Because of this uncertainty, all records for this species complex are given as *B. bakeri* in Table 1.

One additional *Belostoma* species, *B. flumineum*, is found at Ash Warm Springs on the middle White River and at Moapa Warm Springs and Meadow Valley Wash on the lower White River (Figure 2). This species, however, is a transcontinental taxon widespread throughout the Colorado River system and the interior valleys of California and is quite distinct morphologically from the *saratogae/bakeri* complex (Lauck, 1964); thus, its distribution has little bearing on the above analysis.

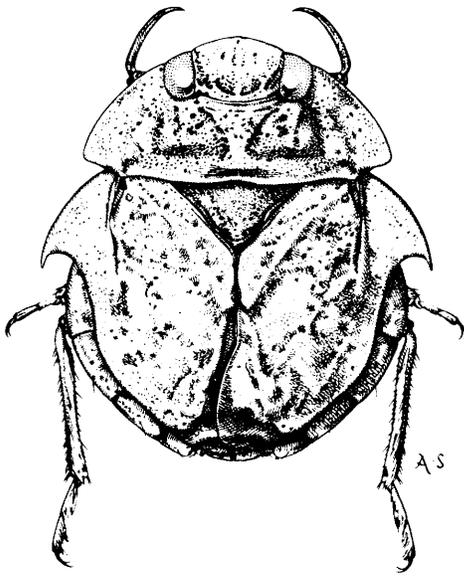


FIGURE 7.—*Limnocoris moapensis* (La Rivers). This creeping water bug is endemic to Moapa Warm Springs in the lower White River basin. This genus is absent in the Colorado River system, with the closest congeners occurring in Texas.

#### NAUCORIDAE

*Limnocoris moapensis* (Figure 7) was described by La Rivers (1950b) from material taken at Moapa Warm Springs, to which the species is endemic. It is one of only two taxa in the subfamily Limnecorinae found in the United States, the other being *Limnocoris lutzi* La Rivers from Texas. The primary character used by La Rivers (1950b) to separate *Limnocoris* from *Usingerina* was the unusual, hooked shape of the hemelytral embolium in *Usingerina*. The suitability of this character as a basis for generic-level separation was subsequently questioned by several authors (De Carlo, 1951; Sites and Willig, 1994), who synonymized *Usingerina* under *Limnocoris*. The presence of *L. moapensis* in southern Nevada provides evidence of former connections between the southern Great Basin and a previously more extensive Rio Grande system. It is also noteworthy that this species has not spread into the Colorado River system, despite the presence of a flowing water connection via the Muddy River.

La Rivers (1948) described *Pelocoris shoshone* (Figure 8) from material taken at Ash Warm Springs along the middle White River, and he subsequently reported additional specimens from Moapa Warm Springs along the lower White River (La Rivers, 1950a). Several years later an additional population of this species was found at Saratoga Spring in Death Valley, which La Rivers (1956) interpreted as a separate subspecies, *P. shoshone amargosus*. These discoveries were remarkable at the time because *Pelocoris* was considered to be a Neotropical genus extending northward only to the southern and eastern United States. Further collecting during the past thirty years,

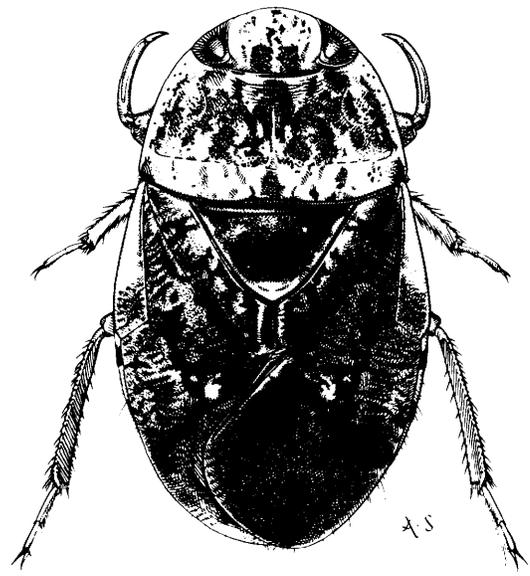


FIGURE 8.—*Pelocoris biimpressus shoshone* La Rivers. This creeping water bug occurs in the Railroad Valley and White River basins of southern Nevada and in Grapevine Springs in northern Death Valley. Populations of the nominate subspecies, *P. biimpressus biimpressus*, occur throughout the remainder of Death Valley and the lower Amargosa River basin. The species is absent from the Colorado River drainage but widespread in northern Mexico and southern Texas.

however, revealed that *Pelocoris* is widespread as a series of disjunct populations throughout the southern Great Basin. By 1994, *P. shoshone* was known not only from the Ash Warm Springs, Moapa Warm Springs, and Saratoga Spring localities that La Rivers reported, but also from Sheep Creek and Grapevine Springs (in Grapevine Canyon) in Death Valley, warm springs in the towns of Tecopa and Shoshone along the middle Amargosa River, many springs at Ash Meadows, and the warm springs at Duckwater in the northern Railroad Valley (see *P. biimpressus shoshone* in Table 1).

La Rivers (1956) suggested that *Pelocoris shoshone shoshone* was confined to the White River drainage, whereas the subspecies *P. shoshone amargosus* occurred in the Amargosa River basin. Although intuitively appealing, this hypothesis of distribution has been disproven by this study of subsequent collections, which demonstrated that the characters used to separate the two subspecies—size and color—intergrade between the many populations now known. If La Rivers' (1956) diagnosis for *P. shoshone amargosus* is strictly applied, the only populations in the southern Great Basin that truly conform to his concept are those from Saratoga Spring, Tecopa Hot Springs, and Shoshone Spring, all lying in the Amargosa basin. This subspecies also occurs in the Atascosa Mountains of far southern Arizona (along southward flowing tributaries to the Río Concepción) and along the western foothills of the Sierra Madre Occidental in Sonora, Mexico (see *P. biimpressus biimpressus* in Figure 3). All of the remaining *Pelocoris* populations in

the southern Great Basin, including those in northern Death Valley, Ash Meadows, Railroad Valley, and the White River drainage, conform to La Rivers' (1948) concept of *P. shoshone shoshone*, a subspecies that does not have a wider distribution (see *P. biimpressus shoshone* in Figure 3).

The taxonomic situation is further complicated by the recent determination that La Rivers' *P. shoshone* is a synonym of *P. biimpressus*, a poorly known species described by Montandon (1898) from Texas (Polhemus and Sites, 1995). As a result of this synonymy and a reanalysis of existing material, we treat the *Pelocoris* populations from the Amargosa River basin, with the exception of those at Grapevine Springs in northern Death Valley, as *P. biimpressus biimpressus*, whereas the populations occurring in the Railroad Valley and White River basins and at Grapevine Springs are considered *P. biimpressus shoshone* (Figure 3). The distribution of the latter taxon suggests that the northern and southern segments of Death Valley had differing biogeographic histories and that the Grapevine Canyon area may have had historical relationships with drainages east of the modern Amargosa River before the creation of the Death Valley trough.

Montandon (1909) described *Ambrysus mormon* (Figure 9) on the basis of a type series collected at St. George, Utah, presumably from the Virgin River or a nearby tributary. This species is widespread throughout the West, exhibiting extensive morphological variation. In particular, populations inhabiting thermal waters tend to be consistently dwarfed and display distinctive morphological features. Two subspecies have been described from such habitats: *A. mormon heidemanni*, from the

Firehole River in the Yellowstone caldera (Montandon, 1910), and *A. mormon minor*, from warm springs along the Owyhee River near Bruneau, Idaho (La Rivers, 1963). Similar trends toward morphological differentiation in thermal springs are also evident in the southern Great Basin, particularly with regard to the populations from Ash Warm Spring and Hot Creek in the White River basin. Decisions as to whether these populations merit recognition as distinct subspecies must await detailed analysis of morphological and molecular variation in *A. mormon* across its entire range.

#### NOTONECTIDAE

*Notonecta unifasciata* (Figure 10) was described by Guérin-Méneville (1857) from specimens taken in central Mexico. Hungerford (1934) listed the range as South America to British Columbia and recognized several subspecies. *Notonecta unifasciata* has been recorded in both hot springs and saline pools (including Francis Lake near Tecopa; Saline Valley in Inyo County) as well as in cool-water habitats. Usinger (1956) treated all populations in mainland California as the subspecies *N. unifasciata andersoni*, but this interpretation does not apply for the populations found in the southern Great Basin. Although *N. unifasciata andersoni* occurs in thermal waters at Hot Creek along the upper White River, other specimens taken in the cool marsh below Moorman Hot Spring, less than 30 km away, represent *N. unifasciata unifasciata*. Analysis of the available collection data indicates that *N. unifasciata andersoni*

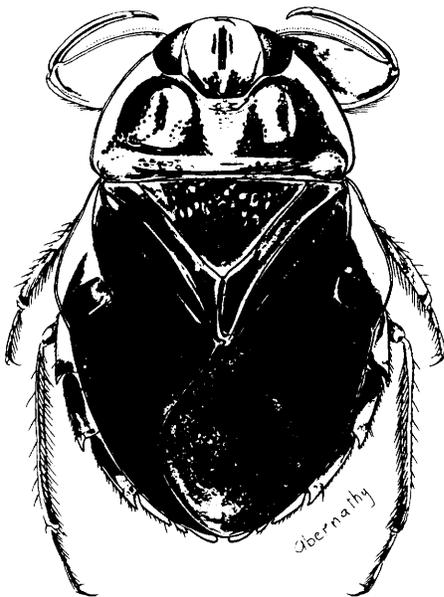


FIGURE 9.—*Ambrysus mormon mormon* Montandon. This is the most widespread creeping water bug in the western United States. Some populations in thermal springs of the Great Basin show morphological divergence indicative of incipient speciation.

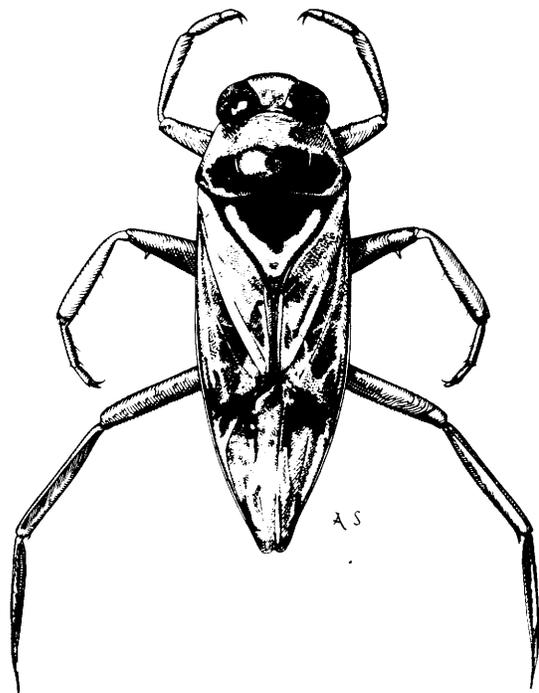


FIGURE 10.—*Notonecta unifasciata andersoni* Hungerford. This backswimmer is widely distributed in the Great Basin and occurs in thermal or saline waters.

inhabits thermal or saline waters in the southern Great Basin, whereas *N. unifasciata unifasciata* lives in cooler waters, such as marshes downstream from thermal springs. These subspecies may be clinal, however, and any firm conclusions regarding habitat partitioning must await resolution of the taxonomic problems involved.

Throughout the southern Great Basin, *N. unifasciata* occurs primarily in thermal springs. It is found at Lockes Ranch and Twin Springs in southern Railroad Valley; Moorman Hot Spring and Hot Creek along the upper White River; Hiko Spring along the middle White River; and several springs in Ash Meadows on the middle Amargosa River. By contrast, cold springs of the upper White River at the towns of Lund and Emigrant (which are in close geographic proximity to the thermal outflows at Moorman Hot Spring and Hot Creek) harbor *Notonecta kirbyi*, a species with a distinct preference for cold waters. Also interesting is the presence of a third species, *N. undulata*, in thermal Saratoga Spring in southern Death Valley, a habitat where one might otherwise expect to find *N. unifasciata*.

The recent discovery of another backswimmer, *Buenoa omani*, near Moapa in the lower White River basin is also of interest. This species is otherwise known only from the southern Coast Range and Los Angeles Basin of California southward into Mexico, where it is widespread—and not from the Colorado River system in the United States.

### Biogeography of the Northern Basins

As noted previously, the aquatic Heteroptera biota of the northern basins consists of widespread generalist species and exhibits no local endemism. Instead, the species assemblage of the Bonneville Basin, Lahontan Basin, and southeastern Oregon basins is composed of north temperate taxa that are broadly distributed across much of the northwestern United States. Although thermal springs are widespread across the region, none contain thermally disjunct or endemic species, possibly because many of these waters were submerged beneath large pluvial lakes in the Pleistocene.

A comparative assessment of distribution patterns in the northern basins also can be made by examining the distributions of Ephmeroptera, or mayflies. Because of their short adult life spans, mayflies are poor dispersers and, given their tolerance for cold waters, might be expected to develop localized endemism in the northern basins. Although 40 genera of mayflies are recorded from Utah, only 23 of these (i.e., 57%) occur in the Bonneville Basin, and only a single species is considered endemic to this basin (G.F. Edmunds, Jr., pers. comm. to DAP, 1998). In most cases, these genera have lower species diversities than they exhibit in areas immediately to the south or east. Similarly, the mountain ranges within the Bonneville and Lahontan Basins contain a depauperate assemblage of genera and species compared with the Sierra Nevada and Wasatch ranges that form the basin borders. Thus, as in Heteroptera, the

mayflies of the northern basins comprise a limited subset of a predominantly widespread north temperate biota.

One aquatic Heteroptera record in the northern basins is worthy of note: the presence of the creeping water bug *Ambrysus woodburyi* in the Sevier River at Junction, Utah, in the far southern Bonneville Basin. This is the only known occurrence of *A. woodburyi* in the northern basins; all other populations occur in the Colorado River system or at isolated localities in several of the southern basins (i.e., Railroad Valley, White River). Given the otherwise southern distribution of this species, its presence in the Sevier drainage is anomalous and suggests that the Sevier River may have captured the headwaters of streams that previously drained southward to the basin of the modern Colorado River.

Another notable aspect of the original aquatic Heteroptera fauna of the northern basins is the general paucity of Veliidae, particularly *Microvelia* and *Rhagovelia* (see Table 1), which are otherwise very widespread and ubiquitous throughout the northern United States. *Rhagovelia distincta* was recently introduced into the eastern Bonneville Basin via water diversions from the Uinta Basin associated with the Central Utah Project (Polhemus, D.A., 1997). This inadvertent introduction illustrates that aquatic insects are often quick to utilize newly established hydrologic dispersal routes between basins, whether these corridors be natural or human-made.

### Biogeography of the Southern Basins

Three of the southern basins lying in California and Nevada contain significant concentrations of thermally endemic or disjunct aquatic Heteroptera: Railroad Valley, the White River basin, and the Amargosa River basin. On the basis of extralimital faunal relationships, we hypothesize that these basins had previous connections either to the Rio Grande system via a drainage network similar to that proposed by McKee et al. (1967) or to other now disrupted drainages that once flowed southward toward Mexico. In some cases (i.e., lower White River) these basins also exhibit apparently recent connections to the modern Colorado River system. Railroad Valley and the White River basins lie in close proximity, being separated by a common drainage divide. The Amargosa River basin, by contrast, is more isolated, being separated from the previous two by the area of sterile basins (Hubbs and Miller, 1948), a region of nearly waterless endorheic basins devoid of native fishes, and by the Las Vegas Wash catchment, which drains to the present Colorado River system (Figure 2).

#### RAILROAD VALLEY

Railroad Valley is an extensive endorheic drainage basin covering approximately 15,540 km<sup>2</sup> (~6000 square miles) in central Nevada. On the basis of biological and geomorphological evidence, Hubbs and Miller (1948) hypothesized that the valley had an historical connection from its southern end to the

Pahranagat Valley (of the middle White River system) via Penoyer and Desert Valleys. This interpretation is supported by the distributions of aquatic Heteroptera. The former stream systems that fed pluvial Lake Railroad are now almost entirely desiccated, as is the lake itself, which exists only in the form of a remnant playa. The two largest thermal springs in the valley are at Duckwater, in the far north, and at Lockes Ranch, along the western edge of the Lake Railroad playa below Black Rock Summit. Other thermal outflows along Hot Creek (not to be confused with a locality of the same name along the upper White River) and at Chimney Hot Springs, in the western and southern sections of Railroad Valley, respectively, have water temperatures too high to naturally support fish or aquatic Heteroptera (although a fish refugium has been constructed below the outflow of the latter). However, complexes of cold springs, some with outflow creeks, occur near Currant along the eastern edge of the Lake Railroad playa and in Hot Creek Canyon above the major thermal outflow. A synopsis of the spring-fed habitats in Railroad Valley and their fish faunas was provided by Williams et al. (1985).

The thermal springs at Duckwater are large and support disjunct populations of a *Belostoma* species in the *bakeri/saratoga* complex (Figure 6) and of *Pelocoris biimpressus shoshone* (Figure 8). Duckwater represents the most northern locality for the latter taxon. The thermal outflow at North Spring in the Lockes Ranch area supports a population of *Nerthra martini* (Figure 11); this locality also represents the most northern record for *N. martini* in North America. Surveys of the cold springs east of the Lake Railroad playa have revealed no unusual aquatic Heteroptera, but the cold spring outflows at misleadingly named Hot Creek contain a disjunct population of the

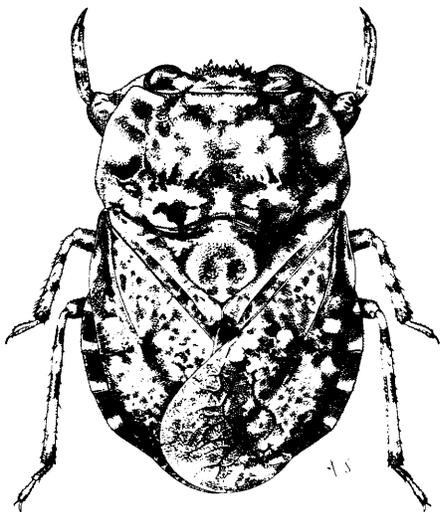


FIGURE 11.—*Nerthra martini* Todd. This littoral toad bug has a patchy distribution from Mexico into the southern Great Basin. Highly isolated populations occur in thermal springs in the Railroad Valley, White River, and Amargosa River basins.

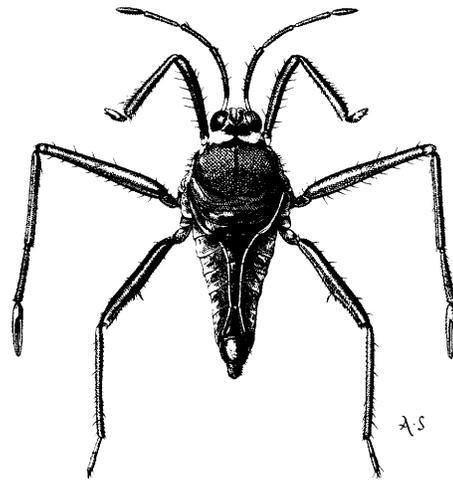


FIGURE 12.—*Rhagovelia distincta* Champion. This small riffle bug is widespread in western North America but rare in the Great Basin. In the northern Great Basin it is known from only a few populations along the Provo and Weber Rivers in Utah, probably the result of recent trans-basin water diversions from the Green River catchment. In the southern Great Basin, by contrast, this species occurs as naturally disjunct populations in thermal springs along the White and Amargosa Rivers.

creeping water bug *Ambrysus woodburyi*, which is typical of the Colorado River drainage but is also known from cold-spring habitats in the White and Sevier River drainages. *Ambrysus mormon* (Figure 9), *Rhagovelia distincta* (Figure 12), and other species represented by disjunct populations in the thermal springs of the adjacent upper White River basin have not been collected in Railroad Valley, although additional surveys are needed, particularly of the Lockes Ranch area and of the cold springs near Currant.

#### WHITE RIVER

The White River is now a desiccated drainage that retains permanent flow only in three separate spring zones. These occur along the upper segment of the drainage in the vicinity of Lund and Sunnyside, along the middle segment of the drainage in Pahranagat Valley, and along the lower reach of the river at Moapa Warm Springs. Each of these spring zones is separated from the others by long, dry sections of ancient river channel, and they contain individually distinctive assemblages of endemic or disjunct aquatic Heteroptera species. In addition, the major eastern tributary of the White River, Meadow Valley Wash, contains several isolated reaches with cold, permanent, spring-fed flow, also separated by long stretches of dry channel.

The upper White River valley contains a large concentration of both cold and thermal springs. The thermal springs emerge on the valley floor to the west of the dry river channel (Figure 2), and the cold springs lie along the base of the Egan Range. An overview of these habitats and their fish faunas was provided by Williams et al. (1985).

The three major thermal outflows occur at Moorman Hot Spring, Hot Creek (not to be confused with the other Hot Creek in Railroad Valley), and Moon River (which lies on private land and has not been accessible for surveys). The spring at Hot Creek, now protected as a fish refuge, is very large and discharges into a deep creek and adjacent cool-water marsh. The outflow supports a disjunct population of *Rhagovelia distincta* (Figure 12), representing the most northern record of this species in Nevada, and a thermally dwarfed population of *Ambrysus mormon*. Moorman Hot Spring is smaller than the Hot Creek outflow but is also in relatively natural condition. A deep pool at the spring head drains into a small, formerly channelized outflow creek that runs for a considerable distance before entering a cool-water marsh. The most notable disjunct faunal element at this site is a *Belostoma* species in the *bakeri/saratogae* complex (Figure 6), which is abundant in the outflow channel.

The cold springs of the upper White River drainage support an aquatic Heteroptera assemblage distinct from that seen in the thermal waters, including populations of certain species adapted to cold waters. Most notable among these is *Ambrysus woodburyi*, which is found at Sunnyside and Flagg Springs; this species also occurs along Meadow Valley Wash in the lower White River basin and, as previously noted, in the cold springs at Hot Creek Canyon in western Railroad Valley. These Nevada records aside, the next closest populations are far to the east, along the lower Virgin River in the Colorado River basin and along the Sevier River at Junction in the Bonneville Basin, suggesting some form of historic linkage between these areas.

The next major spring complex, along the middle course of the White River, consists of three large thermal springs which emerge in Pahranaagat Valley, near Hiko (Figure 2): Hiko Spring, Crystal Spring, and Ash Warm Springs. They contain a diverse array of thermally endemic or disjunct aquatic insect, snail, and fish taxa (Williams et al., 1985). Hiko Spring is on a private ranch and is the most disturbed and least entomologically interesting of the three springs in the valley. Because of the highly altered nature of this habitat and the presence of many introduced fish and aquatic plants, few aquatic insects now occur in the spring except for common generalist species.

Crystal Spring lies in a grove of large cottonwoods and willows just south of the junction of Nevada Highways 375 and 318. Two large spring pools discharge into a complex network of sloughs and flowing channels that finally coalesce into a single outflow, which exits to the east where there is a headgate. The area is in relatively natural condition, although the margins of the outflow channels are heavily overgrown with exotic aquatic plants, and the waters contain numerous introduced fishes, especially the convict cichlid *Cichlasoma nigrofasciatum* (Günther). The large spring pools support *Belostoma* of the *bakeri/saratogae* complex, and the outflow channels contain disjunct populations of *Rhagovelia distincta* (Figure 12) and

*Hydrometra australis* (Figure 13), the latter being found elsewhere in Nevada only in the Muddy River Valley at the lower end of the White River drainage.

Ash Warm Springs is the largest of the Pahranaagat Valley springs. It has been the victim of numerous development attempts over the years, all of which have failed. Several spring outflows emerge from the base of a hill to the east of U.S. Highway 93 and flow into an extensive series of deep, tree-lined ponds. Species present here are *Pelocoris biimpressus shoshone*, which inhabits submerged vegetation along the margins of a small bayou at the northern end of the spring complex, and the thermally disjunct water beetle *Stenelmis callida moapa* La Rivers, found in the clear, flowing water of the spring heads in areas where a substrate of clean sand exists. At the southern end of the ponds the combined waters from all the spring heads drain through a culvert under the highway and form a swift, shaded stream flowing down to the White River. This outflow stream harbors an extremely dense

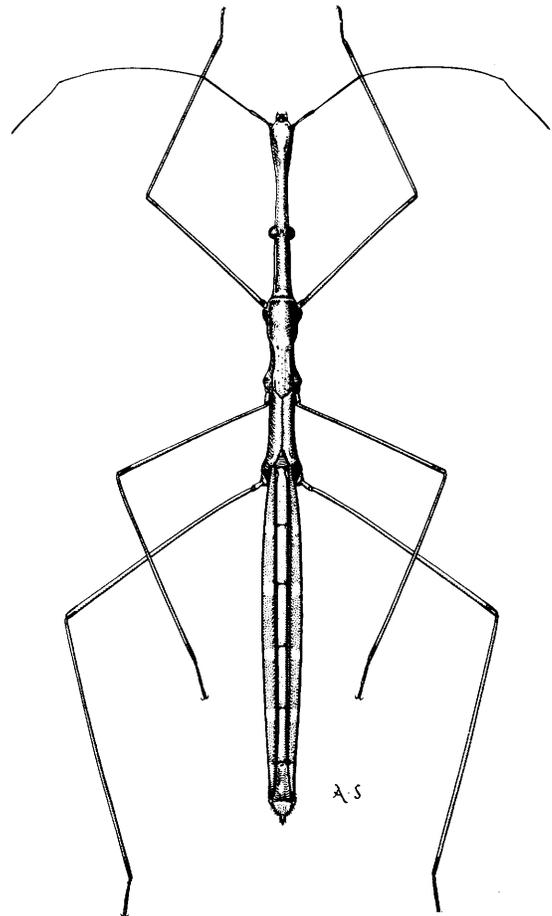


FIGURE 13.—*Hydrometra australis* Say. Although widespread in the southern half of the United States, this delicate, surface-dwelling insect is known from only three areas in the southern Great Basin: Saratoga Spring in southern Death Valley (Amargosa River basin); Crystal Spring along the middle course of the White River; and the Moapa Warm Springs valley along the Muddy River (a part of the lower White River system).

population of *Ambryus mormon*, the individuals of which are morphologically divergent from typical populations of this species (La Rivers, 1953) and which may deserve subspecies status.

The terminal reach of the White River, known as the Muddy River, still connects to the Virgin River and thus to the Colorado River basin. As a result, the lower section of the White River system has had more potential for faunal interchange with the Colorado basin in recent times than any of the other areas under discussion. Nevertheless, Moapa Warm Springs (Figure 2) along this terminal reach retains perhaps the most distinctive aquatic fauna of any spring complex in the region. Many thermal endemics and disjuncts occur at this locality, notably the limnocoarine naucorid *Limnocoaris moapensis* (Figure 7), the riffle bug *Rhagovelia becki* (Polhemus, J.T., 1973) (Figure 4), and the dytiscid beetle *Neoclypeodytes discretus* (Sharp), all of which are unknown elsewhere in the Virgin or Colorado River basins and which have their closest relatives or conspecific populations in eastern Mexico and central Texas. Other Heteroptera disjuncts found here are the backswimmer *Buenoa omani*, known elsewhere only from southwestern California and Mexico, and the toad bug *Nerthra martini* (Figure 11). In addition, several thermally endemic or disjunct water beetle taxa also occur at Moapa Warm Springs, including *Microcyloepus moapus moapus* La Rivers (1949c) and *Stenelmis callida moapa* (La Rivers, 1949b), the latter of which is also found at Ash Warm Springs. Despite occasional collections by numerous specialists over the years and a recently completed year-long study conducted by R. Baumann (R. Baumann, pers. comm. to JTP, 1999), a comprehensive entomological inventory of this spring zone has not yet been published. In addition to the taxa listed above, the thermal outflows in this area also support mosquitoes in the *Uranotaenia anhydora* Dyar complex, the dragonfly *Brechmorhoga mendax* (Hagen), and the mayflies *Isonychia intermedia* (Eaton), *Leptohyphes zalope* Traver, and *Camelobaetis musseri* (Traver and Edmunds), all of which can also be considered thermal disjuncts. The general setting of this spring oasis was described by Williams et al. (1985), and the habitat partitioning exhibited by its naucorid fauna was discussed by La Rivers (1950a).

Near the town of Moapa, the White River is joined by Meadow Valley Wash, a drainage that occupies an extensive catchment along the Utah–Nevada border. Like the White River, this drainage makes a transition from low desert to upland character as one progresses upstream; but unlike the White River, Meadow Valley Wash contains no thermal springs. Instead, several stretches of permanent flow are present from the headwaters to the lower reaches, all fed by cold-water springs. Surveys up the wash from Moapa to Caliente found that these permanent reaches support disjunct populations of *Ambryus woodburyi* and *Belostoma flumineum*, species typical of the Colorado River system.

## AMARGOSA RIVER

The Amargosa River originates in the Bullfrog Hills of Nevada, flows southward for more than 150 km (crossing into California along the way), and hooks abruptly back to the north, terminating in Death Valley (Figure 2). Like the White River, the Amargosa is a desiccated drainage that retains permanent flow in only a few sections. The major thermal springs in the Amargosa system occur along the upper middle section in a former tributary valley at Ash Meadows; on the lower middle section of the river in Tecopa and Shoshone and on a ranch at Resting Spring; and near the southern end of the drainage at Saratoga Spring in Death Valley. In addition, concentrations of thermal springs occur at and near Furnace Creek in the middle section of Death Valley and at Grapevine Springs near the valley's northern end. Cool springs are also present along the upper course of the river near Beatty, but most of these have been extensively disturbed, and surveys have revealed no endemic aquatic Heteroptera in their waters.

The Amargosa River basin is the most isolated of the three drainages under discussion, and it contains the richest concentration of endemic aquatic Heteroptera species. Situated in the lowest and hottest section of the North American continent, the basin undoubtedly retained a warm climate even during the Pleistocene, which, combined with the presence of constant-temperature thermal springs, allowed for the survival of a relict warm-water entomofauna.

The largest concentration of thermal springs in the Amargosa system is found at Ash Meadows, where a complex of more than thirty seeps and springs supports a distinctive assemblage of endemic plants, fish, and insects (Williams et al., 1985). The springs of Ash Meadows form three discrete groups defined by elevation and biota. The highest is Devils Hole Spring, which contains the endemic Devils Hole pupfish *Cyprinodon diabolis* Wales and the endemic riffle beetle *Stenelmis callida callida* Chandler (1949) but no aquatic Heteroptera. At a slightly lower elevation, the second group comprises several thermal springs—including North Scruggs, South Scruggs, North Indian, South Indian, Marsh, and School Springs—which support an endemic naucorid, *Ambryus relictus* (Polhemus and Polhemus, 1994). Many of these springs also harbor thermally disjunct populations of a *Belostoma* species in the *bakeri/saratogae* complex and *Pelocoris biimpressus biimpressus*. The group at the lowest elevation consists of numerous springs with large thermal outflows, including Point of Rock Springs—the sole habitat for the endemic naucorid *Ambryus amargosus*, whose habitat preferences were described in detail by La Rivers (1953). Many of the larger springs in Ash Meadows, including Point of Rock, were extensively modified in past decades to support planned agricultural and residential developments. As a result, *Ambryus amargosus* was driven nearly to the point of extinction (Polhemus, D.A., 1993) and is now classified as a Federally threatened species; the disjunct populations of *Rhagovelia distincta* and

*Pelocoris biimpressus biimpressus* that formerly occurred at Point of Rock Springs were extirpated.

The thermal springs of the middle Amargosa River are concentrated in the towns of Shoshone and Tecopa and at the nearby ranch at Resting Spring. All have suffered from municipal, recreational, or agricultural development. Access to Resting Spring, which lies on private land, has been restricted by the ranch owner. The only aquatic Heteroptera species recorded from the site is the riffle bug *Rhagovelia distincta*, collected in 1956. Although widespread in the western United States, this species is found only as extremely localized populations in isolated thermal waters within the Great Basin (see previous discussion concerning this species in the White River system). Because all known localities for *R. distincta* in the southern Great Basin support additional thermal disjuncts or endemics, its presence at Resting Spring implies that this site may harbor additional Heteroptera of interest.

The springs at Tecopa, a few miles west of Resting Spring, are the hottest in the Amargosa system, having an emergent temperature of 43° C; they previously supported an endemic pupfish subspecies that is now extinct. Pools near the spring sources also supported extremely large concentrations of *Pelocoris biimpressus biimpressus* in the past, but its habitat there was completely eliminated in the course of development of recreational spas. Other less disturbed thermal outflows lie to the north of the Tecopa Hot Springs resort along the paved highway between Shoshone and Tecopa, and these support species of both *Pelocoris* and *Belostoma*, although the occurrence of the latter appears to be seasonal (D. Threlhoff, pers. comm. to DAP and JTP, 1999).

The thermal spring at Shoshone was similarly modified for municipal use: the spring head was boxed and the outflow creek is mostly piped to supply a local swimming pool. A small section of less disturbed habitat, consisting of a deep pond and a short stretch of flowing channel, remains between the spring head and the pipe collector system. The pond supports a population of *Pelocoris biimpressus biimpressus*, and the flowing channel contains *Ambrysus mormon*.

Along the lower Amargosa River, the most notable thermal site is Saratoga Spring, which emerges at the base of the Ibex Hills; this spring habitat was described in detail by Belkin and McDonald (1956). The aquatic Heteroptera fauna of the spring is unique and distinctive, including a highly disjunct population of the giant water bug *Lethocerus angustipes* (Figures 5, 14), which is otherwise not known outside of central Mexico (Menke, 1963). Other disjunct species here are *Pelocoris biimpressus biimpressus*, *Belostoma saratogae* (for which this is the type locality), *Nerthra martini*, and *Hydrometra australis* (see Table 1), plus a population of metallic-colored mosquitoes in the *Uranotaenia anhydor* complex (Belkin and McDonald, 1956).

A second focus of endemism in the lower Amargosa River basin is found along the course of Furnace Creek. The thermal outflows concentrated in this area—most notably Travertine, Cow Creek, and Limestone springs—harbor the endemic nau-

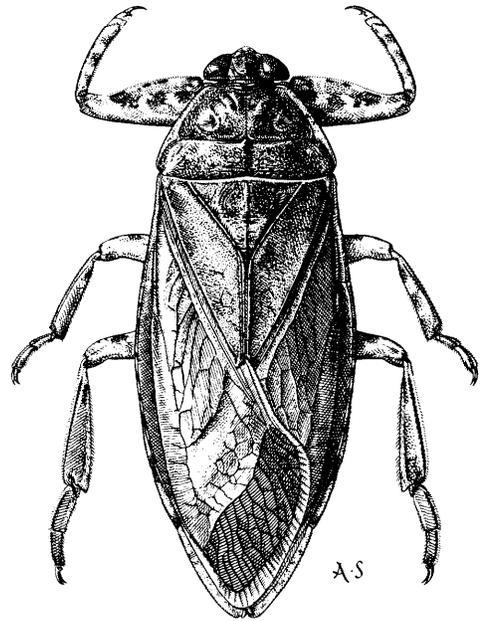


FIGURE 14.—*Lethocerus americanus* (Leidy). This giant water bug ranges across temperate North America, including the northern portion of the Great Basin. It is absent in the southern Great Basin, where the genus is represented by only a single highly disjunct population of *L. angustipes* (Mayr) in the Amargosa River basin; the closest known populations of this latter species are found in central Mexico.

corid *Ambrysus funebris* and a disjunct population of *Nerthra martini* (Figure 11). The spring habitat at Cow Creek was described in detail by La Rivers (1949a, 1951).

The most significant thermal springs in northern Death Valley are found at Grapevine Springs, which consist of many small thermal outflows perched on a bench above the valley floor northeast of Stovepipe Wells. The overall habitat here is in good condition, although many of the spring heads are covered by introduced palms and other encroaching vegetation and, thus, do not present an original aspect. Similar outflows once occurred along the bed of Grapevine Creek in Grapevine Canyon to the east, but these were extensively altered and diverted during the last hundred years to supply the small settlement at Scotty's Castle; as a result, they are not known to retain any of their former thermally dependant aquatic Heteroptera species. The remaining outflow channels in the Grapevine area are, for the most part, heavily overgrown and thus are difficult to sample. At a few spots the waters have pooled to form small ponds that support populations of *Pelocoris biimpressus shoshone*. This is the most northerly occurrence of the genus in California and the only place in the Amargosa River basin where *P. biimpressus shoshone* occurs. All other thermal outflows in this basin instead support *P. biimpressus biimpressus* (Figure 3), suggesting that the Amargosa basin may be a composite drainage, with its northwestern limb having had a separate history more closely linked to the Railroad Valley and White River drainages.

### Biogeographic Implications

The various internal drainages of the Basin and Range Province grouped under the term "Great Basin" form a definable unit in a topographic sense, but not biologically. As we have shown, the aquatic Heteroptera that are the subject of this paper exhibit an obvious faunal dichotomy between the cold basins to the north of the Caliente–Enterprise accommodation zone, many of which formerly drained to the Snake or Columbia Rivers, and the warm basins to the south, some of which have had ancient drainage relationships with the Colorado or Mojave Rivers, or even the Rio Grande (McKee et al., 1967; Lucchitta, 1990). The northern basins contain a broadly distributed cold-water biota devoid of notable endemic or disjunct species, whereas the thermal refugia of the southern basins harbor many such taxa. As a result, the northern basins provide little in the way of a compelling biogeographic story, whereas the southern basins contain intriguing faunal evidence of drainage basin development and capture during the Tertiary.

Two competing hypotheses may be advanced to explain the current distribution of disjunct faunal elements in the southern basins: long-distance dispersal and vicariance. The first postulates intermittent chance colonizations of drainage systems over time by faunal passage across existing barriers, such as deserts or drainage divides. The latter implies an initial widespread distribution of biotas, followed by subsequent fragmentation due to the imposition of barriers produced by tectonic or climatic events. A corollary axiom is that, in general, individual species will tend to disperse, at widely separate times, whereas entire communities will vicariate, more or less simultaneously.

We favor the vicariance hypothesis to explain the distributions of thermal relicts in the southern Great Basin, because this fauna represents entire disjunct communities of aquatic organisms with common geographic affinities—not the result one would expect from multiple episodes of chance long-distance dispersal. In addition to the evidence from aquatic Heteroptera presented in this paper, analyses of mitochondrial DNA variation in Death Valley pupfishes also support the hypothesis of an eastern ancestor for some of these pupfish species, with the sister group of the Amargosa River basin component of this radiation apparently occurring in the Laguna de Guzman area, east of the present continental divide in northern Mexico, rather than in the Colorado River basin (Echelle and Dowling, 1992). Similarly, Parenti (1981) presented a morphologically based phylogenetic analysis showing that the cyprinodontiform fish genera *Empetrichthys* and *Crenichthys*, endemic to the southern Great Basin, had their sister group relationships with the Goodeidae of the Mexican Plateau. On the basis of morphological evidence, Hershler and Pratt (1990) also hypothesized an eastern derivation for the ancestors of spring snail species now found at Moapa and Ash Meadows, via southeastward drainage connections across Arizona in the Miocene.

A vicariance scenario accommodating these relationships requires initial dispersal from the southeast, followed by subsequent isolation. The geological evidence is quite clear that in the

late Oligocene to early Miocene, before the onset of crustal extension in the Great Basin, the terrain west of the Colorado Plateau was higher than the plateau itself, and sedimentation occurred in an easterly direction—a pattern that continued at least until the emplacement of the Peach Springs Tuff at 18 Ma (Young, 1970; Lucchitta, 1990). Certain authors have proposed that what is now the upper basin of the Colorado River drained eastward during that period, possibly to the Rio Grande via the Little Colorado River (McKee et al., 1967; Nilsen and McKee, 1979) (Figure 15), and that Oligocene drainage networks in southern Nevada could have been integrated with it. Such a scenario is consistent with the current distributions of *Pelocoris* and *Limnocois*, which are absent in the warm streams of central Arizona (Figure 3), indicating that they dispersed from southeast to northwest along drainages lying north of the current Gila River.

Any southeast-flowing connection to the Rio Grande, if it existed, was probably severed in the late Oligocene to early Miocene by a region-wide episode of rifting, orogeny, and volcanism associated with the extension of the Basin and Range Province (Mutschler et al., 1998), in particular the eruption of the Mogollon–Datil volcanic field, which emplaced lava 3–5 km thick over southwestern New Mexico between 36 and 24 Ma (Schneider and Keller, 1994) (Figure 15). Subsequent tertiary volcanism in this region underwent a progressive northward migration out of the Arizona section of the Basin and Range Province and onto the southern margin of the Colorado Plateau from 15 to 2 Ma, further altering the course of the Little Colorado River (Moyer and Nealey, 1989; Mutschler et al., 1998). During this period, and before the establishment of a westward-flowing Colorado River, there is evidence that a formerly eastward-flowing drainage may have pooled in the Hopi Buttes area from 12 to 4 Ma, forming the lacustrine facies of the Bidahochi Formation in northeastern Arizona and northwestern New Mexico (Hunt, 1969; Miller, 1981; Love, 1989). The postulated Lake Bidahochi, depicted in Figure 15, thus could have continued to provide potential aquatic stepping stones for fauna moving northwestward from the Rio Grande Rift until 4 Ma, by which time the formation of the Grand Canyon and the gradual westward reorganization of regional drainage was well underway (Lucchitta, 1990).

After crustal extension, we hypothesize that vicariance occurred as Railroad Valley and the White River both became isolated endorheic basins, probably by the end of the Miocene, with the latter finally reestablishing an outlet to a reorganized, westward-flowing Colorado system via headwater extension of the Virgin River sometime in the Pliocene. The stratigraphic character of the Muddy Creek Formation in the Grand Wash Trough indicates interior drainage at the lower end of the White River basin throughout the Miocene, with through drainage to the Colorado River occurring no earlier than 5–6 Ma (Lucchitta, 1972, 1990; Bohannon et al., 1993). The absence of any of the signature Railroad Valley and White River thermal endemics or disjuncts in the current Colorado system (Figures 3,

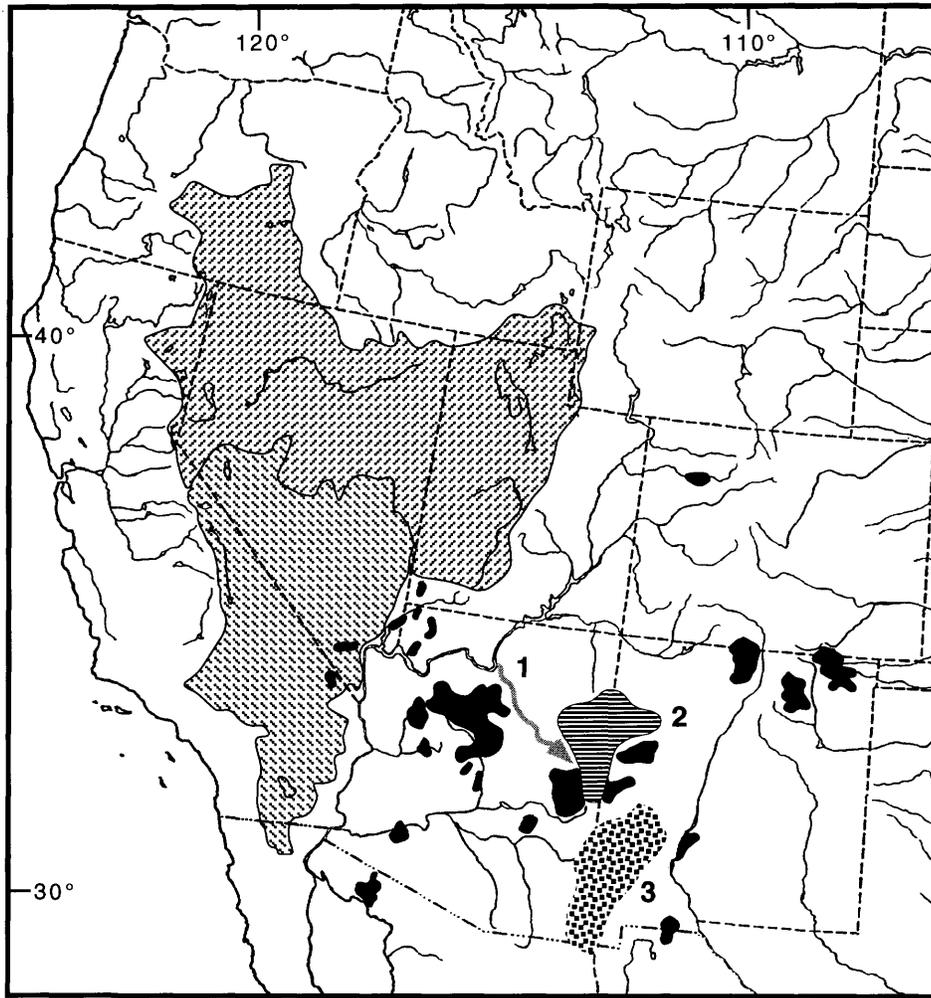


FIGURE 15.—Late Miocene to Late Pliocene topographic features in southwestern North America. The present Great Basin is also depicted, with division into northern basins (area marked by right-leaning slashes) and southern basins (left-leaning slashes) as discussed in text. Black shading indicates Late Cenozoic basalt flows, emplaced 25–4 Ma (after Mutschler et al., 1998). Numbered features are as follows: 1 = course of Little Colorado River (gray line with arrowhead indicates hypothesized direction of southeasterly drainage toward the Rio Grande system (after McKee et al., 1967); 2 = hypothesized location of Lake Bidahochi (horizontal lines), 12–4 My (after Hunt, 1969; Love, 1989); 3 = location of Mogollon–Datil volcanic field (square dots), emplaced 36–24 Ma (after Schneider and Keller, 1994; Mutschler et al., 1998).

4), despite the modern-day presence of a flowing-water link via the Muddy River, argues that the reconnection of the lower White River may have come very late; the current outlet lies along the highly active Lake Mead fault zone, where crustal blocks such as Frenchman Mountain have been transported up to 80 km from their former location east northeast of their present position in the last 14 My (Duebendorfer et al., 1998), resulting in extensive rearrangement of local drainage networks.

The Amargosa River basin may have had a more isolated position, as indicated by its faunal endemism, but it nevertheless exhibits faunal ties to the White River catchment and Railroad Valley. The distribution of *Pelocoris* subspecies (Figure 3) sug-

gests that the current basin is a composite and that the northern section of Death Valley near Grapevine Canyon was previously linked in some fashion to the Railroad Valley and White River drainage system. Additional surveys of warm springs in the basins northeast of the Amargosa drainage would prove useful in determining if *Pelocoris* populations are present in those areas, which might indicate a corridor that linked the Grapevine Springs populations to those of Railroad Valley and the White River.

The presence of strikingly disjunct populations of otherwise Mexican taxa in the southern end of the Amargosa system (Figure 5), coupled with the absence of strong relationships to the modern Colorado River basin, again indicates the relative

youth of the Colorado River in its current, westward-flowing configuration and suggests a former Amargosa River outlet to the south or southeast. One clue regarding the location is provided by the presence of another set of Mexican disjuncts along the upper Verde River system in central Arizona. This area contains populations of the backswimmer *Martarega mexicana* Truxal and the riffle bug *Rhagovelia choreutes* Hussey, both of which are typically Mexican taxa that do not occur elsewhere in Arizona or the Colorado River system (Menke and Truxal, 1966; Polhemus, J.T., 1966; Polhemus, D.A., 1997). Although neither of these species occurs in the Amargosa River basin, their presence as another cluster of disjunct Mexican taxa nevertheless suggests that a warm-water corridor to northern Mexico once ran through that region.

Superimposed upon these presumably Oligocene to Pliocene warm-water vicariance patterns is another, apparently more recent pattern involving the isolation of cold-water taxa at various widely separated localities in the southern Great Basin, as exemplified by the distribution of *Ambrysus woodburyi* discussed previously. This newer pattern may have resulted from the existence of cold-water drainage networks that formed during wet periods in the Pleistocene or late Pliocene. We infer that these conjectured drainages were not extensive or persistent enough to permit invasion into the southern basins by most of the aquatic insect biota of the modern Colorado River, and they were evidently too cold for utilization by species associated with thermal waters. Our entomological evidence implies this second round of vicariance events occurred in the White River and Railroad Valley basins at some point after the fragmentation of the warm-water biota. This hypothesis also implies that the Railroad Valley and White River drainage systems were hydrologically integrated in post-Miocene times, and perhaps as late as the Pleistocene.

Biological evidence for the sequence of events that eventually isolated the southern basins from each other and from the previous river systems to the south may be difficult to deduce from phylogenetic analyses of the aquatic Heteroptera species involved. The thermal disjuncts do not form monophyletic clades, but instead they are either endemic isolates within genera with many other widespread species or locally disjunct populations which, though profoundly isolated, have not undergone extensive morphological differentiation. In some taxa, such as the *Belostoma* species, there is evidence of incipient speciation that has not developed into any geographic pattern. Molecular approaches offer the promise of additional resolution of relationships between such potentially confusing and yet apparently conspecific populations. Until such data are available, however, our current biogeographic analysis of these basins, at least in terms of the evidence from aquatic Heteroptera, must rest primarily on faunal similarity and sister group distributions, an approach which, though less rigorous than strict cladistic biogeography, can still discern the large-scale patterns of historical relationship within these systems.

Many of the discoveries upon which the foregoing zoogeographic hypotheses are based were made only during the last decade. Given the size and complexity of the Great Basin and the number of springs remaining to be sampled for aquatic insects, it is likely that important information will come to light in the future. As with all such hypotheses, our zoogeographic interpretations are open to further testing as additional collections and analyses are made. We have little doubt that new evidence of the faunal signatures left by ancient lake and river systems will continue to be uncovered amid the basins and ranges of this most remote segment of the American West.

### Biogeographic Summary

In sum, the following biogeographic patterns are suggested by the distributions of aquatic Heteroptera in the Great Basin:

1. The northern Great Basin, consisting of the Bonneville Basin, Lahontan Basin, and the basins of southeastern Oregon, contains a widespread assemblage of typical north-temperate species and lacks significant regional endemism.
2. The Sevier River, draining into the Bonneville Basin, contains species shared with the southern Great Basin and the Colorado River system and absent elsewhere in the northern Great Basin, indicating that this river may have had an historical relationship with the upper Virgin River drainage.
3. Railroad Valley and the White River basin contain a unique set of disjunct taxa allied to species occurring in Texas and northern Mexico but absent in the Colorado River basin, indicating that these units had an historical relationship with the Rio Grande drainage and that modern integration of the White River and the Colorado River via the Virgin River is of very recent origin.
4. The Amargosa River basin contains a distinctive assemblage of endemic and disjunct taxa absent in the Colorado River basin but in some cases found in northern and western Mexico, thus indicating that this basin was isolated before formation of the modern Colorado River and also that it had an historic outlet to the south or southeast.
5. Northern Death Valley contains taxa also found in Railroad Valley and the White River basin but absent in the remainder of the Amargosa River system, suggesting that modern Death Valley is a composite of previously distinct drainage basins that had disparate histories.

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# Biogeography of Great Basin Aquatic Snails of the Genus *Pyrgulopsis*

*Robert Hershler and Donald W. Sada*

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## ABSTRACT

Snails of the genus *Pyrgulopsis* (Caenogastropoda: Hydrobiidae) are among the richest elements of aquatic biodiversity in the Great Basin (80 Holocene species), with most species endemic to single springs, spring systems, or drainage basins. *Pyrgulopsis* is an old Great Basin group, with a fossil record extending into the late Miocene (Truckee Formation). These tiny, gill-breathing gastropods (commonly known as springsnails) are obligately aquatic throughout their life cycle which, together with the above features, suggests that their biogeographic patterns are highly informative with respect to late Cenozoic hydrographic history.

Distributions of *Pyrgulopsis* species define seven regions of endemism within the Great Basin. Five of these correspond to drainages harboring concentrations of other endemic aquatic biota (Death Valley system, Lahontan Basin, Bonneville Basin, Railroad Valley, upper White River basin), whereas snail endemism in Dixie and Steptoe basins appears to be unique. Each of the three largest regions (Death Valley system, Lahontan Basin, Bonneville Basin) contains two or three subregions of *Pyrgulopsis* endemism, most of which are not paralleled by other aquatic biota.

*Pyrgulopsis* biogeography in part conforms to currently accepted interpretations of pluvial drainage in the Great Basin, but locally suggests different, presumably older relationships. Various historical relationships with adjacent external drainages are implied, although snail biogeography provides surprisingly little evidence of prior linkage with the Sacramento and upper Colorado River basins. In contrast to the fish-hook track, which is attributed to various mollusks and fishes and links the Snake River basin with the eastern Bonneville and western Lahontan Basins, *Pyrgulopsis* provides evidence of more continuous prior drainage integration across the northern boundary of the Great Basin.

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## Introduction

Gastropods of the family Hydrobiidae (commonly known as springsnails) are a highly suitable group for biogeographic evaluation of historical relationships among drainages of the Great Basin. These gill-breathing snails are obligate to permanent waters and disperse only through their habitat (Taylor and Bright, 1987).<sup>1</sup> Because of the antiquity (late Miocene) of these snails and their tight linkage with aquatic habitats, their patterns of phylogenetic relationships and distributions likely reflect late Cenozoic regional hydrographic history. Native distributions of these snails in the Great Basin appear to have been little affected by introduced species in contrast to fishes (particularly salmonids; Behnke, 1992). The diverse hydrobiid fauna of the Great Basin includes many locally endemic forms, suggesting a complex evolutionary history that can provide a rich source of biogeographic information.

For this contribution we focus on the hydrobiid *Pyrgulopsis*, the most speciose genus of aquatic snails in North America. Our purposes are to describe the regions of endemism defined by Holocene *Pyrgulopsis* species in the Great Basin and to review the distributions and the inferred phylogenetic relationships of these snails as they relate to current interpretations of drainage history.

*Pyrgulopsis* is a North American group of 131 described species that are considered valid, 61% of which live in the Great Basin. Members of the genus are found throughout much of western North America from the Rio Grande basin west to the California coast and from the Snake River–Columbia River basin south to the Bolsón de Mapimí depression in Chihuahua and Coahuila states, northern Mexico (Figure 1).<sup>2</sup> The scope of *Pyrgulopsis* remains incompletely known because many species are undescribed, including sizable faunas in northern Mexico and the northwestern United States. The Great Basin contains the greatest diversity of *Pyrgulopsis* (80 species), followed by a far smaller fauna in the Colorado River drainage (20 species). Allopatry of congeners is typical, although two or three species occasionally are sympatric, usually in large springs.

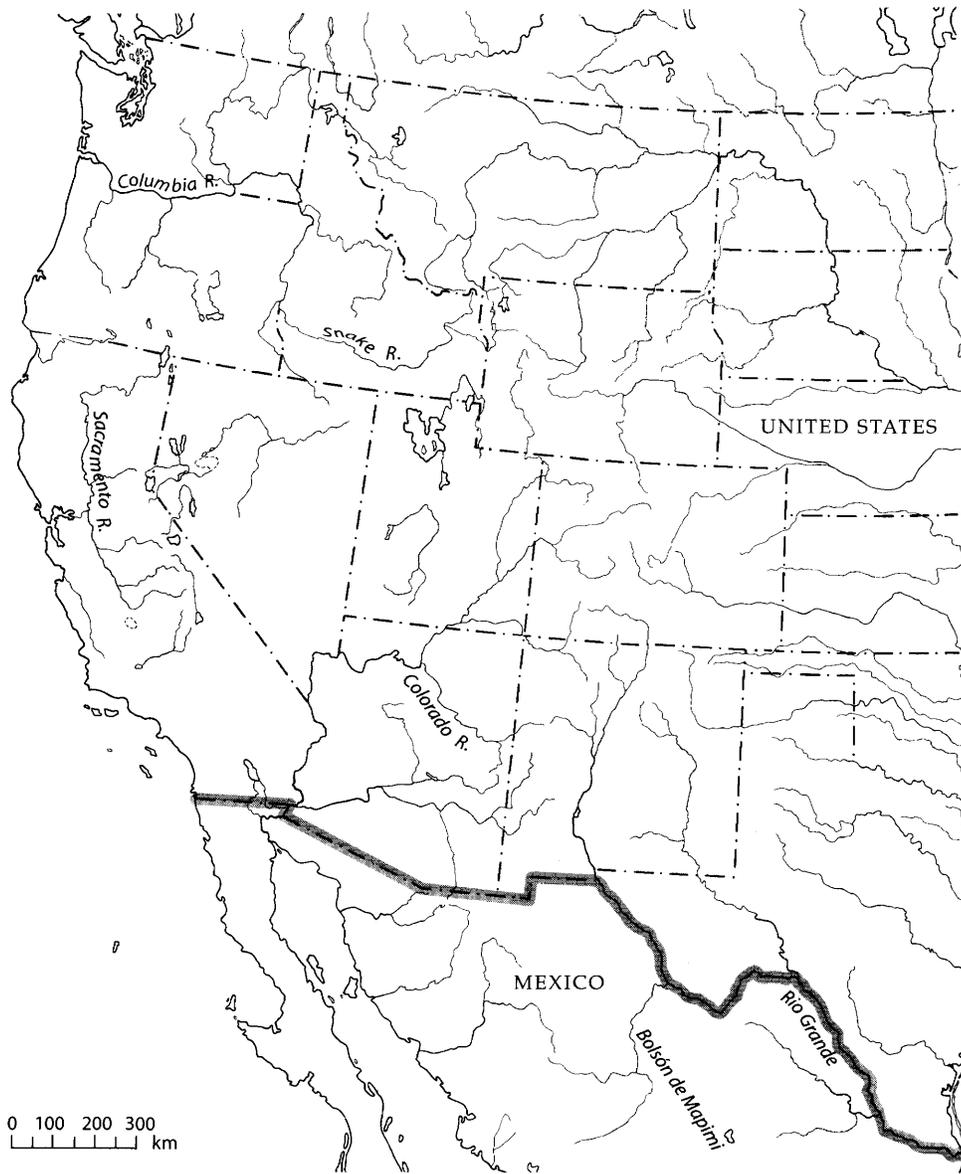
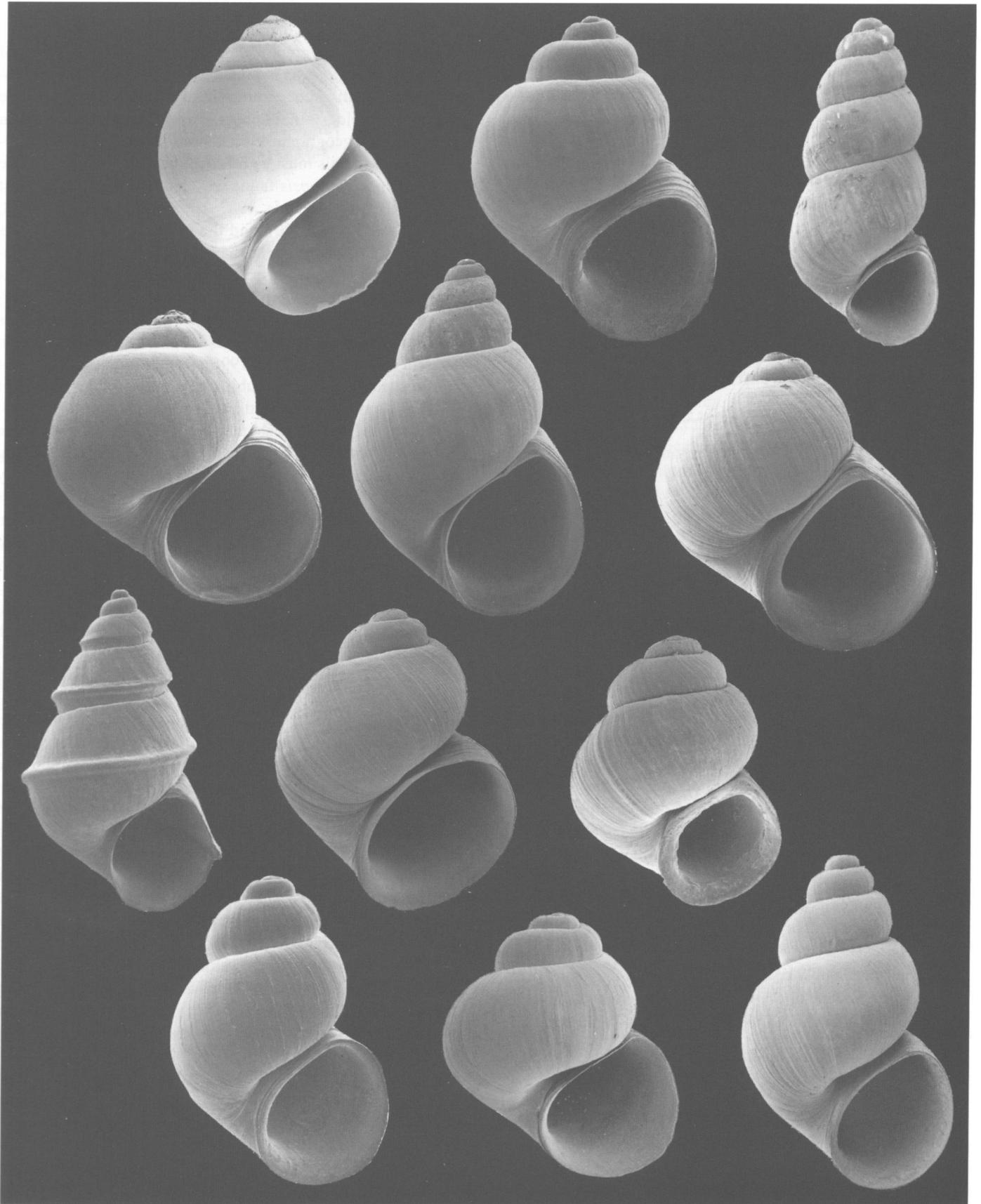


FIGURE 1.—The general distribution of *Pyrgulopsis* (shaded area) throughout the western United States and northern Mexico. The southern limit of the genus in Mexico is uncertain.

*Pyrgulopsis* is composed of small snails (1–8 mm in maximum shell dimension) having a smooth or weakly sculptured shell that ranges from low trochiform to narrow-conic in shape (Figure 2). Throughout the West *Pyrgulopsis* is a locally abundant member of benthic communities, living on rock or aquatic vegetation and grazing on periphyton (Mladenka, 1992). Females are oviparous and deposit egg capsules on hard substrates. Larval development is direct, with “crawl-away” young emerging from the egg capsules. *Pyrgulopsis* typically lives in springs ranging from tiny seeps to large rheocrenes and limnocrenes. Snails generally are concentrated near spring sources, with their density declining downflow (e.g., Noel, 1954)—a pattern that surely contributes to their tendency for local differ-

entiation. A few species live in lakes, rivers, and larger streams. Although some species live only in basin floor habitats, many others live in middle- and high-elevation springs and streams along montane slopes, suggesting that faunal

FIGURE 2 (opposite).—Scanning electron micrographs of shells of selected *Pyrgulopsis* species. Top row (left to right): *P. breviloba* (USNM 873174, shell height 1.8 mm), *P. bryantwalkerii* (USNM 874305, 2.3 mm), *P. dixensis* (USNM 874391, 2.0 mm); second row: *P. erythropoma* (USNM 857864, 2.2 mm), *P. hendersoni* (USNM 874386, 5.1 mm), *P. merriami* (USNM 873395, 2.5 mm); third row: *P. nevadensis* (USNM 590364, 4.6 mm), *P. notidicola* (USNM 873215, 1.8 mm), *P. orbiculata* (USNM 873196, 1.4 mm); bottom row: *P. owensensis* (USNM 857955, 2.3 mm), *P. papillata* (USNM 873185, 2.0 mm), *P. turbatrix* (USNM 883978, 2.9 mm).



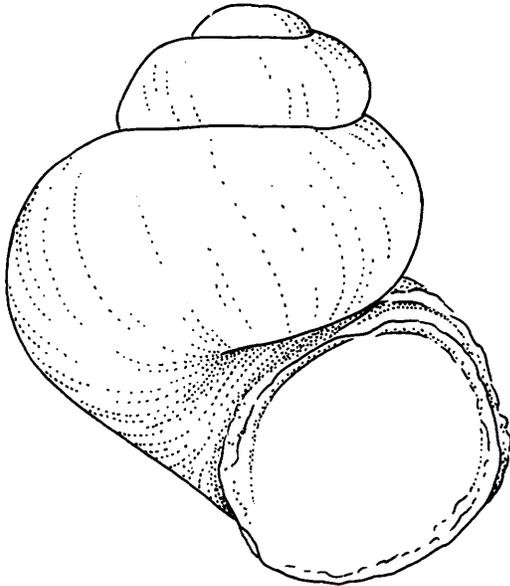


FIGURE 3.—*Pyrgulopsis truckeensis*, from the Truckee Formation (late Miocene), Churchill County, Nevada (holotype, USNM 560438). Shell height 2.2 mm.

movement has been achieved by upland headwater transfers (e.g., stream capture) as well as by basinal integration.

Whereas extant species typically live in small springs, fossil shells referable to the genus routinely are found in late Cenozoic lacustrine deposits (Taylor, 1966a). Paleoecological studies that delineate habitat use by these snails are lacking. The known ecology of extant congeners allows us to conjecture that *Pyrgulopsis* was not widely dispersed in paleolakes but instead was restricted to well-oxygenated littoral zones or lived in springs or wetlands closely associated with these lakes. The fossil record of *Pyrgulopsis* is limited in utility because of the weak phylogenetic signal provided by the simple shells of these snails (Taylor, 1987:5). Nevertheless, the occurrence of *P. truckeensis* (Figure 3) in the Truckee Formation (stratigraphy discussed by Firby, 1993) in the northwest Great Basin suggests that the genus dates at least to the late Miocene (Yen, 1950; see Gregg and Taylor, 1965, for assignment of this species to *Fontelicella* (= *Pyrgulopsis*)).<sup>3</sup> It has been suggested that Holocene (presumably cold-water) species in the genus generally may be Pliocene in origin and that western hydrobiids living in thermal springs (which include many *Pyrgulopsis* species) are generally ancient, perhaps middle Tertiary in age (Taylor, 1987:5, as *Fontelicella*). The antiquity of this group suggests that, as in the case of Great Basin fishes (e.g., Smith, 1978; Minckley et al., 1986), ancestral biotic ranges were affected not only by extensive integration and subsequent fragmentation of Late Quaternary pluvial drainage, but also by the spectrum of tectonic and volcanic events that shaped the modern regional landscape during the past 17–18 My.

## Methods

A rigorous biogeographical analysis (e.g., Wiley, 1988) of Great Basin *Pyrgulopsis* is precluded by the paucity of phylogenetic information concerning these snails, and although we discuss morphological groupings of species (as summarized in Appendix), biogeographic conclusions derived from distributions of these snails must be refined in the future. Most of the Great Basin *Pyrgulopsis* fauna was described during the past decade (Hershler and Sada, 1987; Hershler, 1989, 1995, 1998; Hershler and Pratt, 1990), and the study of these snails lags well behind that of regional aquatic vertebrates. Taxonomic reanalysis of relatively widespread and/or morphologically variable forms will be necessary, as evidenced by a recent allozymic study of *P. wongi* from the southwestern Great Basin; this study revealed fixed-allele differences among populations from different drainages (Hamlin, 1996), suggesting the presence of cryptic species. The only published phylogenetic analysis of *Pyrgulopsis* species provided little resolution (Hershler, 1994, fig. 31) and did not establish monophyly of the genus within the subfamily Nymphophilinae.<sup>4</sup> Morphological diversity among species assigned to *Pyrgulopsis* is pronounced, particularly with respect to glandular penial ornament (Figure 4). Species groupings in use are based on very few characters (mostly from penial form and ornament) that often are noncongruent, and many snail species are strongly differentiated by autapomorphies.

We thus rely heavily on the technique of inferring past drainage relationships on the basis of biotic distributions, although we acknowledge the inherent limitations of this method (Platnick and Nelson, 1978). A biotic distribution encompassing several now-isolated drainages may suggest previous integration or connection of these waters (and/or relatively vagile organisms), but this assumes that biotic components automatically expand or contract their ranges in concert with potential habitat. The extent to which this assumption is realistic depends greatly on ecological characteristics of species in question. Biotic distributions do not reveal relative timing of historical relationships among inhabited areas, whereas fossils and/or a well-resolved cladogram might provide this information. Relatively broadly distributed taxa are useful within this context, but locally endemic forms provide no information in the absence of phylogenetic resolution. (In contrast, broadly distributed taxa have little utility for vicariance biogeography.) Despite these drawbacks, earlier efforts using this methodology often have been insightful for Great Basin aquatic biogeography, as exemplified by seminal works on fishes (Hubbs and Miller, 1948; Hubbs et al., 1974).

We follow King's (1982) definition of the Great Basin (which, in turn, was based on that of Frémont, 1845) as all contiguous areas of currently internal drainage between the Sierra Nevada and Rocky Mountains. Thus, areas that may have had recent external drainage but now are endorheic, such as the Salton Trough and disrupted drainage of the Colorado River in southeast Nevada, are treated as Great Basin. Drainage maps

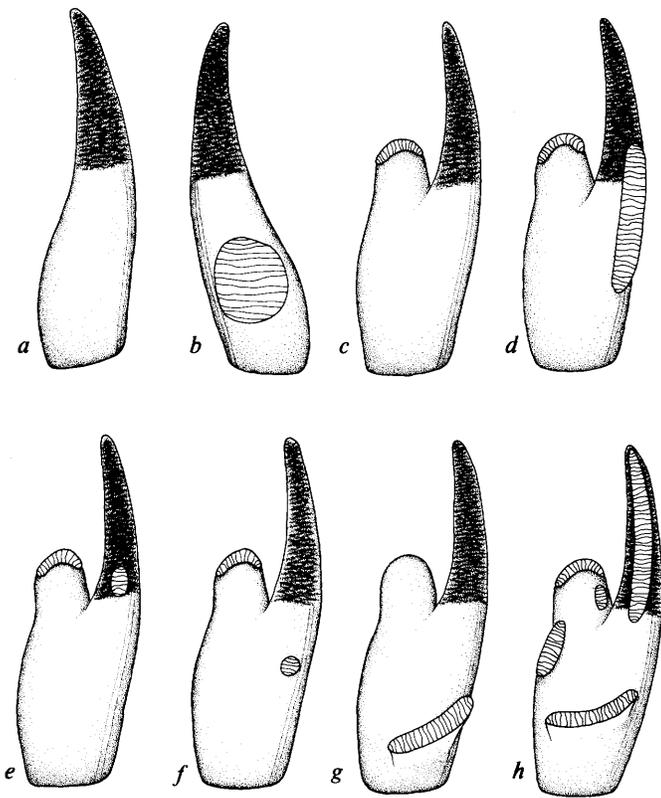


FIGURE 4.—Representative variation in penial glandular ornament among *Pyrgulopsis* species groups (see Appendix for names of species exhibiting each form): *a*, simple penis lacking glands (group 1); *b*, ornament of a superficial ventral gland (group 2); *c*, ornament of a terminal gland (group 3); *d*, ornament of a terminal gland and elongate Dg1 abutting filament (group 4); *e*, ornament of a terminal gland and small, basal penial gland (group 5); *f*, ornament of a terminal gland and weak, dot-like Dg1 (group 6); *g*, ornament of a raised Dg1 (group 8); *h*, ornament of a full complement of glands (group 9). The schematic drawings are not to scale.

were constructed by using United States Geological Survey (USGS) 1:2,000,000 line graph data as base. Drainage basins and their boundaries were digitized from USGS 1:500,000 (state) hydrologic unit maps. The fit of hydrographic boundaries onto the drainage base is not exact because these two sets of data were originally of different scales and map projections. Final maps were prepared using Adobe Illustrator (version 7.0). Regions of endemism refer to drainages having two or more endemic species and should not be confused with “areas of endemism,” which imply congruence of distributional and phylogenetic pattern among taxa (Harold and Mooi, 1994).

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row (NMNH) inked anatomical drawings and assisted with preparation of plates. Fiscal support was provided by two awards from the Smithsonian Institution Scholarly Studies Program. This paper benefited from detailed and very useful criticisms from Marith Reheis, Richard Vari, and two anonymous reviewers. We also acknowledge an intellectual debt to Dwight W. Taylor, whose pioneering studies of western American freshwater molluscan biogeography (notably Taylor, 1960, 1966a, 1985; Taylor and Smith, 1981; Taylor and Bright, 1987) paved the way for the present work.

#### Biogeography

*Pyrgulopsis* is widespread in the Great Basin (Figure 5) and even occurs in some poorly watered, fishless regions such as the “area of sterile basins” of southern Nevada (Hubbs and Miller, 1948:45). We know of no major sampling gaps, although distributions of many species may be imprecisely known because of nonexhaustive local fieldwork and probable undocumented extinctions in historic time.

Distributions of Great Basin species are given in Table 1. Most of the fauna is endemic to single springs, spring complexes, or drainage basins. Only 16 of the 80 species range across major drainage divides and, as mentioned above, a re-evaluation of the purported conspecificity of populations is necessary in these cases. *Pyrgulopsis* species describe seven major regions of endemism within the Great Basin (Figure 6), five of which correspond to drainages harboring other endemic biota (e.g., fishes; Smith, 1978; Minckley et al., 1986). On the other hand, snail endemism in Dixie and Steptoe Basins is not matched by any other aquatic organism. Species of *Pyrgulopsis* also define subregions of endemism within the largest of these drainages (Bonneville Basin, Lahontan Basin, Death Valley system); most of these subregions have no parallel among other aquatic biota.

**DEATH VALLEY SYSTEM.**—Treatment of this fauna partly reiterates that of Hershler and Pratt (1990). The three components (Owens Valley, Amargosa River basin, and Mohave Desert) of the Death Valley hydrographic system contain a total of 14 species of *Pyrgulopsis*, all but four of which are endemic. Endemic species are concentrated in two subregions, upper Owens Valley and the Amargosa River basin (Figure 7), both of which harbor other endemic biota (Sada et al., 1995).

The upper Owens Valley subregion contains an endemic flock of three species—*P. aardahli*, *P. owensensis*, *P. perturbata*—that are most similar to the widespread Lahontan species *P. gibba*. The distribution of another species from this subregion, *P. wongi* (Figure 8a), suggests prior integration among upper Owens Valley—the southeastern Lahontan region (Carson and East Walker River basins); Mono Valley, which comprised the uppermost segment of the pluvial Owens River drainage (Putnam, 1949); and several valleys to the east (Deep Springs Valley, Huntoon Valley, Fish Lake Valley, Teels Salt Marsh). Reheis et al. (2002) present shoreline evidence that

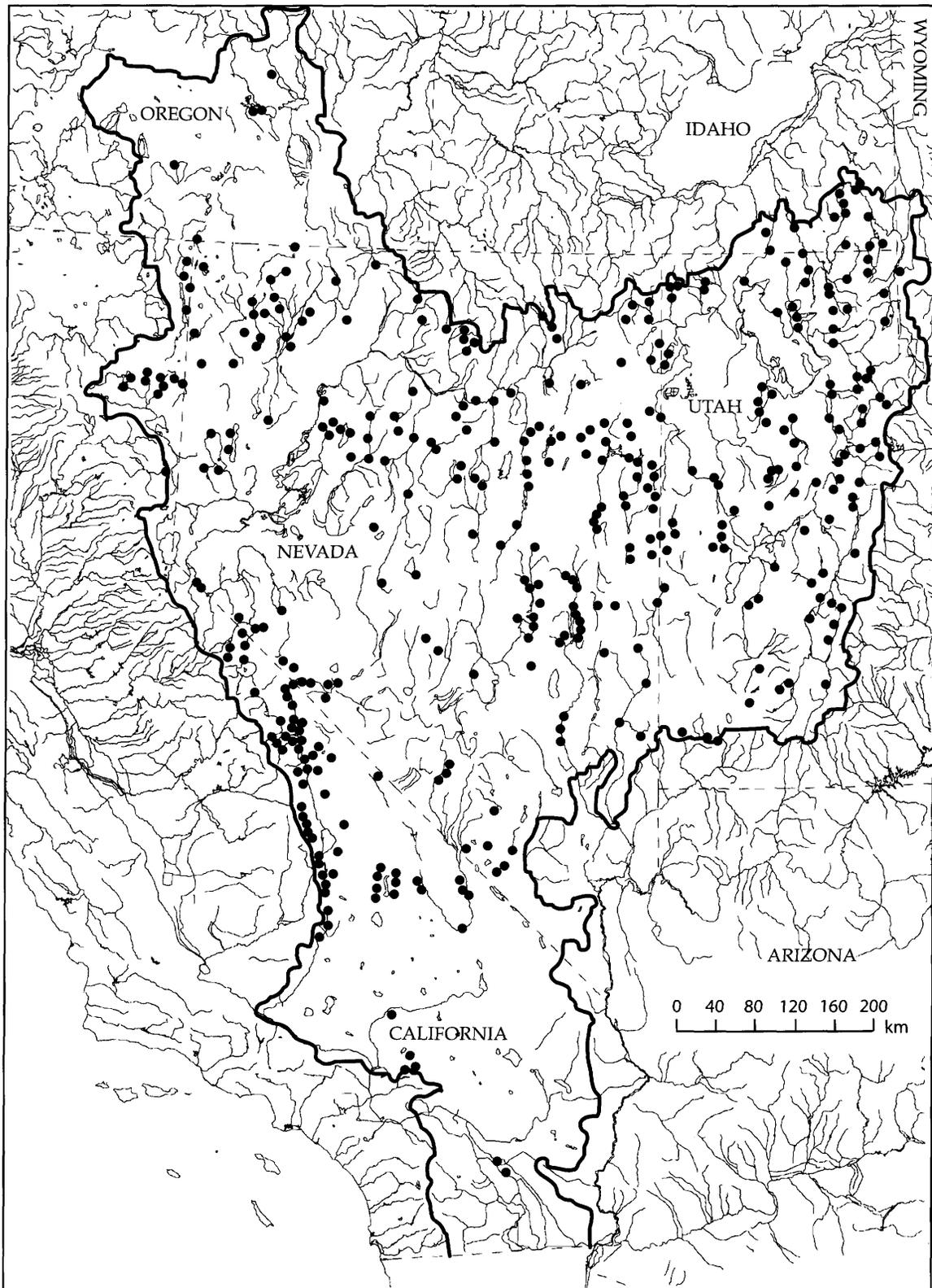


FIGURE 5.—Distribution of *Pyrgulopsis* in the Great Basin of the western United States. Dots often represent more than one locality. The heavy line shows the boundary of the Great Basin hydrographic system.

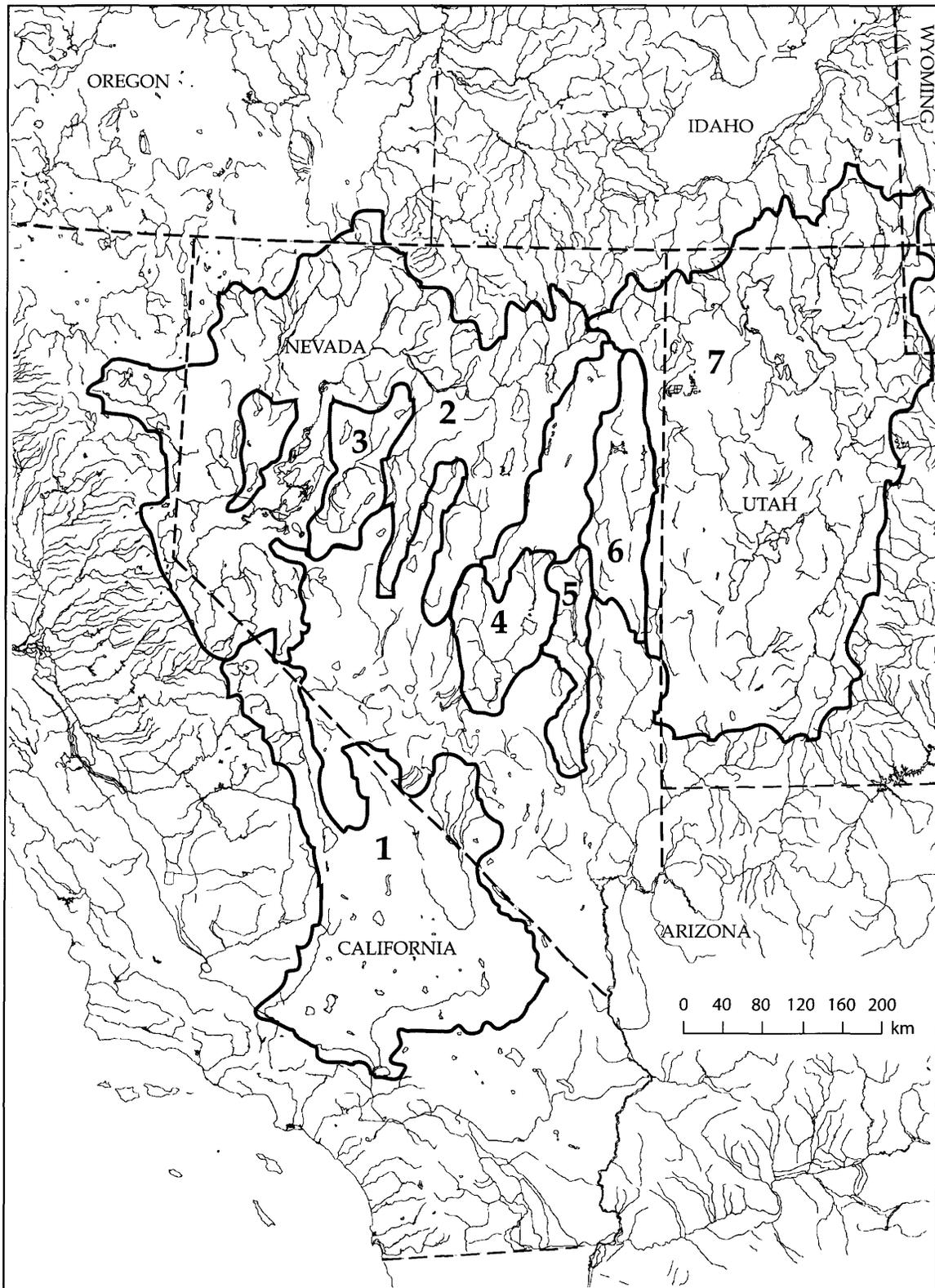


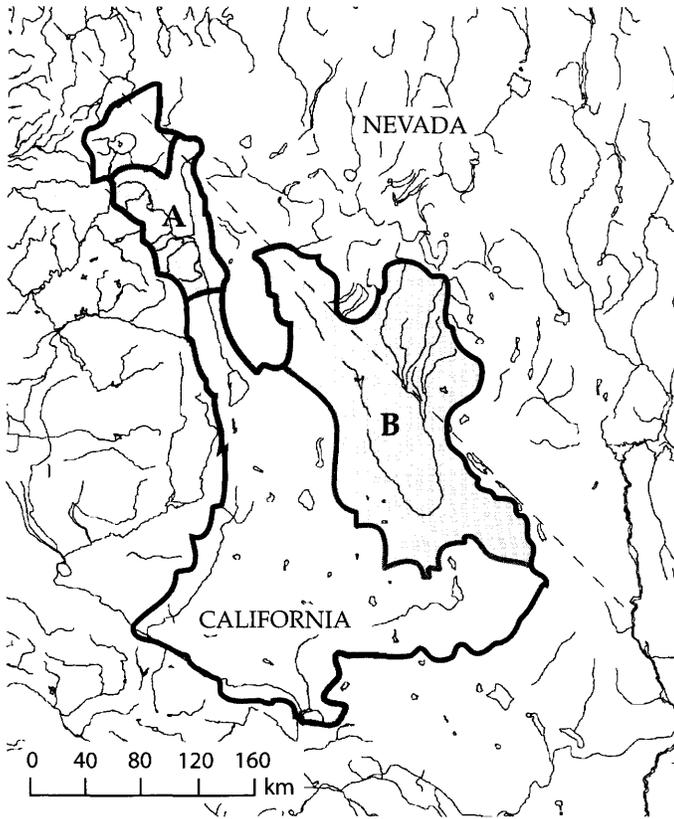
FIGURE 6.—Regions of endemism represented by *Pyrgulopsis* in the Great Basin. 1, Death Valley system; 2, Lahontan Basin; 3, Dixie Basin; 4, Railroad Valley; 5, upper White River basin; 6, Steptoe Basin; 7, Bonneville Basin.



TABLE 1.—Continued.

Species	Drainage												
	Great Basin									Extralimital			
	DV	LA	RB	ST	DX	WR	IB	BO	OL	SA	CA	SN	CO
<i>papillata</i>	—	—	X	—	—	—	—	—	—	—	—	—	—
<i>peculiaris</i>	—	—	—	—	—	—	—	X	—	—	—	—	—
<i>pellita</i>	—	X <sup>1</sup>	—	—	—	—	—	—	—	—	—	—	—
<i>perturbata</i>	X	—	—	—	—	—	—	—	—	—	—	—	—
<i>pictilis</i>	—	X <sup>1</sup>	—	—	—	—	—	—	—	—	—	—	—
<i>pilsbryana</i>	—	—	—	—	—	—	—	X	—	—	—	—	—
<i>pisteri</i>	X	—	—	—	—	—	—	—	—	—	—	—	—
<i>planulata</i>	—	—	—	X <sup>1</sup>	—	—	—	—	—	—	—	—	—
<i>plicata</i>	—	—	—	—	—	—	—	X <sup>1</sup>	—	—	—	—	—
<i>ruinosa</i>	—	—	—	—	—	—	Y <sup>1</sup>	—	—	—	—	—	—
<i>sadai</i>	—	X	—	—	X	—	—	—	—	—	—	X	—
<i>sathos</i>	—	—	—	—	—	X	—	—	—	—	—	—	—
<i>saxatilis</i>	—	—	—	—	—	—	—	X <sup>1</sup>	—	—	—	—	—
<i>serrata</i>	—	—	—	X	—	—	—	—	—	—	—	—	—
<i>sterilis</i>	—	—	—	—	—	—	X	—	—	—	—	—	—
<i>sublata</i>	—	—	—	—	—	—	X <sup>1</sup>	—	—	—	—	—	—
<i>sulcata</i>	—	—	—	X	—	—	—	—	—	—	—	—	—
<i>transversa</i>	—	—	—	—	—	—	—	X	—	—	—	—	—
<i>turbatrix</i>	X	—	—	—	—	—	X	—	—	—	—	—	X
<i>umbilicata</i>	—	X	—	—	—	—	—	—	—	—	—	—	—
<i>variegata</i>	—	—	—	—	—	—	—	X	—	—	—	X	—
<i>villacampae</i>	—	—	X	—	—	—	—	—	—	—	—	—	—
<i>vinyardi</i>	—	X	—	—	—	—	—	—	—	—	—	—	—
<i>wongi</i>	X	X	—	—	—	—	X	—	—	—	—	—	—

<sup>1</sup>Species is endemic to a single spring.



Mono Valley’s pluvial Lake Russell may have had an interval of northern drainage to the East Walker River basin, and Russell (1889:299–301) implied earlier integration of Mono Valley and the Lahontan Basin prior to disruption by Quaternary volcanics. Perhaps early integration between Mono and Huntton Valleys also occurred, because their divide is only slightly above the highest shoreline (~2257 m; Reheis et al., 2002) documented for Lake Russell. Distribution of *P. wongi* in isolated valleys to the east of the Owens Valley trough correlates, in part, with an emerging concept that Lake Lahontan may have extended sufficiently south of Walker Lake to integrate with Fish Lake Valley (Mifflin and Wheat, 1979; Reheis and Morrison, 1997; Reheis et al., 2002). However, integration of this conjectured drainage with Deep Springs Valley would have been unlikely, because pluvial Deep Spring Lake was isolated by very high divides during the late Pleistocene (Miller, 1928). A fossil *Pyrgulopsis* (*Fontelicella* sp.; Taylor, 1966a:67) was recorded from the Waucoba Lake beds (fide Walcott, 1897), which contain tephra layers from 2.22–2.17 Ma (A. Sarna-Wojcicki, in litt., August, 1998) that are now uplifted above

FIGURE 7 (left).—Regions of endemicism by *Pyrgulopsis* within the Death Valley system. A, upper Owens Valley (north of Tinemaha Reservoir); B, Amargosa River basin (including its terminus, the Death Valley trough). The heavy line shows the boundary of the Death Valley pluvial drainage system.

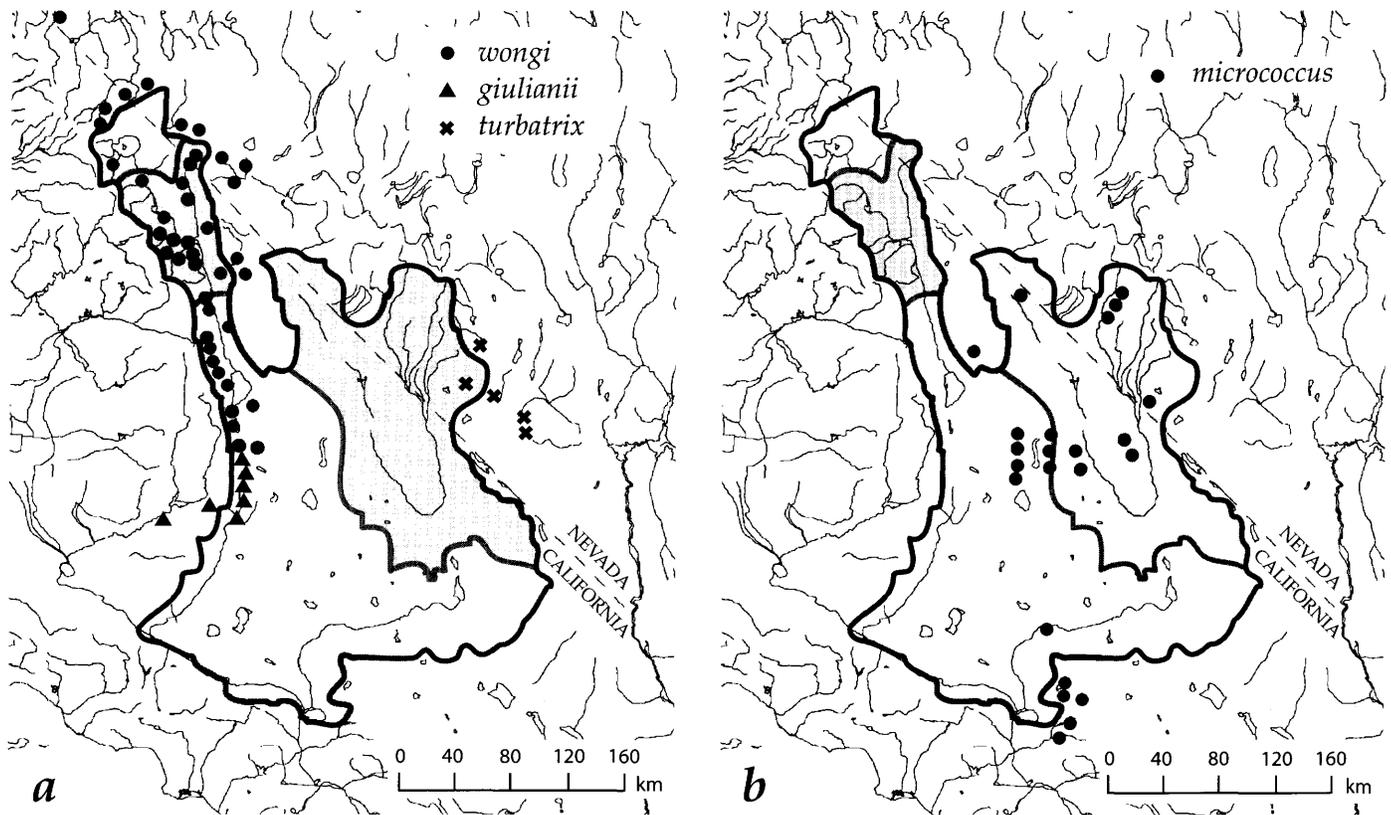


FIGURE 8.—Distributions of selected *Pyrgulopsis* species of the Death Valley System: a, *P. giulianii*, *P. turbatrrix*, *P. wongi*; b, *P. micrococcus*. Shading indicates the regions of endemism (from Figure 7).

eastern Owens Valley. This record suggests that *P. wongi* may have dwelled early in the proto-Sierra Nevada/White Mountain block and attained current distribution as a result of later tectonic events that created Owens, Deep Springs, and Fish Lake Valleys during the past 2.3 My (Bachman, 1978; Reheis and Sawyer, 1997; also see Lueddecke et al., 1998). This hypothesis is supported by allozyme evidence that *P. wongi* populations of Deep Springs Valley are more similar to snails of Owens Valley than to samples from upper segments of the pluvial Owens River drainage (Hamlin, 1996).

*Pyrgulopsis giulianii* (Figure 8a), which is morphologically very similar to the upper Owens Valley species flock described above, lives in Sierra Nevada streams that drain to Indian Wells Valley, into which pluvial Lake Owens spilled. Records of this species along the south fork of the Kern River west of the Sierra Nevada suggest prior transmontane drainage across the Sierra Nevada divide (also indicated by Dibblee, 1967, figs. 79, 80), which presumably was disrupted by uplift and westward tilting of the southern portion of this range since the late Neogene (Loomis and Burbank, 1988; Unruh, 1991; Christiansen and Yeats, 1992).<sup>5</sup>

Of the seven species endemic to the Amargosa River basin, six are restricted to the Ash Meadows spring oasis, several of which (*P. crystalis*, *P. erythropoma*, *P. pisteri*) form a putative

clade closely similar to *P. avernalis* from Moapa Valley in southeast Nevada (Colorado River basin).<sup>6</sup> The seventh species endemic to the Amargosa River basin, *P. amargosae*, lives in springs along the lower Amargosa River and most closely resembles a species from the Snake River basin (*P. bruneauensis*). This putative relationship is suggestive of the fish-hook distributional pattern described for various freshwater mollusks and fishes (Taylor 1960, 1966a), although this possibility would be bolstered by presence of linking populations or species in the large intervening area.<sup>7</sup>

The distribution of another snail, *P. turbatrrix* (Figure 8a), also implies that the Amargosa River basin had a previous drainage relationship with the Colorado River basin as well as with several isolated valleys to the east. *Pyrgulopsis turbatrrix* lives along slopes of the Spring Mountains in Amargosa Flat (which drains to Ash Meadows), isolated Indian Springs and Pahrump Valleys, and Las Vegas Valley (Colorado River basin). (Note that another congener, *P. deaconi*, also lives along the western and eastern flanks of the Spring Mountains in Pahrump and Las Vegas Valleys, respectively.) *Pyrgulopsis turbatrrix* also lives in a single spring in Frenchman Flat, a small, isolated basin west of Indian Springs Valley. Many have speculated that the Death Valley system had a past connection with the Colorado River basin (see Miller, 1946); although an

oft-postulated connection via spilling of the integrated pluvial lake system to the south (through Bristol, Cadiz, and Danby Lake basins) is unlikely (Brown and Rosen, 1995; Hooke, 1998), other forms of integration may have occurred. Distribution of *P. turbatrrix* conforms in part to previous integration of the Amargosa River basin and Las Vegas Valley around the north flank of the Spring Mountains, as proposed by Hubbs and Miller (1948:101–102; also see Nolan in Gilluly, 1929:682). This integrated system presumably was disrupted as a result of stream captures across the low, largely alluvial divides in the region. Hubbs and Miller (1948:85) argued that “Lake Pah-rump” spilled to the Amargosa River basin, but Mifflin and Wheat (1979) denied existence of a late Pleistocene pluvial lake in this valley. Integration of the drainage postulated above with that of Frenchman Flat may have occurred via the low divides separating the Amargosa River basin from Rock and Mercury Valleys to the west (which in turn are weakly separated from Indian Springs Valley). Alternatively, drainage integration may have been disrupted by the several kilometers of movement along local, northeast-trending strike-slip faults, at least some of which occurred after the Miocene (Carr, 1984; Stewart, 1988). Distribution of *P. turbatrrix* along flanks of the Spring Mountains also could have arisen via transmontane stream capture, perhaps associated with late Cenozoic tilting of this range (Burchfiel et al., 1983).

*Pyrgulopsis micrococcus* (Figure 8b) lives in all three components of the Death Valley hydrographic system, although it is found in only a lower segment of the pluvial Owens River drainage, Panamint Valley. The distribution of this snail provides a possible exception to the assertion by Taylor (1985: 317–318) that “spillover from Lake Panamint into Death Valley, and into Lake Manly in Death Valley, had no recognizable effect on mollusc distribution.” However, this species lives in high-elevation springs in the Panamint Mountains, and its distribution across this divide may reflect headwater transfer as opposed to pluvial dispersal. Distribution of this snail also implies early (before the late Pleistocene) drainage integration of the Death Valley system with both Saline Valley (northwest of Panamint Valley) and the California coastal drainage south of the Transverse Ranges. Saline Valley, a small, profoundly closed basin that lacked a pluvial lake, perhaps integrated with Panamint Valley before the faulting that was responsible for basinal development during the past 3.0 My (Burchfiel et al., 1987). The distribution of *P. micrococcus* is paralleled by another prosobranch snail, *Assimineia infima*, which lives in Saline (Hershler, unpublished) and Panamint Valleys (as Holocene fossil; Taylor, 1966b:208), as well as in the Amargosa River basin (Hershler, 1987). The transmontane distribution of *P. micrococcus* in the San Bernardino Mountains implies early presence in the region—before the late Miocene to early Pliocene uplift, which truncated and reversed the southward Mojave drainage (Meisling and Weldon, 1989).<sup>8</sup>

*Pyrgulopsis* biogeography (1) implies various prior drainage connections between the Death Valley system and other,

mostly adjacent, areas and (2) suggests that the upper Owens Valley and Amargosa River basin subregions of endemism do not share a close historical relationship. Interestingly, early drainage integration between the northwest portion of the Death Valley system and the Sacramento Valley before the late Cenozoic Sierra Nevada uplift (e.g., Huber, 1981) is not well reflected in *Pyrgulopsis* biogeography. The complete absence of species overlap and the entirely different sets of historical drainage relationships implied by the *Pyrgulopsis* faunas of Owens Valley and the Amargosa River basin are striking, given the pluvial integration of these drainages, yet they agree with the distribution patterns of other mollusks (Taylor, 1985) and of fishes (Minckley et al., 1986; also see Echelle and Dowling, 1992). Taylor (1985:317) suggested that the disparity of freshwater mollusks from west and east of Death Valley may reflect a dispersal barrier provided by extension of the Miocene proto-Gulf of California into the area. Although fossils may imply presence of a late Cenozoic estuary in portions of the Mojave Desert (Durham and Allison, 1960; Smith, 1970; disputed by Spencer and Patchett, 1997), no physical record of such conditions has been found in the Death Valley region (Buising, 1990, fig. 1), and the local fossil record is equivocal in this regard.<sup>9</sup> Physical evidence of middle Pleistocene integration of the Owens and Amargosa River basins is clear (Smith, 1976; Jan-nik et al., 1991; Fitzpatrick and Bischoff, 1993), yet hydro-graphic conditions nonetheless may have provided a barrier to aquatic dispersal (Miller, 1981) that perhaps was positioned between Indian Wells and Panamint Valleys.

LAHONTAN BASIN.—This large region harbors 22 species of *Pyrgulopsis*. Four endemic species of fishes also live in this basin (Hubbs et al., 1974; Deacon and Williams, 1984). The 16 endemic species of *Pyrgulopsis* are concentrated in four subregions (Figure 9), only one of which, the Black Rock Desert, harbors other endemic aquatic biota. *Pyrgulopsis* biogeography implies considerable prior drainage integration within the Lahontan Basin and between this and several adjacent drainages.

A southwest extension of Reese River Valley (Antelope Valley) contains two endemic species (*P. augustae*, *P. pictilis*) that are morphologically very similar to other Lahontan snails. Basin floor springs in the Carico Lake basin (part of the middle segment of the Humboldt River basin) harbor two endemic species (*P. basiglans*, *P. bifurcata*) that form a putative clade similar to the group of snails from the Amargosa and White River basins discussed above. Two snails (*P. bryantwalkeri*, *P. humboldtensis*) belonging to large groups of similar species are endemic to the upper Humboldt River basin. The distribution of another snail, *P. leporina* (Figure 10a), implies that drainage of the upper Humboldt River basin (Lamoille Valley) was previously integrated (before the late Pleistocene) with that of northern Ruby Valley, perhaps reflecting spill of pluvial Lake Franklin into Lake Lahontan via Lake Clover as suggested by Snyder et al. (1964; but disputed by Mifflin and Wheat, 1979:57). Soldier Meadows, a prominent zone of thermal springs that drains south to the floor of Black Rock Desert via Mud Meadows

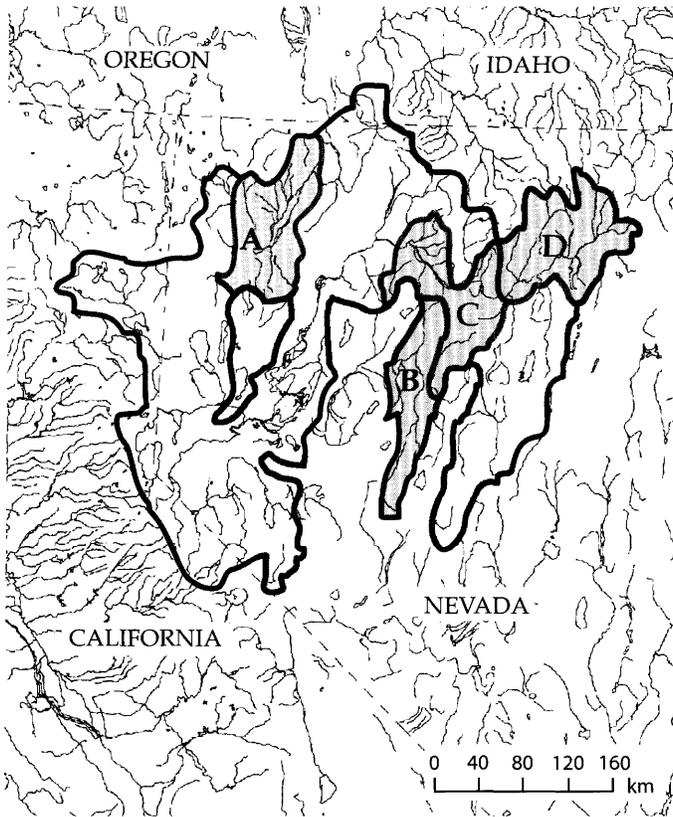
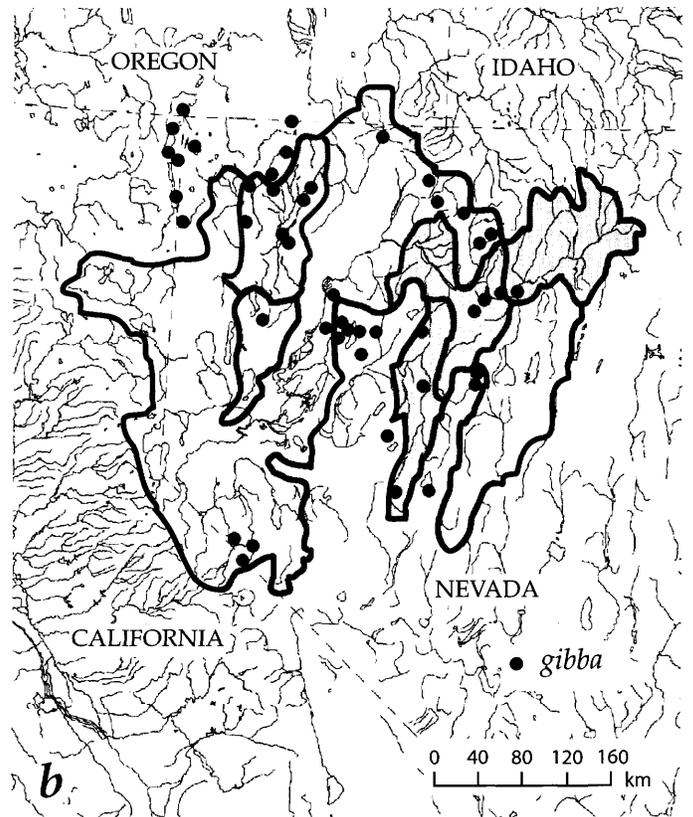
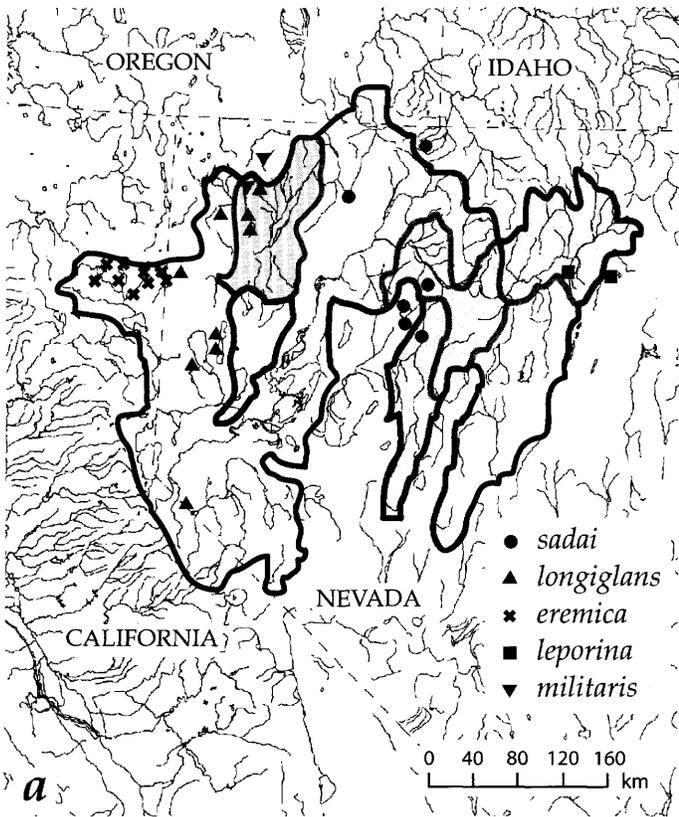


FIGURE 9 (left).—Regions of endemism by *Pyrgulopsis* within the Lahontan system. A, Black Rock Desert; B, Reese River basin; C, middle Humbolt River basin (includes the section of river from Palisade to Golconda Summit; also Carico Lake, Crescent, and Pumpnickel Valleys); D, upper Humboldt River basin (includes Marys River drainage). The heavy line shows the boundary of the Lahontan pluvial drainage system.

FIGURE 10 (below).—Distributions of selected *Pyrgulopsis* species of the Lahontan system: a, *P. eremica*, *P. leporina*, *P. longiglans*, *P. militaris*, *P. sadai*; b, *P. gibba*. Shading indicates the regions of endemism (from Figure 9).



Creek, contains a presumed flock of three endemic species (*P. limaria*, *P. notidicola*, *P. umbilicata*), which closely resemble an eastern Lahontan (Squaw Valley) species. Soldier Meadows also contains an endemic species of desert dace (Nyquist, 1963). Distribution of a fourth snail (*P. militaris*) belonging to this local group implies earlier drainage integration between Soldier Meadows and Alvord Basin to the north (Figure 10a), which in turn had (at least temporarily) a pluvial connection with the Snake River basin during the late Pleistocene (Lindberg and Hemphill-Haley, 1988). Snail transfer also could have been mediated through intervening Summit Lake basin, which Mifflin and Wheat (1979:27, 30) suggested had a complex Quaternary history that included intervals of drainage to Soldier Meadows and Alvord Basin. Note that Soldier Meadows springs are associated with a lineament extending through the Alvord Basin, which Garside and Schilling (1979:38–39, fig. 28) interpreted as a fault trace.

In addition to the endemic faunas described above, the Lahontan Basin harbors scattered locally endemic species. Of particular note is *P. nevadensis*, which lived in several western Lahontan lakes but is now probably extinct (Hershler, 1994). This snail is closely similar to *P. archimedis* from Klamath Lake basin, and the implied historical drainage relationship between these areas is part of the fish-hook track described by Taylor (1960, fig. 1; 1985, fig. 17) for these and other species having similar shell sculpture. We are not confident, however, that other components of this track, consisting of fossil taxa from the Snake River region and southern California, are closely related to these living species because development of carinate shell sculpture has been subject to homoplasy in this group (Hershler, 1994, 1998).

Several widespread snails also reflect considerable past connectivity of drainage in the Lahontan region. *Pyrgulopsis wongi*, discussed above, lives in both the Carson River and East Walker River basins (Figure 8a). *Pyrgulopsis longiglans* (Figure 10a) is distributed in a north–south manner in the western portion of the Lahontan Basin (overlapping the Black Rock Desert) whereas *P. sadai* (Figure 10a) is distributed in a similar fashion in the central Lahontan area (overlapping the Reese River and the middle Humboldt subregions). Distribution of this species also implies prior drainage integration between the Lahontan Basin and the Snake River basin in northeast Nevada, although the single locality in the Snake River drainage (at the base of the Santa Rosa Range) is suggestive of a headwater transfer. The distribution of *P. eremica* (Figure 10a) in the western Lahontan Basin conforms to interpretations that Eagle Lake and Horse Lake basins (north of Honey Lake Valley), both of which contained pluvial lakes, overflowed to Lake Lahontan (Gester, 1962; Snyder et al., 1964; Morrison, 1991). In the Eagle Lake basin, this snail lives along Willow Creek, which may have drained pluvial Lake Acaps’kati to the south before the damming caused by Quaternary basalt flows (Gester, 1962). *Pyrgulopsis gibba* lives throughout much of the western Lahontan Basin, including all of the subregions of endemism (Figure 10b). Distribution of this snail implies past connections be-

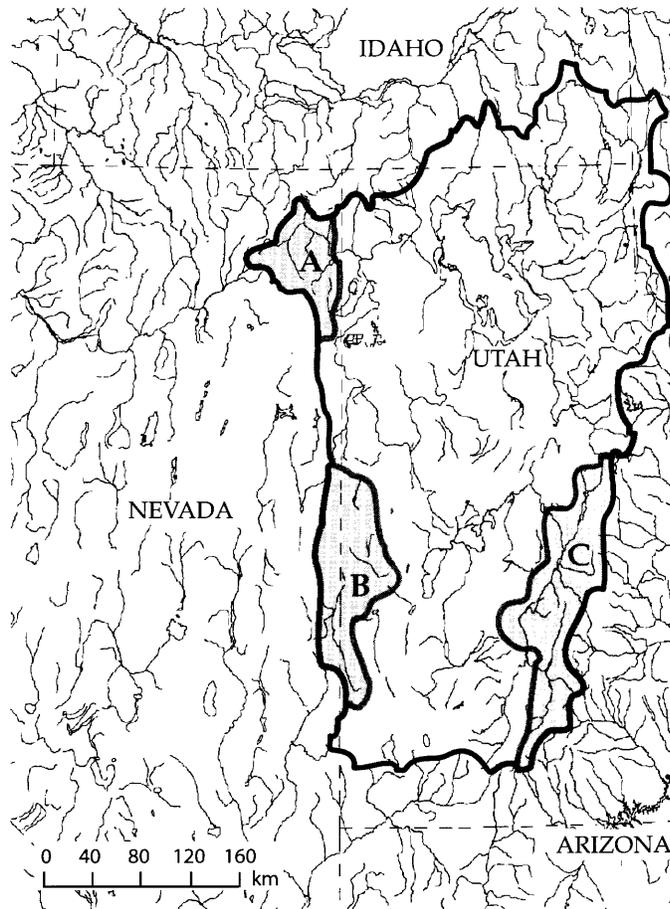


FIGURE 11.—Regions of endemism by *Pyrgulopsis* within the Bonneville Basin. A, Thousand Springs basin (includes Pilot Creek, Tecoma, and Thousand Springs Valleys); B, Snake Valley (includes Hamlin and Snake Valleys); C, upper Sevier River basin (extending to Sevier Bridge Reservoir above Gunnison; exclusive of the West Fork Sevier River below Piute Reservoir). The heavy line shows the boundary of the Bonneville pluvial drainage system.

tween the Lahontan Basin, several closely proximate Nevadan valleys (Big Smokey, Dixie, Granite Springs, and Grass Valleys), and the “Oregon Lakes” region, although the northern component of this distribution also may be attributed to drainage disruption caused by tens of kilometers of right-lateral slip (Miocene to Holocene) along the Eugene–Denio fault zone (Lawrence, 1976).

**BONNEVILLE BASIN.**—Taylor and Bright (1987) previously discussed the aquatic molluscan biogeography of this region (although not focusing on *Pyrgulopsis*), which constitutes the largest drainage unit in the Great Basin. The Bonneville Basin harbors 17 species of *Pyrgulopsis*, 14 of which are endemic. This basin also contains eight endemic species of fishes (Smith, 1978). The *Pyrgulopsis* fauna is very distinct from that of the Lahontan Basin (paralleling that of fishes), and only a single species ranges across both regions. Endemic species are concentrated in three subregions (Figure 11), of which only the Snake Valley (along the Nevada–Utah border, east of the Snake

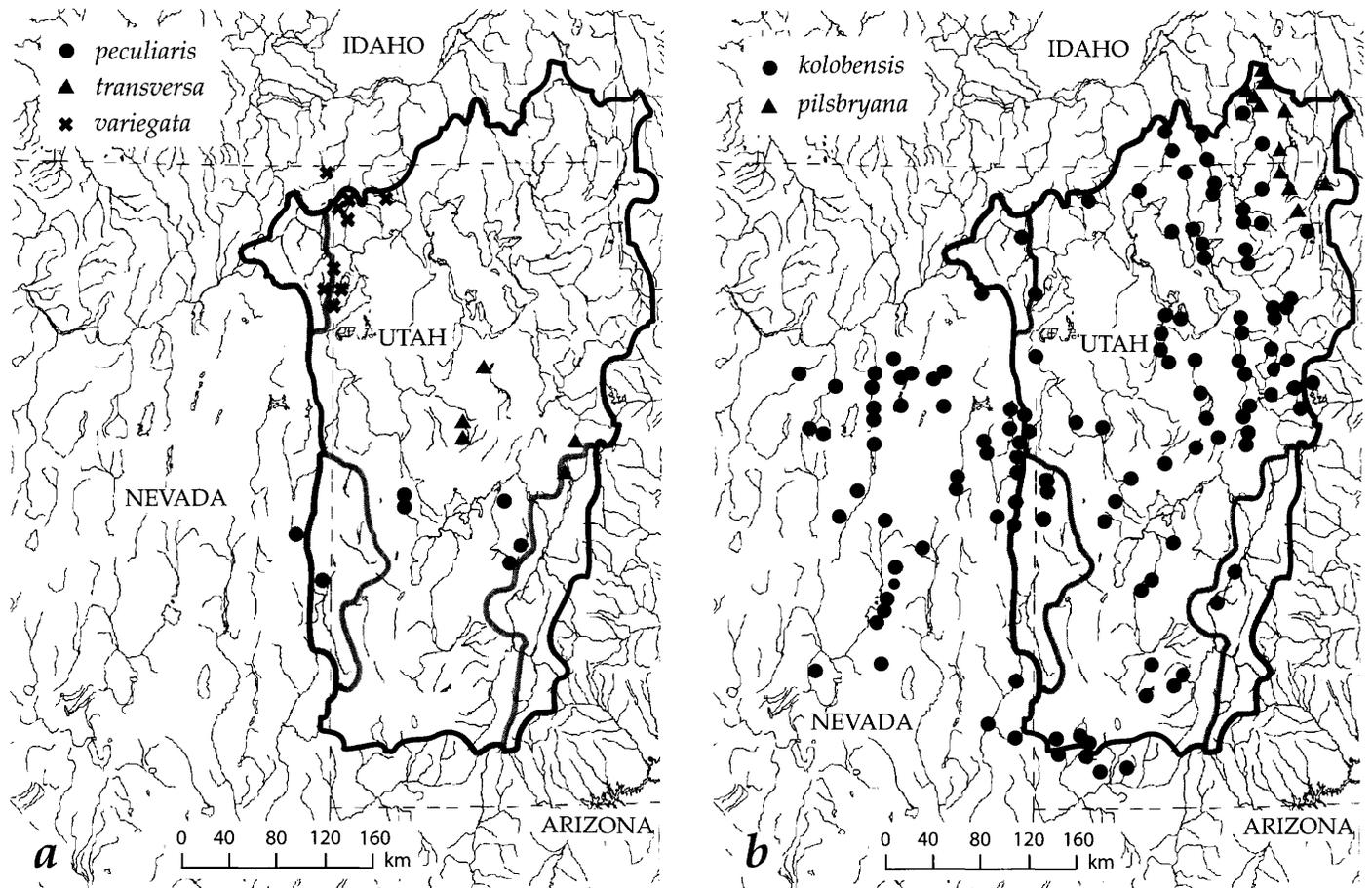


FIGURE 12.—Distributions of selected *Pyrgulopsis* species of the Bonneville Basin: a, *P. peculiaris*, *P. transversa*, *P. variegata*; b, *P. kolobensis*, *P. pilsbryana*. Shading indicates regions of endemism (from Figure 11).

Range; not to be confused with the Snake River basin to the north) contains other endemic biota.

The Thousand Springs subregion harbors five species, including three endemics (*P. hovinghi*, *P. lentiglans*, *P. millenaria*) distributed along segments of the Thousand Springs Creek drainage. Although relationships of these endemic snails are uncertain, the distribution of another snail, *P. variegata* (Figure 12a), suggests a prior drainage relationship existed with an adjacent portion of the northwest Bonneville Basin and Goose Creek, which is in the Snake River basin to the north. Physical evidence also suggests that Goose Creek was part of the Bonneville drainage basin before the late Miocene drainage reversal that was associated with passage of the Yellowstone Hot Spot (Hildebrand and Newman, 1985; Rodgers et al., 1991).

Three species are locally endemic in the Snake Valley subregion (see Figure 11). One of these, *P. hamlinensis*, is closely similar to *P. montana*, which lives in the uppermost portion of Meadow Valley Wash (a disrupted segment of Colorado River drainage) just over the White Rock Mountain divide to the west. Distributions of these species may reflect past historic upland stream capture between these drainages. *Pyrgulopsis*

*saxatilis* is most similar to a species from the White River valley to the west (*P. lata*), whereas the third endemic, *P. anguina*, is most similar to *P. chamberlini* from the Sevier River basin to the east. Prior drainage integration with areas to the west and east is also implied by the distribution of *P. peculiaris* (Figure 12a), which lives in the Snake Valley as well as in the lower segment of the Sevier River basin and the isolated Spring Valley in eastern Nevada. Five species are endemic in the upper segment of the Sevier River basin in southern Utah, confirming the distinctiveness of this fauna as noted by Taylor and Bright (1987). Affinities of these species imply prior historical relationships with other segments of the Bonneville Basin, as does the distribution of *P. transversa* (Figure 12a).

The distribution of *P. kolobensis* suggests extensive prior connectiveness of Bonneville Basin drainage (this snail overlaps all three subregions of endemism) as well as integration with the eastern Lahontan Basin, isolated valleys situated between these two regions, and the Colorado River basin (Figure 12b). (This snail exhibits considerable morphological differentiation across its broad range and almost certainly represents a species complex.) Past integration with the Colorado River ba-

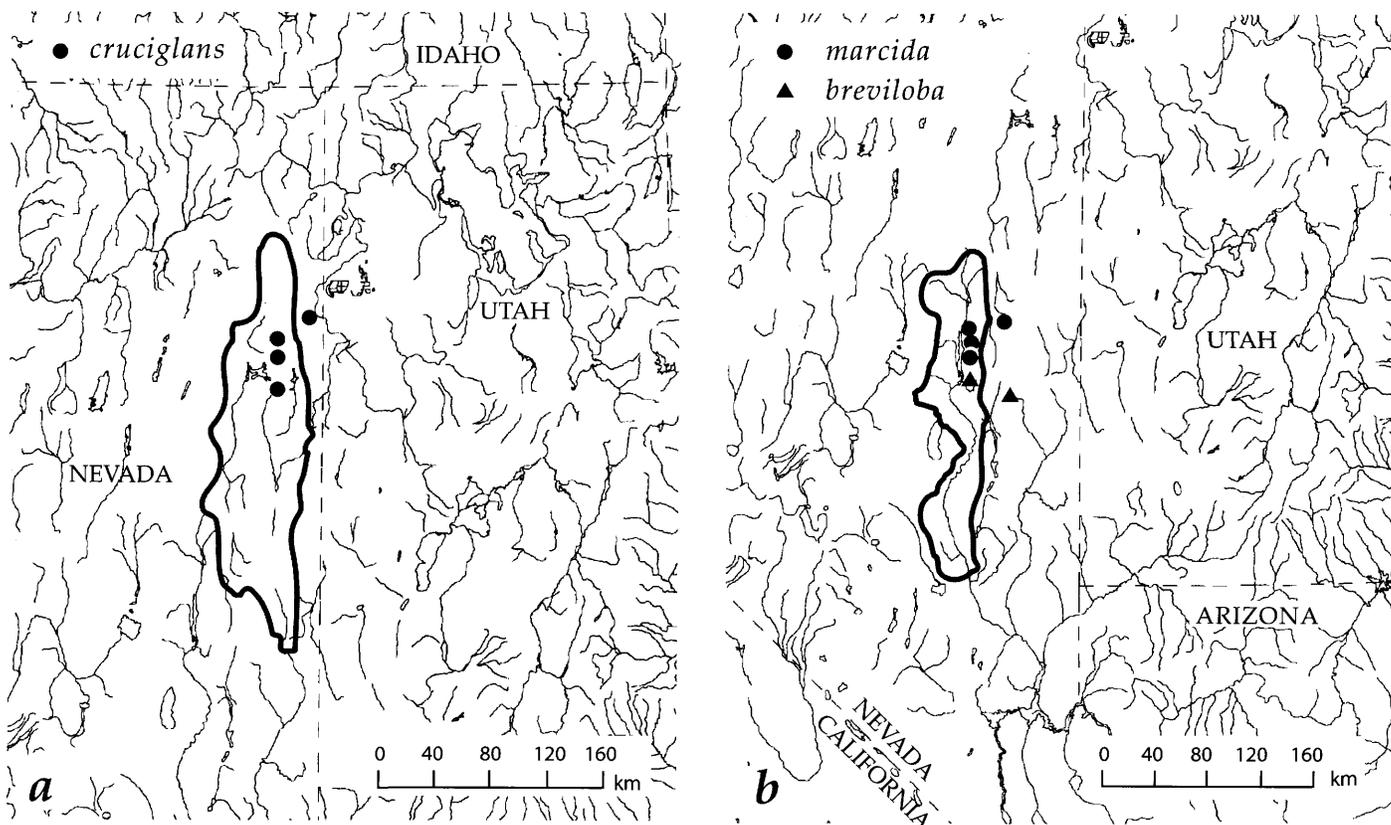


FIGURE 13.—Distributions of selected *Pyrgulopsis* species in Steptoe Basin (a, *P. cruciglans*) and in the upper White River basin (b, *P. marcida*, *P. breviloba*). The heavy lines show the boundaries of these drainage basins.

sin (in southern Utah) probably represents headwater transfers, for which there is also ichthyological evidence (Hubbs and Miller, 1948:29–30) as well as physical evidence (Averitt, 1962; Anderson and Mehnert, 1979). Undescribed material (USNM collection) from the Snake River basin of southeast Idaho is closely similar to or possibly conspecific with this snail, conforming with the physical record of early southerly drainage of southeast Idaho basins (Ore, 1982; Bobo, 1991; Osier, 1995).<sup>10</sup> The distribution of *P. pilsbryana* reflects integration of the Bear Lake and Bear River basins (Figure 12b) and is noteworthy in that this snail does not range below the Oneida Narrows, which comprised the divide between pluvial Lake Thatcher and the Bonneville Basin (Bright, 1963).

**STEPTOE BASIN.**—This large Nevadan basin (which includes Antelope, Goshute, Spring, and Steptoe Valleys) contains eight species, six of which are endemic. Endemic species are concentrated in the northern and southern segments of this drainage, and only the widespread *P. kolobensis* lives in both areas. Five of the endemic species are localized in a large basin floor spring province along the east flank of the Egan Range north of Ely. These snails are united by several unique features and probably represent a species flock, the affinities of which are not clear. The distribution of *P. cruciglans* in the northern segment of Steptoe Basin (Figure 13a) and in the adjacent western

Bonneville Basin is enigmatic because shorelines indicate that although pluvial Lake Waring was relatively deep, its high stand was well below basinal sills, and it did not integrate with Lake Bonneville during the late Pleistocene (Hubbs et al., 1974; Currey et al., 1984). Note that the sole native fish living in the Steptoe Basin, *Relictis solitarius*, does not cross the Bonneville divide but instead ranges to the west and south (Butte and Ruby Valleys; Hubbs et al., 1974; Deacon and Williams, 1984).

**UPPER WHITE RIVER BASIN.**—This large area includes Pahranaagat and White River Valleys (above Pahranaagat Wash) but excludes Moapa Valley (the lowermost segment of the White River basin), which maintains external drainage to the Colorado River basin. DiGuseppi and Bartley (1991) suggested that the White River drainage was internally drained before capture by the Colorado River during the Quaternary. This region contains eight species (five endemic); this fauna neither overlaps nor shows affinities with the two species living in Moapa Valley, which instead have affinities with snails in the Amargosa River basin (*P. avernalis*) and Colorado River basin of northern Arizona (*P. carinifera*). The upper White River basin also contains an endemic species of cyprinid fish (Miller and Hubbs, 1960). Of the endemic snails for which affinities are clear, *P. merriami* is most similar to fauna of the Rio Grande and upper

Gila River basins, whereas *P. lata* is most similar to *P. saxatilis* from the Bonneville Basin.

Distributions of two nonendemic species (Figure 13b) suggest prior relationships between the White River region and two fishless valleys to the east (Cave and Dry Lake Valleys) despite physical evidence that the pluvial lakes of these small valleys did not overflow during the late Pleistocene (Mifflin and Wheat, 1979). The distribution of *P. marcida* supports the contention of Hubbs et al. (1974:65) that, although Cave Valley appears to be part of a structural trough including Steptoe Valley to the north, Cave Valley instead probably drained early (i.e., prior to the late Quaternary pluvial period) to the White River valley. We were unable to confirm the assertion of Hubbs and Miller (1948:98) that there may be a low, alluvial saddle separating the southern portion of Cave Valley from the White River valley; maps indicate that these valleys instead are separated in this area by middle Tertiary andesite flows. The distribution of *P. breviloba* (Figure 13b) conforms to an interpretation (Hubbs and Miller, 1948:98) that Dry Lake valley (therein referred to as Bristol Valley) may have drained early, south to the White River valley via Delamar Valley. Drainage integration between these valleys may have been disrupted by significant late Cenozoic lateral slip along the northeast-trending Pahrangat Fault Zone (Rowan and Wetlaufer, 1981; Jayko, 1990).

**RAILROAD BASIN.**—Railroad Valley in south-central Nevada is closed to the east, north, and west principally by the Grant, White Pine, and Pancake Ranges, respectively, but it opens to the southwest into a large basin comprising Reveille, Hot Creek, and Little Fish Lake valleys (Figure 6). Mifflin and Wheat (1979:30) suggested that Big Sand Springs Valley also may have opened southeast to Railroad Valley before the Late Quaternary emplacement of the Lunar Crater Volcanic Field (see Scott and Trask, 1971; Luedke and Smith, 1991). The northern segment of Railroad Valley harbors six endemic species of *Pyrgulopsis*, and widespread *P. kolobensis* also occurs locally, both in Railroad and Reveille Valleys. Four of the local endemics—*P. aloba*, *P. carinata*, *P. lockensis*, *P. papillata*—belong to a group represented in western California and the Lahontan Basin, northern Bonneville Basin, Snake River basin, and Colorado River basin. Three of these snails compose a morphologically distinct subgroup confined to thermal limnocrenes.

**DIXIE BASIN.**—This large, Nevada basin includes Buffalo, Buena Vista, Dixie, Edwards Creek, Fairview, and Pleasant Valleys. It contains two dissimilar endemic species—*P. aurata*, *P. dixensis*—that closely resemble other Lahontan forms. The only endemic fish in this drainage is an undescribed subspecies of *Gila bicolor*, which Hubbs and Miller (1948) suggested was closely related to Lahontan taxa. In support of these connections, Reheis et al. (2002) infer that a high stand of Lake Lahontan flooded into Dixie Basin during the middle Pleistocene.

**OREGON LAKES.**—*Pyrgulopsis* is poorly represented in this large region, which consists of a series of valleys and pluvial lakes in northeast California and southeast Oregon. Only four

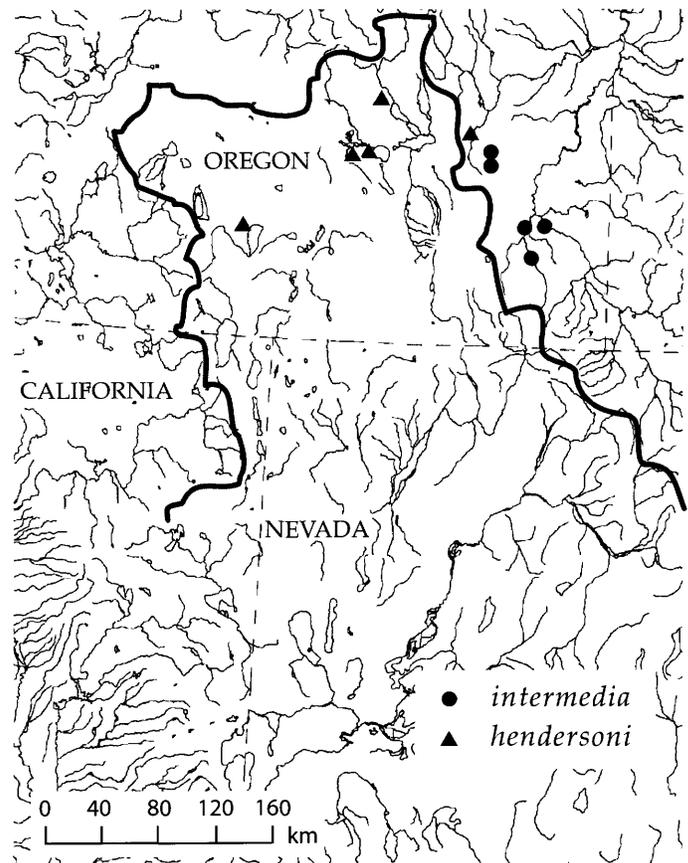


FIGURE 14.—Distributions of *Pyrgulopsis intermedia* and *P. hendersoni* of the "Oregon Lakes" region. The heavy line shows the northwest boundary of the Great Basin.

species are present, none of which are endemic, and relatively large areas (e.g., Goose Lake and Fort Rock basins) apparently lack *Pyrgulopsis*. Biogeographic patterns of these snails, nevertheless, are informative, suggesting past integration of component valleys as well as relationships with both the Lahontan Basin (as discussed above) and the Snake River basin. The distribution of *P. gibba* (Figure 10b) suggests prior integration of Long and Surprise Basins, whose pluvial lakes apparently did not overflow during the late Pleistocene (Mifflin and Wheat, 1979; Allison, 1982, respectively). The snail also lives in Coleman Valley, a small endorheic basin that Hubbs and Miller (1948:65) suggested was flooded by an arm of pluvial Lake Warner. However, Weide's (1974, fig. 19) map of the lake indicates that this did not occur in the late Pleistocene. The distribution of *P. hendersoni* (Figure 14) suggests prior integration of the widely separated Lake Abert and Malheur Lake basins, which is also suggested by the distribution of the fish *Gila bicolor* (Minckley et al., 1986). This snail also lives in springs along the Malheur River, conforming to the oft-postulated prior drainage relationship between the Oregon Lakes region and the Snake River basin (e.g., Wheeler and Cook, 1954; Taylor and Smith, 1981; disputed by Repenning et al., 1995). Shoreline

evidence suggests that pluvial Lake Malheur probably spilled east to the Malheur River (Gehr and Newman, 1978), and a similar eastward drainage through Malheur or Crane Gaps may have occurred earlier, before late-Pleistocene emplacement of lava flows (Piper et al., 1939; Bisson and Bond, 1971; Baldwin, 1976). The distribution of *P. intermedia* also suggests a prior relationship between regional drainage and the Snake River basin. This snail lives in Crooked Creek, a tributary to the Owyhee River (Snake River basin), as well as in Barren Valley, a small basin often depicted on maps as draining to the Snake River basin (e.g., Snyder et al., 1964; Williams and Bending, 1984) but which, in fact, is endorheic and seemingly a northern extension of the Alvord Basin trough. Snail populations from the Pit River and Klamath Lake basins are similar to *P. intermedia*—although probably not conspecific, as suggested by Taylor (1985:309).

### Conclusions

*Pyrgulopsis* biogeography within the Great Basin conforms in part to current interpretations of pluvial drainage configurations, but in many cases it defines additional or more complicated patterns that presumably reflect older relationships. Various drainage relationships between the Great Basin and adjacent regions also are implied by these data, although there is surprisingly little evidence of past integration between the Great Basin and the Sacramento River basin to the west and the

upper Colorado River basin to the northeast. This may partly reflect inadequate sampling of these extra-limital areas. In contrast to previous suggestions that the Great Basin had prior connections along its northeast and northwest boundaries with the Snake River basin (Taylor, 1966a, 1985; Minckley et al., 1986; Taylor and Bright, 1987), *Pyrgulopsis* biogeography suggests a more continuous pattern of northern integration.

As mentioned above, a more rigorous biogeographic analysis of *Pyrgulopsis* must await preparation of a well-corroborated phylogeny for its species, which will prove difficult using morphological criteria alone and thus will probably require the use of DNA sequence data. Determination of cladistic structure among Holocene species of this group can provide a hierarchical depiction of historical relationships among drainages, but the fossil record also must be better utilized to constrain the chronology more tightly. Given that hydrobiids are difficult to identify at the species and, often, generic ranks based on traditional shell characters, new methods will be needed to extract a phylogenetic signal from fossils, perhaps from details of shell structure or composition of preserved organic shell components. Ecological characteristics of fossil *Pyrgulopsis* also must be better understood if we are to determine, for instance, whether interbasinal patterns reflect vicariance of pluvial lake biota or transmontane headwater transfers. This information may perhaps be obtained from a combination of environmentally sensitive isotopes preserved in shell fabric and more detailed study of sedimentary facies.

## Appendix

### Species Groups of *Pyrgulopsis*

The informal groups described below are defined mostly by characters of penial form and ornament. We follow the terminology of Hershler, 1994.

1. A small number of species, mostly from the Great Basin, share a simple penis bereft of distal lobe and glands (Figure 4a). These snails otherwise closely resemble typical *Pyrgulopsis*, and a close relationship is inferred, although separate generic status for some or all of these may be suggested upon cladistic analysis. Subgroups are discernable on the basis of shape of shell and penial filament. Species included are *aloba*, *augustae*, *carinata*, *coloradensis* (Virgin River basin), *dixensis*, *eremica*, *greggi* (Kern River basin), *lockensis*, *millenaria*, and *papillata*.
2. Snails of this group have a glandular ornament of a single, superficial ventral unit (Figure 4b). This gland differs in appearance from the narrow, raised ventral gland typical of *Pyrgulopsis* and resembles that of eastern American *Birgella* (Thompson, 1984, figs. 81, 82) and *Rhapinema* (Thompson, 1970, fig. 3D,E). With the exception of *P. arizonae*, the snails of this group also lack a penial lobe, per-

haps indicating a close relationship with the group described above. Subgroups are recognizable on the basis of shell shape and gland position and size. Species included are *arizonae* (Gila River basin), *avernalis* (Colorado River basin), *basiglans*, *bernardina* (Río Yaqui basin), *bifurcata*, *crystalis*, *erythropoma*, and *pisteri*.

3. A large number of species share a relatively narrow, distally bifurcate penis ornamented with a terminal gland along the distal edge of the rather small lobe (Figure 4c). Other dorsal glands are absent in these snails, although some species have a single ventral gland. The terminal gland is often oriented longitudinally rather than transversely, as in groups described below. In some species the terminal gland is weakly developed (e.g., *stearnsiana*) or often absent (*bryantwalkerii*). This group conforms in large part to the "*Fontelicella stearnsiana* series" described by Taylor (1987:10). Subgroups are recognizable on the basis of shell shape, shape of penial lobe and filament, and development of the terminal gland. Species included are *amargosae*, *aurata*, *bacchus* (Colorado River basin), *brandi* (Río Casas Grandes basin), *breviloba*, *brunEAUensis* (Snake River basin), *bryantwalkerii*, *carinifera* (Colorado River basin), *conica* (Colo-

rado River basin), *fairbanksensis*, *hamlinensis*, *hubbsi*, *imperialis*, *isolata*, *lentiglans*, *manantiali* (Cuatro Ciénegas basin), *micrococcus*, *montana*, *morrisoni* (Verde River basin), *nanus*, *nonaria*, *sathos*, *simplex* (Verde River basin), *sola* (Verde River basin), *stearnsiana* (California coastal drainage), *thompsoni* (Gila River basin), and *transversa*.

4. A medium-sized group comprises species in which the outer edge of the dorsal penis has an elongate gland (Dg1) abutting or slightly overlapping the filament (Figure 4d). Penial ornament in this group is otherwise variable, although most species have a terminal gland, ventral gland, and sometimes additional dorsal glands. The penial lobe of these snails often is enlarged relative to the filament. This group includes the large snails allocated to the subgenus *Natricola* Gregg and Taylor, 1965, except for *intermedia*. Species included are *glandulosa* (Verde River basin), *hendersoni*, *hovinghi*, *idahoensis* (Snake River basin), *inopinata*, *montezumensis* (Verde River basin), *pecosensis* (Rio Grande basin), *pellita*, *robusta* (Snake River basin), and *sublata*.
5. Another large group consists of snails in which the penis has a short penial gland at the base of the filament and generally no other dorsal glands other than a terminal gland and occasionally a ventral gland (Figure 4e). Subgroups are recognizable on the basis of shell sculpture, shape of penial lobe and filament, development of terminal gland, presence of additional dorsal glands, and position of ventral gland. Species included are *anatina*, *archimedis* (Klamath Lake basin), *diablensis* (Sacramento River basin), *fusca*, *humboldtensis*, *kolobensis*, *lata*, *leporina*, *limaria*, *longae*, *marcida*, *militaris*, *nevadensis*, *notidicola*, *pictilis*, *pilsbryana*, *saxatilis*, *serrata*, *sterilis*, *taylori* (California coastal drainage), *trivialis* (Gila River basin), *turbatrix*, *umbilicata*, *variegata*, and *vinyardi*.
6. Six species have a penis with a well-developed terminal gland, a ventral gland, and a weakly developed additional dorsal gland corresponding to Dg1 (Figure 4f). Species

included are *aardahli*, *gibba*, *giulianii*, *owensensis*, *perturbata*, and *ruinosa*.

7. The five species locally endemic in southwestern Steptoe Valley are united by strong protoconch microsculpture, a broadly conical or subglobose shell, and unique features of the central radular teeth (fused lateral cusps, basal cusps absent or very weakly developed, elongate basal tongue). Although penial form and ornament varies considerably among these species, we nevertheless interpret the group as a strongly differentiated clade based on the synapomorphic radular features. Species included are *landyei*, *neritella*, *orbiculata*, *planulata*, and *sulcata*.
8. Two Great Basin species share a distinctive pattern of penial ornament consisting of a large, raised, proximal dorsal unit (Figure 4g). These species are *cruciglans* and *plicata*.
9. A large number of species share a massive penis having a long gland on the dorsal surface of the penial filament (Pg); typically they also share a terminal gland (typically transverse, and often U-shaped), one or two ventral glands, and one or more additional dorsal glands (Figure 4h). Members of this group usually have an enlarged, pyriform bursa copulatrix and a narrow bursal duct. The seminal receptacle is often very small relative to the bursa copulatrix and usually is well posterior in position, broadly overlapping the bursa copulatrix. This group corresponds, at least in part, to the "californiensis series," as defined by Taylor (1987). Subgroups are recognizable from the presence of secondary dorsal glands and from the shape and multiplication of penial glands. Species included are *anguina*, *californiensis* (California coastal drainage), *chamberlini*, *chihuahua* (Rio Carmen basin), *chupadera* (Rio Grande basin), *davisi* (Rio Grande basin), *deaconi*, *deserta* (Virgin River basin), *fausta* (Colorado River basin), *gracilis*, *intermedia*, *longiglans*, *longinqua*, *metcalfi* (Rio Grande basin), *neomexicana* (Rio Grande basin), *peculiaris*, *roswellensis* (Rio Grande basin), *sadai*, *thermalis* (Gila River basin), *ventricosa* (Sacramento River basin), *villacampae*, and *wongi*.

## Notes

1. Ponder et al. (1994) suggested that passive dispersal on birds may be a significant factor in biogeography of some Australian hydrobiids.

2. Twelve eastern American species currently are allocated to the genus (Hershler and Thompson, 1987; Hershler, 1994; Thompson, 1995); recent morphological studies indicate that this fauna is a distinct clade that is not closely related to *Pyrgulopsis* (Thompson and Hershler, In press).

3. Tall-spined western Paleogene hydrobiids, usually allocated to *Hydrobia* or *Micropyrgus* (e.g., from Flagstaff Formation; La Rocque, 1960), approach the range of shell variation of modern *Pyrgulopsis*, but they probably represent other clades (Taylor, 1975).

4. Other genera in the subfamily are *Birgella*, *Cincinnatia*, *Notogillia*, *Nymphophilus*, *Rhaphinema*, *Spilochlamys*, and *Stiobia* (Thompson, 1979).

5. These and other early concepts of extent and timing of late Cenozoic uplift of the Sierra Nevada (e.g., Axelrod, 1962; Huber, 1981) have recently been dis-

puted (Small and Anderson, 1995; Wernicke et al., 1996; Wolfe et al., 1997).

6. An earlier conjecture (Hershler and Pratt, 1990:292) that all of the endemic *Pyrgulopsis* in Ash Meadows were derived from taxa in the White River Valley (whose lowermost segment is Moapa Valley) to the east was premature.

7. This refers to a distributional track encompassing the Bonneville Basin, the middle Snake River drainage, the Lahontan Basin, and the Death Valley system.

8. Nagy and Murray (1996) suggested that this drainage reversal may not have occurred before 0.5 Ma.

9. Late Cenozoic fossil Foraminifera from Panamint Valley may have lived in a saline lake instead of in an estuary (Smith, 1960).

10. Whether or not the late Pleistocene Bonneville Flood (Malde, 1968; O'Connor, 1993) also contributed to snail exchange with the Snake River basin is conjectural.

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# Anthropogenic Changes in Biogeography of Great Basin Aquatic Biota

*Donald W. Sada and Gary L. Vinyard*

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## ABSTRACT

The Great Basin, the most arid region in North America, has small, widely spaced wetlands compared with those in more mesic regions. These wetland habitats generally support aquatic taxa that are widespread throughout North America. Recent work has complemented the studies of endemic fishes by Carl Hubbs and Robert Miller and has served to identify a diverse fauna of insects and mollusks endemic to the Great Basin. The presence of this fauna in comparatively small wetlands shows that habitat size is not a good indicator of the importance of these wetlands to unique biological communities.

Historical and current records show that anthropogenic activities during the last 120 years have modified the structure of Great Basin aquatic communities by altering habitats and by the translocation of species. Fifty nonnative fish taxa and several invertebrate taxa have been introduced into the region by the public and/or by fishery management agencies. Twenty-four fish taxa endemic to the Great Basin also have been translocated into habitats both within and outside of their native range. Most of these translocations were undertaken to create refuge populations and, thus, to reduce the possibility of extinction.

Within the Great Basin, introductions of nonnative species and habitat modification have caused the extinction of 16 endemic species, subspecies, or other distinctive populations (12 fishes, three mollusks, and one aquatic insect) since the late 1800s. Declines in abundance or distribution were attributable (in order of decreasing importance) to water flow diversions, competitive or predatory interactions with nonnative species, livestock grazing, introductions for sport fisheries management, groundwater pumping, species hybridization, timber harvest, pollution, recreation, and habitat urbanization. Most affected taxa were influenced by more than one of these factors.

The temporal pattern of decline in endemic taxa was examined by determining the calendar decades of first population loss, of major decline (loss of one-half of either a taxon's distribution or abundance), and of extinction for 199 endemic taxa (102 fishes, 85 mollusks, nine aquatic insects, two amphibians, and one fairy shrimp). Population loss has affected approximately 50 percent of taxa for which information was available (135 distinct taxa: 99 fishes, 24 mollusks, and all taxa in the three other aquatic animal groups), and 58 percent of these taxa have suffered major declines. Differences among rates of population loss, major decline, and extinction were not significant (ANCOVA,  $p > 0.05$ ). Declines and extinctions were first recorded in the late 1800s. Rates peaked first after World War I and again in the 1970s after a long increase that began after World War II. Status was comparatively static during both World Wars. This pattern indicates that declines can be attributed to regional economic conditions and increased immigration. Declines slowed in the 1980s and 1990s because most taxa had previously declined, not because threats had diminished.

Declines during the last 120 years have been greatest in the most narrowly distributed and vulnerable populations. All extinct taxa and most taxa suffering major declines (68 percent) had fewer than five populations. If past trends continue into the future, additional extinctions will occur (primarily in narrowly distributed taxa), and extinctions also may begin to affect widespread taxa. These changes will accompany environmental change that characterizes consumption patterns of increasing human populations. Avoiding future changes in Great Basin biogeography that result from declines in taxon status will require new, innovative programs that protect wetland habitats from environmental degradation and the deleterious effects of nonnative species while allowing appropriate human uses of wetland resources.

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## Introduction

The Great Basin, the driest physiographic province in North America, contains fewer small rivers, lakes, streams, springs, and marshes than do more mesic regions, and all of these waterbodies are more widely dispersed in the Great Basin than elsewhere. Aquatic communities in the region include species common to other North American wetlands as well as a diverse fauna of endemic fishes, mollusks, and aquatic insects predominantly associated with springs. Although these unique characteristics have long been recognized (Gilbert, 1893; Brues,

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1932), recent surveys have revealed a surprisingly high diversity of additional endemic macroinvertebrates (e.g., Hershler and Sada 1987; Shepard, 1990; Hershler, 1998). We examine herein the major causes of historical change in biodiversity in an effort to understand the predominant ways in which anthropogenic uses of wetlands have affected Great Basin biogeography.

Humans have used Great Basin wetlands since the early Holocene (Janetski and Madsen, 1990). Intermittent settlement near wetlands and daily activities of hunting and gathering naturally tended to focus upon the biotic resources concentrated at these habitats. For a short period before the region was settled by European immigrants, a few indigenous tribes also diverted water to irrigate land and increase production of commonly eaten native plants. The Fremont Tribe diverted water from large rivers near the Wasatch Range (Madsen, 1989), and the Owens River basin Paiutes diverted streams from the east flank of the Sierra Nevada (Steward, 1933). Great Basin wetlands also produced food organisms, such as *Cyprinodon radiosus* (Owens pupfish), *Catostomus tahoensis* (Tahoe sucker), *Chasmistes cujus* (cui-ui), *Oncorhynchus clarki henshawi* (Lahontan cutthroat trout), *Gila bicolor* (tui chub), and *Ephydra hians* (brine fly), which were eaten by Paiutes along the eastern Sierra Nevada (Steward, 1933; Knack and Stewart, 1984). Excavation of sites known to have been inhabited by Fremont Tribe members revealed that their diet included *Catostomus ardens* (Utah sucker), *Gila atraria* (Utah chub), and *Oncorhynchus clarki utah* (a cutthroat trout subspecies) (Janetski, 1990). Greenspan (1990) also documented fish remains from archaeological sites in the Great Basin of Oregon, and Drews (1990) reviewed the dietary role of Great Basin shellfishes.

Although Native Americans used and altered Great Basin wetlands, the major anthropogenically induced changes to aquatic biogeography accompanied habitat alterations and introductions of nonnative taxa during the last 120 years. Since the beginning of the twentieth century, most rivers in the region have been dammed and diverted for irrigation, flood control, or power generation (La Rivers, 1962; Sigler and Sigler, 1987). Many springs and streams have been modified by livestock grazing, water flow diversion, and groundwater use (see Miller, 1961; Dudley and Larson, 1976; Fleischner, 1994). Native aquatic biota also have been affected by the introduction of 50 nonnative fish species for sport, pest management (Sigler and Sigler, 1987), and unspecified recreational or commercial interests (Moyle, 1984). Fisheries management agencies have enhanced nonnative sport fish populations by poisoning thousands of miles of streams, causing the consequent reduction or elimination of native fish and macroinvertebrate populations (Moyle et al., 1986; Rinne and Turner, 1991; Andersen and Deacon, 1996). These habitat modifications and introductions have caused the decline of many populations of native taxa and have driven some species to extinction (Minckley and Deacon, 1968; Williams et al., 1985; Miller et al., 1989; Minckley and Douglas, 1991).

The changing status of fishes and their habitats have been reported as discrete events affecting localized habitats or individual taxa (e.g., Williams et al., 1985; Williams et al., 1989; Moyle et al., 1995). The status of endemic invertebrates and the effects of human activities on smaller aquatic habitats (e.g., springs not occupied by native fishes) have not been examined in detail. We assess herein how habitat modifications and species translocations have affected Great Basin aquatic biogeography by altering the historical distribution of endemic species. This information was then used to examine the temporal pattern of past changes as a means of providing insight into potential future changes in the biogeography of aquatic animals endemic to the Great Basin.

### Habitat and Biotic Diversity

Taxonomic studies during the last 140 years have consistently increased recognition of endemic plants and animals in Great Basin wetlands (see Hubbs and Miller, 1948a; Hershler, 1998). Although many taxa have been described, a number of additional populations may qualify for recognition as either endemic species or endemic subspecies (see Hubbs et al., 1974; Deacon and Williams, 1984; Sada et al., 1995; Hamlin, 1996). Recent descriptions of mollusks and insects (e.g., Hershler and Sada, 1987; Shepard, 1990; Hershler, 1998) indicate that additional undiscovered aquatic macroinvertebrates in Great Basin springs may exist. Currently, 118 species (two amphibians, 23 fishes, 84 mollusks, eight insects, and one fairy shrimp) and 45 subspecies (one aquatic insect and 44 fishes) are endemic to the Great Basin. We also studied 36 additional endemic forms that have been identified in published and unpublished reports as morphologically or genetically distinct. All of these described and undescribed forms will be collectively referred to herein as "distinctive taxa."

Distinctive taxa occupy a wide diversity of habitats including rivers, lakes, and streams, as well as cold and thermal springs (La Rivers, 1962; Sigler and Sigler, 1987; Hershler, 1998). Most of these taxa occupy habitats below 2200 m in elevation, where wetlands are most common and the historical use of water by humans has been greatest. Most distinctive taxa occupy specific habitats. Several taxa are primarily lentic but require lotic habitats for spawning (e.g., *Catostomus warnerensis*, *Chasmistes cujus*, *Chasmistes liorus*), and some continuously inhabit both lentic and lotic habitats (e.g., *Catostomus ardens*, *Richardsonius egregius*). Others only inhabit thermal springs (e.g., *Cyprinodon diabolis*, *Eremichthys acros*, *Gila boraxobius*, *Pyrgulopsis militaris*) or cold springs (e.g., *P. ruinosa*, *P. wongi*). *Cyprinodon radiosus* and *Lotichthys phlegethontis* occupy both lentic and spring habitats. Most endemic macroinvertebrates are restricted to springs, but several are lentic (e.g., *P. nevadensis*, *Capnia lucustra*, *Artemia monica*). The primary habitats of most distinctive taxa are springs (153 taxa), followed by lotic (18 taxa) and lentic (10 taxa) habitats; 10 taxa are lentic species that require lotic spawning habitat; and eight

taxa are equally abundant in both springs and streams (see Appendix). Many habitats are occupied by a single endemic, and many habitats support several endemics. Communities with the highest diversity of endemics are concentrated in thermal springs of southern Nevada (e.g., Ash Meadows, Pahranaagat Valley), which support endemic fishes, mollusks, and aquatic insects (Hershler and Sada, 1987; U.S. Fish and Wildlife Service, 1990; Polhemus and Polhemus, 1994; Hershler, 1998).

The unique aspects of these wetland communities are not limited to the aquatic animals inhabiting them. Great Basin wetlands of Nevada and southeastern Oregon also support 19 endemic plant species and five endemic plant varieties (Nevada Heritage Program Data Base, unpublished; Oregon Heritage Program Data Base, unpublished); four endemic vole subspecies—namely, *Microtus californicus vallicola* (Owens vole), *M. c. scirpensis* (Amargosa vole), *M. montanus fucosus* (Pahranaagat vole), and *M. m. nevadensis* (Ash Meadows vole)—inhabit southern Nevada and southern California wetlands (Bailey, 1898; Hall, 1946). No endemic plants or mammals, however, are known from wetlands in the Utah portion of the Great Basin.

### Introductions and Translocations

Many nonnative species have been introduced into North American waters, and these introductions have changed the structure of native vertebrate and invertebrate communities and caused extinctions of native biota through predation, hybridization, and competition (see Courtenay and Stauffer, 1984; Mooney and Drake, 1986; Moyle et al., 1986; Johnson and Padilla, 1996). Nonnative aquatic species in the Great Basin were introduced from other parts of North America and from Europe, Asia, Africa, and South America (Deacon and Williams, 1984; Sigler and Sigler, 1987). Many of these introduced species are now widespread, and most Great Basin fish assemblages are dominated by nonnative taxa. Deacon and Williams (1984) and Sigler and Sigler (1987) identified 50 nonnative fish taxa in the region, which exceeds the number of native Great Basin fish taxa (43 species). Most intentional introductions were made to accommodate the recreational sport-fishing industry, but some fishes were introduced as biological control agents. Some fish species were released from home aquaria, and others escaped from commercial aquaculture facilities (Courtenay et al., 1985; U.S. Fish and Wildlife Service, 1997a).

Little is known about nonnative invertebrate introductions; several introduced species, however, have become widespread in the region, including *Procambarus* sp. and *Pacifastacus lenusculus* (crayfishes), *Corbicula manilensis* (Asian clam), and *Thiara* (= *Melanoides*) *tuberculata* (red-rimmed thiara, a snail). Crayfish introductions may have reduced refuge populations of *Cyprinodon radiosus* (U.S. Fish and Wildlife Service, 1998a); *T. tuberculata* may have contributed to declines in springsnail populations in southern Nevada (Hershler and Sada, 1987); and

the disappearance of *Anodonta californica* (California floater, a bivalve mollusk) from the Owens River basin may have been caused by *Corbicula manilensis*. Disappearance of *Daphnia* sp. (ostracode) from Lake Tahoe is attributed to the introduction of *Mysis relicta* (oppossum shrimp) (Richards et al., 1975; Morgan et al., 1978).

No private or state programs exist to translocate endemic Great Basin macroinvertebrates or amphibians, and no records indicate that these species have been translocated. However, several state and Federal programs have actively translocated 24 endemic Great Basin fishes into refuges both within and outside of their native ranges (Appendix). Most fishes were translocated to expand their distributions and minimize threats, thus reducing the possibility of extinction. Other translocations were conducted to enhance sportfishing opportunities (e.g., *Oncorhynchus clarki henshawi*). Some species were established in single refuges whereas others have been broadly introduced (e.g., *O. c. henshawi* into 33 refuges). Some of these translocations probably prevented imminent extinction (e.g., *Cyprinodon radiosus*, *Empetrichthys latos latos* (Pahrump poolfish), and *Crenichthys baileyi grandis* (Hiko White River springfish)).

Refuge populations may influence biogeography in several ways. They may expand distributions and confound future biogeographic interpretations. Also, many refuges have been established with very few individuals, which presumably represents a comparatively small portion of the genome of the species. These factors suggest that caution should be used when interpreting biogeographic information accumulated from refuge populations. In addition, refuge construction may adversely affect other native taxa. Hershler (1989) reported that *Pyrgulopsis perturbata* (Fish Slough springsnail) disappeared from a spring that had been impounded to create a refuge for *Cyprinodon radiosus*. Effects of refuge development probably have been greatest when construction modified a previously unaltered habitat (e.g., channelized or impounded spring brooks), thus causing functional changes in the aquatic ecosystem's community structure.

### Status Changes

We sought to determine the extent of decline for all aquatic taxa endemic to the Great Basin. Status information was gathered from personal communications and from approximately 100 published and unpublished survey reports (undertaken within the private sector and by federal and state agencies) written during the last 120 years. Early records were first prepared before widespread settlement of the region (Frémont, 1845; Beckwith, 1855; Merriam, 1893; Davidson, 1976), and they frequently have been used to compare historical and current distributions of most taxa. Distributional information was also gathered from early taxonomic surveys (e.g., Gilbert, 1893; Hubbs and Miller, 1948a). Most information provided by early records is less comprehensive than that from contemporary

records, which frequently describe demography and distribution of extant populations. Early records, however, usually provide baseline distributional information that can be effectively contrasted with current distributions.

For each distinctive taxon, we identified the year in which taxonomic distinction was initially recognized. We then sought to determine the calendar decade(s) in which three possible levels of decline had occurred (if any): the first population loss (loss of first population, i.e., reduced distribution and absolute abundance), a decrease in historical distribution or absolute abundance by at least one-half (a "major decline"), and extinction. Factors that affected the status of each taxon (i.e., threats, when known) were also identified.

All known distinctive aquatic taxa in the Great Basin were considered: 102 fishes, 85 mollusks, nine aquatic insects, two amphibians, and one fairy shrimp. Status surveys, however, had not been conducted for all distinctive taxa (surveys have assessed the status of few recently described taxa), thus status could be reviewed for only 135 taxa—99 fishes, 24 mollusks, and all taxa in the three other aquatic animal groups. By determining the year that each distinctive taxon was identified, we could assess the relationships between changes in status and taxonomic recognition. These dates often predated formal taxonomic descriptions, and they were selected for analysis because Federal and state agencies frequently have initiated status surveys soon after distinctive populations were identified. Relationships between status changes and recognition of distinction may facilitate our understanding of temporal trends in status change. Positive correlation between these factors may indicate that status changes occur quickly after recognition of distinctive taxa. Either a negative correlation or the absence of correlation may suggest that decline rates occur sporadically, regardless of when distinctiveness is recognized. Data for each distinctive taxon are summarized in the Appendix.

The information provided by these records has limitations. Surveys usually have been qualitative, and status changes are rarely quantified. It is also difficult to precisely identify when populations disappeared or declined because surveys have been sporadic as a result of budget limitations and changing agency priorities. Taxonomic studies have also revealed many endemic taxa (approximately 90 mollusks and aquatic insects since 1990) that were uncollected and undescribed until recently (e.g., Shepherd, 1992; Hamlin, 1996; Hershler, 1998). Many of these populations occupy springs that are in poor condition, and traditional human uses of these wetlands have caused several taxon extinctions and population losses in the last five years (Sada and Nachlinger, 1996; Hershler, 1998). Although it is not possible to determine how many extinctions of uncollected taxa have occurred, recent extinctions and population losses suggest that current status information may underestimate the total number of historical Great Basin extinctions. Despite of these limitations, adequate status information was obtained for a sufficient number of taxa such that a meaningful analysis could be conducted.

The status reports identified 10 factors (threats) that influenced abundance and distribution of distinctive endemic aquatic taxa: water flow diversions (affected 90 taxa), nonnative species (78 taxa, which include introductions for fisheries management purposes as well as other other nonnative taxa; e.g., Asian clam and crayfishes, mentioned above in "Introductions and Translocations"), livestock grazing in riparian zones (54 taxa), introductions for sportfisheries management (33 taxa), groundwater pumping (17 taxa), hybridization of species (eight taxa), timber harvest (four taxa), pollution and recreation (three taxa each), and urbanization of habitat (two taxa). Most affected taxa were influenced by more than one factor: two affected 37 taxa, three affected 26 taxa, four affected 12 taxa, and five affected five taxa, whereas 67 taxa were affected by only one factor. This suggests synergistic effects may affect status changes—e.g., the combined effects of degraded habitats and nonnative species on endemic taxa may be greater than the summed effect of individual threats (Moyle and Light, 1996). Nonnative species, water flow diversions, and groundwater use caused most extinctions, whereas livestock grazing and pollution each caused a single extinction. All extinct taxa and most (68%) of the taxa experiencing major decline were narrowly distributed within the Great Basin (<5 populations each); this indicates that taxa with limited distribution are acutely vulnerable to catastrophic changes in status.

Sixty-eight distinct taxa (50% of those reviewed) lost at least one population during the last 140 years, 78 experienced a major decline (58%), and 16 became extinct. Only 28 taxa maintained what is believed to be their approximate historical abundance and distribution. Incidences of first population loss, major decline, and extinction occurred irregularly throughout the period of record (Figure 1). Rates of decline increased and decreased three times since the late 1800s; however, differences among the rates of population loss, major decline, and extinction from the late 1800s through the late 1990s were not significant (analysis of covariance (ANCOVA): slopes,  $p > 0.05$ ; regression,  $p < 0.05$ ), indicating that changes in these rates followed similar temporal trends. The first rate increase began before the turn of the twentieth century, another began during the early decades after the turn of the century, and the third began during the 1950s. Decline rates peaked sharply and then leveled off somewhat for several decades. Both the frequencies of increasing decline rates and amplitudes of the three rates increased with time, indicating that periods of rapid declines have become more frequent.

Several factors may explain general trends in the changes of status. Increases in the rates of decline appear to coincide with periods of human population expansion and economic growth. Status declines were most rapid during the 1890s, 1930s, and 1970s—periods that are associated (respectively) with the greatest revenues from mining and completion of the transcontinental railroad in the late 1800s (Hulse, 1991), the population expansion before the Great Depression, and the growing economy prior to the 1970s recession. Conversely, rates of decline

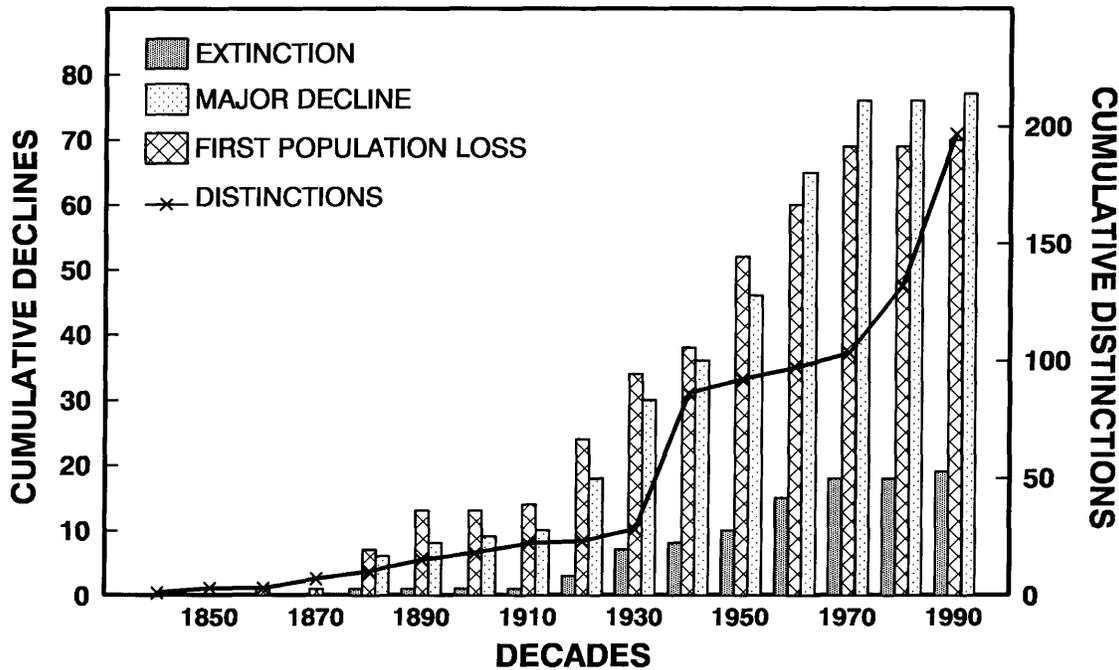


FIGURE 1.—Cumulative percent decline (by calendar decade) of aquatic animals endemic to the Great Basin since the 1850s, as shown by percent of taxa affected by first population loss, major decline (a decrease in historical distribution or abundance by at least one-half), and extinction. Differences among rates of first population loss ( $y = 0.516x - 967.0$ ,  $r^2 = 0.88$ ), major decline ( $y = 0.587x - 1101.8$ ,  $r^2 = 0.87$ ), and extinction ( $y = 0.143x - 268.4$ ,  $r^2 = 0.84$ ) are not significant. “Cumulative distinctions” illustrate the cumulative increases (by decade) in the identifications of 199 endemic taxa determined in published and unpublished taxonomic studies to be distinct within the Great Basin. See “Status Changes” in the text for a description of distinctive taxa.

were slowest during the period before the region was actively settled (pre-1850), during the second decade of the twentieth century (during World War I), and in the 1940s (during World War II). During the last century, status was most stable during both World Wars, when the national economy focused on armament production and when immigration was constrained by fuel shortages and rationing. After World War II, status declines increased through the 1970s to an unprecedented level, and most taxa known in 1980 had either lost one population (68 taxa) or suffered major decline (78 taxa). Rates of decline slowed again during the 1980s and 1990s. This decrease in the decline of taxa coincides with enactment of environmental legislation (i.e., Endangered Species Act, Clean Water Act, National Environmental Policy Act, and many similar state statutes) and with initiation of many state, Federal, and private conservation programs, which seems to suggest these programs are successful. It is problematic, however, to attribute these decreases solely to conservation programs because most distinctive taxa had already declined before these decades, leaving a comparatively smaller portion of endemic taxa to suffer their first population loss and/or major decline. In the future, major declines and the first population loss of a taxon will be recorded mostly for newly discovered taxa. Nonetheless, the high number of extant taxa (199 distinct forms) com-

pared with the numbers of distinct taxa having lost a population (68) and having undergone major decline (78) suggests that these conservation programs may have lowered the extinction rate.

### Discussion

Composition and distribution of Great Basin aquatic communities, and the patterns of human resource use, both reflect the influence of regional aridity. Although Great Basin wetlands are small and isolated, they provide most of the water in a dry region and they contain a more diverse flora and fauna than other habitats (Thomas et al., 1979; Brode and Bury, 1984). Riparian vegetation provides nesting, roosting, and migratory habitat for resident and migratory birds and provides food and cover for mammals. Importance of these wetlands to terrestrial wildlife and to the endemic aquatic fauna shows that even small aquatic habitats are important to Great Basin biodiversity. Water has also been a focus for human activities in the Great Basin. Hunter-gatherers frequently placed their settlements near rivers, marshes, and springs (Fowler and Fowler, 1990), and all of the largest contemporary cities are proximal to large water resources (e.g., the Humboldt, Carson, and Truckee Rivers, Utah Lake, etc.).

Anthropogenic use has affected terrestrial and aquatic ecosystems in many ways. Hypotheses relating the extinction of mammals and birds to the arrival of humans approximately 10,000 years ago suggest that some declines were attributed to human predation or climate change (Martin, 1990; Grayson, 1991). A thorough assessment of these impacts is beyond the scope of this paper, and additional evidence is needed to better understand how humans effected Holocene biotic changes in the Great Basin. However, information compiled during the last 120 years shows that historical status declines and extinctions began soon after the region was first settled by European immigrants. Evidence that the impacts of recent human activities on biogeography greatly exceeded those of hunter-gatherers is indicated by archaeological and fossil records and by taxonomic studies.

Wetlands have continuously provided important resources for humans in the Great Basin. Hunter-gatherers did not live in permanent settlements because food resources were frequently scarce and movement was necessary to maximize foraging opportunities that changed seasonally. In wet years, they utilized higher elevations to harvest piñon (*Pinus monophylla* and *P. edulis*) nuts. When food was scarce (e.g., during droughts) they temporarily settled near wetlands (Yellen, 1977; Fowler and Fowler, 1990). Springs and marshes bordering pluvial lakes supported small animals, tubers, and seeds that were foods unavailable in other places (Janetski and Madsen, 1990). Halford (1998) identified a number of edible plant species (e.g., currant, *Ribes* sp.; elderberry, *Sambucus* sp.; and wild rose, *Rosa woodsii*) from pack-rat middens that were located near small springs and an ephemeral lake in the west central Great Basin.

Hunter-gatherers affected endemic aquatic taxa by manipulating habitats and by harvesting fish and shellfish. It is difficult to assess the effects that these activities had on Great Basin biogeography because little information exists that indicates the response of aquatic taxa to human activities. Mehringer and Warren (1976) found that fire was used periodically to clear mesquite (*Prosopis* spp.) bosques and to increase food availability in Ash Meadows, a spring province in southern Nevada. Although fire may dramatically affect riparian vegetation, and fish populations have been extirpated by fire in the southwest (Rinne, 1996), little information suggests that it has been a major cause of extinction. Scoppettone et al. (1998) observed declines in native fish abundances after a fire along spring brooks in southern Nevada, but no extinctions were documented and populations soon recovered to preburn levels. The minimal impact of fire on Great Basin macroinvertebrates was also indicated by the presence of large populations of the springsnail *Pyrgulopsis gibba* in a small, recently burned spring in northern Nevada (Sada, field notes, 1996). Owens Basin Paiutes and the Fremont Tribe manipulated aquatic habitats by diverting streams for irrigation to increase the abundance of edible native vegetation (Steward, 1933; Madsen, 1989). These activities may have affected

aquatic taxa by drying streams and by creating barriers that interrupted spawning migrations. The amount of habitat affected by these activities and the abundance and wide distribution of taxa affected by these diversions during early taxonomic surveys indicate that these activities did not cause extinction.

A number of Native American tribes also harvested shellfishes and endemic fishes (Steward, 1933; Knack and Stewart, 1984; Drews, 1990; Greenspan, 1990; Janetski, 1990). The abundance of shellfishes and endemic fishes among midden fossils (Dansie, 1990; Greenspan, 1990; Janetski, 1990; Schmitt and Sharp, 1990) suggests that hunter-gatherers actively harvested aquatic taxa. Harvesting did not cause extinction because the midden fossils are all extant taxa that also were collected during initial taxonomic surveys. The occurrence of extinct taxa in middens would suggest that harvesting or other Holocene events caused extinction. There can be little doubt that harvest and habitat manipulation by hunter-gatherers affected the abundance of aquatic taxa and that similar manipulations since the beginning of the twentieth century have extirpated many populations of aquatic taxa within the Great Basin (Minckley and Deacon, 1968; Williams et al., 1985; Miller et al., 1989; Hershler, 1998); however, no evidence documents extirpations that may have been caused by hunter-gatherer harvesting and habitat manipulations. Early Holocene extinctions of aquatic species are not likely attributable to hunter-gatherers because of their transitory settlement behavior, their limited ability to manipulate large amounts of aquatic habitat, and the large size of habitats that supported harvested populations. Although hunter-gatherers affected the abundance of some endemic aquatic species, it is unlikely that their activities extensively affected aquatic biogeography.

Biogeography could have been affected by hunter-gatherers who transported aquatic species outside of their native range, thus establishing new populations. Translocations may have been inadvertent (e.g., accidental captures in water containers when settlements were moved) or intentional. Effects of these translocations on biogeography are also difficult to determine, but their possible influence is indicated by several factors. If movement was accidental, a wide diversity of taxa (e.g., fishes, mollusks, and aquatic insects) would have been involved because endemic aquatic species occupy many aquatic habitats that would have been encountered because of the transitory lifestyle of hunter-gatherers. These taxa could have been accidentally captured in water jugs or carried in moist clothing and moved to new locations. Intentional translocations would have served a purpose such as broadening the distribution of food fishes, which suggests that a small number of taxa would have been selected. If intentional translocations were common, it is doubtful that they were limited to intrabasin movements. Interbasin translocations from the diverse fish assemblages in surrounding basins (e.g., Colorado River, Klamath River, Sacramento River, and Columbia River basins) would have been likely, and representatives of these faunas

would have been recorded in the Great Basin during the early biological surveys.

Evidence that hunter-gatherers translocated aquatic taxa is equivocal. Unintentional capture and movement was highly probable for some taxa, but establishment of viable populations would have been less likely because of differences among aquatic habitats (e.g., water chemistry, water temperature, current velocity, etc.) and competitive interactions that discourage colonization. Translocation of springsnails would have been unlikely; they can persist for several hours in moist, cool conditions but do not appear to survive by rapidly acclimating to waters with chemistries different from their founder habitat (Sada, unpublished data). Unintentional fish translocations likely would have been infrequent because of fish requirements for adequate water and tolerable temperatures and dissolved oxygen concentrations. Water quality differences also may have limited aquatic insect translocation. If unintentional translocation had been common, interbasin genetic differences between populations could not be easily detected and there would be little pattern that could be described by pluvial-period interbasin connectivity.

Evidence for intentional translocations is also weak. Most aquatic taxa of the Great Basin were either too small or too scarce to be used by hunter-gatherers; this suggests that movement of larger fish and invertebrates (e.g., California floater *Anodonta californica*) was more likely. The paucity of large Great Basin taxa also indicates that the efficacy of translocation would have been enhanced if species had been brought in from surrounding basins. There is little evidence, however, that intentional movement was common; the distribution of endemic taxa within the Great Basin can usually be explained by models describing the fluvial connectivity of basins during the Pleistocene (Echelle and Dowling, 1992; Smith, 1992; Hamlin, 1996), and the Great Basin fish fauna has few taxa in common with surrounding basins. Many aquatic species in the Great Basin instead are derived from ancestral taxa occupying surrounding basins (Smith, 1978; Minckley et al., 1991).

Unassisted entrance of aquatic taxa into the Great Basin is shown by the fossil record. Pliocene and Miocene fish and mollusk fossils indicate past connectivity between the Great Basin and its surrounding basins (e.g., Miller and Smith, 1981; Smith, 1981; Taylor and Smith, 1981; Taylor, 1985). Firby et al. (1997) recorded bones of *Oncorhynchus* (trout) and *Catostomus* (subgenus *Pantosteus*) (sucker) from 695,000–725,000 year-old sediments in Owens Lake, California. Neither of these taxa inhabit the Owens Basin today, but closely related taxa are found in the Lahontan Basin to the north and in coastal drainages of southern California (Smith, 1966). Past occurrence and extirpation of these fishes before the arrival of humans indicates that these fish moved into the Great Basin during pluvial periods and became extinct without the influences of hunter-gatherer activity.

European immigrants had an immediate effect on Great Basin aquatic biogeography when they first settled the region during the nineteenth century. Expansion of the livestock industry, which began in the middle 1800s, resulted in some of the first disturbances of many aquatic habitats and riparian communities (Davis, 1977; Mack, 1981). Introductions of nonnative fishes also began in this period, when interest in sportfishing accompanied the expanding population that pursued the silver and gold mining bonanzas then underway (Hulse, 1991; Dill and Cordone, 1997). The resulting effects on biogeography were greater than those caused by hunter-gatherers, because the settlers used technologies that caused large-scale habitat modifications (e.g., pipes, dredging, dams, impoundments) and they introduced species from throughout the world. As a result, many existing wetlands probably bear little resemblance to their condition prior to settlement by the European Americans and immigrants. Water flow diversion and introduced species have degraded most large wetlands, whereas smaller habitats—streams and springs—have been perturbed by water diversion and riparian zone trampling that accompanies pastoral activities. These changes have reduced the distribution and abundance of most endemic aquatic taxa and the aquatic biodiversity within the Great Basin.

Historical declines in Great Basin endemic aquatic taxa can be attributed to a comparatively small number of factors (e.g., water diversion, livestock use, and introduction of nonnative species). The scarcity of proposals for ecologically beneficial changes in future land use, the increasing demands for water, and the changes in abundance and distribution of most endemic species during the last 100 years all indicate that these factors can be expected to cause additional extinctions (primarily in narrowly distributed taxa) and changes in biogeography. Continued declines in abundance and distribution may begin to affect widespread taxa as well, which will limit our ability to interpret pluvial climates and interbasin connectivity; and a natural laboratory will be eliminated wherein the ecology, diversity, and speciation of the aquatic fauna within the Great Basin—almost 20 percent of the area of the United States—can be examined.

The small size of most Great Basin wetlands and the small number of activities causing status declines indicate that stopping the losses of aquatic taxa does not require substantial funding or a large commitment of natural resources. Conserving these habitats requires innovative programs to allow reasonable human uses of wetland areas while protecting Great Basin aquatic ecosystems from further degradation. To meet this challenge, land and resource management strategies must be developed that will allow use of resources while conserving Great Basin biota. This can be accomplished only by increasing ecological knowledge of endemic species and by using this information to create innovative techniques that allow wetland use by humans while providing for conservation of fauna and flora unique to the Great Basin. Experimental work that examines interactions between native and exotic macroinvertebrates

is also needed to determine mechanistic causes for interactions between native aquatics and nonnative invertebrates so that effective conservation strategies can be developed.

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## Appendix

### Primary Habitat and Status of Known Distinctive Aquatic Biota in Great Basin Wetlands

Distinct biota are either described taxa or potential, undescribed taxa whose morphological or genetic distinctiveness has been recognized in published or unpublished reports. Potential taxa are identified by their geographic location in quotes after the taxon name. In parentheses are numbers of translocated populations (if known). The year distinctiveness was first recognized (Distinct); the calendar year or decades of first population loss (First Loss), major decline, and extinction; and the anthropogenic activities causing status change

(Threats) are shown for each form. A dash (–) indicates no population loss, major decline, extinction, or threats are known. Threats: 1 = livestock grazing, 2 = nonnative species introduction, 3 = sport fisheries management, 4 = water diversion, 5 = groundwater pumping, 6 = urbanization, 7 = hybridization, 8 = timber harvest, 9 = pollution, 10 = recreation. A question mark (?) denotes instances in which population translocation, status change, or threats are probable but existing information is insufficient for an accurate assessment.

Distinct biota	First Major						References
	Habitat	Distinct	loss	decline	Extinct	Threats	
Amphibians							
<i>Bufo exsul</i>	Spring	1942	–	–	–	1	Szewczak, 1997
<i>Bufo nelsoni</i>	Spring	1893	1980	1980	–	1,2,4	Altig, 1981; Maciolek, 1983; Hoff, 1993; Heinrich, 1996
Fishes							
<i>Catostomus ardens</i>	Lotic/Lentic	1881	1930	–	–	4	Kershner, 1995
<i>Catostomus clarki intermedius</i>	Lotic	1942	1960	1960	–	2,3,4	Courtenay et al., 1985
<i>Catostomus clarki</i> 'Meadow Valley'	Lotic	1948	1950	–	–	2,4	Hubbs and Miller, 1960; Stein, 1997
<i>Catostomus fumeiventris</i> (4)	Lotic	1948	?	1940	–	1,2,3,4	Moyle et al., 1995; USFWS, 1998a
<i>Catostomus occidentalis lacusanserinus</i>	Lotic/Lentic	1948	1940	1940	–	1,2,4,8	J.E. Williams, pers. comm., 1996
<i>Catostomus platyrhynchus lahontan</i> (?)	Lotic	1903	–	–	–	2,3,4	Decker, 1989
<i>Catostomus platyrhynchus platyrhynchus</i>	Lotic	1874	1900	–	–	3,4	Kershner, 1995
<i>Catostomus tahoensis</i> (?)	Lotic/Lentic	1878	1900	–	–	1,2,3,4	La Rivers, 1962
<i>Catostomus warnerensis</i> (1)	Lotic/Lentic	1908	1940	1940	–	1,2,3,4,8	Andraesen, 1975; Kittredge, 1987; Williams et al., 1990
<i>Catostomus</i> 'Wall Canyon'	Lotic	1948	?	?	–	2	Hubbs and Miller, 1948a; Heinrich, 1993
<i>Chasmistes cujus</i>	Lotic/Lentic	1883	–	1930	–	2,3,4,6	Scopettone and Vinyard, 1991; USFWS, 1992
<i>Chasmistes liorus liorus</i>	Lotic/Lentic	1981	1900	1930	1930	2,3,4	Sharp, 1905; Miller and Smith, 1981
<i>Chasmistes liorus mictus</i> (3)	Lotic/Lentic	1981	–	1950	–	2,3,4	Sharp, 1905; Miller and Smith, 1981; Kershner, 1995
<i>Cottus bairdi</i> 'Mahleur'	Lotic	1948	1960	1940	–	1,2,4,8	Bond, 1974; C.E. Bond, pers. comm. with J.E. Williams, 1996
<i>Cottus echinatus</i>	Lentic	1963	1890	1900	1930	2,4	Heckman et al., 1981; Miller et al., 1989
<i>Cottus extensus</i> (1)	Lentic	1963	–	–	–	–	Sharp, 1905; Holden et al., 1996
<i>Cottus pitensis</i>	Lotic	1963	1940	1890	–	1,2,8	Oregon Department of Wildlife files, 1992
<i>Crenichthys baileyi albivallis</i>	Spring	1981	1970	–	–	1,2,3	Williams and Wilde, 1981; Courtenay et al., 1985
<i>Crenichthys baileyi baileyi</i> (1)	Spring	1981	–	1960	–	1,2,4	Williams and Wilde, 1981; Courtenay et al., 1985; USFWS 1998b
<i>Crenichthys baileyi grandis</i> (1)	Spring	1981	1960	1960	–	1,2,3	Williams and Wilde, 1981; Courtenay et al., 1985; USFWS 1998b
<i>Crenichthys baileyi moapae</i>	Spring	1981	1960	–	–	2,4,5	Williams and Wilde, 1981; Courtenay et al., 1985
<i>Crenichthys baileyi thermophilus</i>	Spring	1981	1960	–	–	2,3,4	Williams and Wilde, 1981; Courtenay et al., 1985; Heinrich, 1993
<i>Crenichthys nevadae</i> (4)	Spring	1932	–	1980	–	2,3,4	Williams and Williams, 1981; USFWS, 1997a
<i>Cyprinodon diabolis</i> (2)	Spring	1930	1970	1970	–	5	Deacon, 1979; Heinrich, 1993
<i>Cyprinodon nevadensis amargosae</i> (3)	Spring	1948	–	–	–	2,4	Moyle et al., 1989; Sada et al., 1997
<i>Cyprinodon nevadensis calidae</i>	Spring	1948	1950	1950	1970	4,7	Miller et al., 1989; Moyle et al., 1995
<i>Cyprinodon nevadensis mionectes</i> (2)	Spring	1948	1960	1970	–	2,4,5	Williams and Sada, 1985; Scopettone et al., 1995
<i>Cyprinodon nevadensis nevadensis</i>	Spring	1948	–	–	–	–	Deacon and Deacon, 1979; Sada et al., 1997

APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
<b>Fishes (continued)</b>							
<i>Cyprinodon nevadensis pectoralis</i>	Spring	1948	1970	—	—	2	USFWS, 1976; Soltz and Naiman, 1978; Scopettone et al., 1995
<i>Cyprinodon nevadensis shoshone</i>	Spring	1948	1940	1960	1960	2,4	Taylor et al., 1988; Moyle et al., 1995
<i>Cyprinodon radiosus</i> (4)	Spring/Lotic	1948	1930	1940	—	2,4	Miller, 1948; 1961; Miller and Pister, 1971; USFWS, 1998a
<i>Cyprinodon salinus milleri</i>	Spring	1972	—	—	—	—	LaBounty and Deacon, 1972; Sada and Deacon, 1995
<i>Cyprinodon salinus salinus</i>	Spring	1943	—	—	—	—	Miller, 1943; Sada and Deacon, 1995
<i>Empetrichthys latos concavus</i>	Spring	1948	1940	1950	1950	5	Miller, 1948; Sokol, 1954; Miller, 1961
<i>Empetrichthys latos latos</i> (3)	Spring	1948	1970	1970	—	2,5	Miller, 1948; Minckley and Deacon, 1968
<i>Empetrichthys latos pahump</i>	Spring	1948	1940	1950	1950	5	Miller, 1948; Sokol, 1954; Miller, 1961
<i>Empetrichthys merriami</i>	Spring	1893	1930	1930	1950	2,5	Miller, 1948; Sokol, 1954; Miller, 1961; Miller, 1969
<i>Eremichthys acros</i>	Spring	1948	—	—	—	1,4	Hubbs and Miller, 1948b; Vinyard, 1996; USFWS, 1997b
<i>Gila alvordensis</i>	Spring/Lotic	1972	1960	—	—	1,2,4	Williams and Bond, 1983
<i>Gila bicolor euchila</i>	Spring	1948	—	1970	—	1,2,3,4	Hubbs et al., 1974; Baugh et al., 1986
<i>Gila bicolor eurysona</i>	Spring	1948	—	1890	—	1	Williams et al., 1980; Williams and Bond, 1981
<i>Gila bicolor isolata</i>	Spring	1948	—	1970	—	1,2,4	Hubbs et al., 1974; Vinyard, 1984; Heinrich, 1993
<i>Gila bicolor mohavensis</i>	Lotic	1938	1930	1940	—	2,4,7	Hubbs and Miller, 1943; USFWS, 1984
<i>Gila bicolor newarkensis</i>	Spring	1948	1950	—	—	1	Hubbs et al., 1974; Hardy, 1980; Haskins, 1996
<i>Gila bicolor obesa</i>	Lotic	1856	1890	1940	—	1,2,3,4	La Rivers, 1962; Snyder, 1917a
<i>Gila bicolor oregonensis</i>	Spring/Lotic	1977	—	1890	—	1,4	Bills, 1977; J.E. Williams, pers. comm., 1997
<i>Gila bicolor pectinifer</i>	Lentic	1917	—	—	—	3,4	La Rivers, 1962
<i>Gila bicolor snyderi</i> (3)	Lotic	1948	1940	1940	—	2,3,4,7	Snyder, 1917b; Miller, 1973; USFWS, 1998a
<i>Gila bicolor vaccaceps</i>	Spring	1948	—	—	—	1,4	Bills and Bond, 1980; Moyle et al., 1995
<i>Gila bicolor</i> 'Big Smokey Valley'	Spring	1948	1960	1980	—	1,2,5	Deacon and Pedretti, 1984; Pedretti et al., 1987
<i>Gila bicolor</i> 'Blue Eagle Spring'	Spring	1948	1970	1970	—	4	J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Bull Creek'	Spring	1948	—	—	—	—	D.W. Sada, field notes, 1995; J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Butterfield Spring'	Spring	1948	—	—	—	—	J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Catlow Valley'	Spring	1948	—	1890	—	1,4	Bills, 1977; J.E. Williams, pers. comm., 1997
<i>Gila bicolor</i> 'Diamond Valley'	Spring	1948	?	?	—	?	Hubbs et al., 1974
<i>Gila bicolor</i> 'Dixie Valley' (2)	Spring	1948	—	—	—	2	Rissler et al., 1991; Vinyard, 1994
<i>Gila bicolor</i> 'Eagle Lake'	Spring	1943	—	1910	—	2,3	Kimsey, 1954; Moyle et al., 1991
<i>Gila bicolor</i> 'Fish Lake Valley'	Spring	1948	1960	1980	—	2,3	D.W. Sada, field notes, 1993
<i>Gila bicolor</i> 'Green Springs'	Spring	1948	—	—	—	—	D.W. Sada, field notes, 1995; J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'High Rock'	Spring	1948	1980	1980	1980	2	Moyle, 1993
<i>Gila bicolor</i> 'Hot Creek Valley'	Spring	1948	1970	—	—	1	J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Hutton Spring'	Spring	1948	—	—	—	—	Bills, 1977; J.E. Williams, pers. comm., 1997
<i>Gila bicolor</i> 'Kate Springs'	Spring	1948	—	—	—	—	J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Little Fish Lake Valley'	Spring	1948	—	—	—	—	J.R. Stein, pers. comm., 1997
<i>Gila bicolor</i> 'Pleasant Valley'	Spring	1948	1970	1980	—	2,3	Nevada Division of Wildlife files, 1995
<i>Gila bicolor</i> 'Railroad Valley'	Spring	1948	—	—	—	1,2,3	Williams and Williams, 1981
<i>Gila bicolor</i> 'Summer Valley'	Spring	1948	1930	1960	—	1,2,3,4,7	Bills, 1977; J.E. Williams, pers. comm., 1997
<i>Gila boraxobius</i> (1)	Spring	1980	—	—	—	5	Williams and Bond, 1980; 1983; USFWS, 1987
<i>Gila robusta jordani</i> (1)	Spring	1950	1960	1940	—	2,4	Courtenay et al., 1985; USFWS, 1986, 1998b
<i>Iotichthys phlegethontis</i> (1)	Spring/Lotic	1874	1900	1900	—	2,3,4,6	Kershner, 1995; USFWS, 1995a
<i>Lampetra tridentata</i> 'Goose Lake'	Lentic	1948	—	1940	—	2,4	J.E. Williams, pers. comm., 1997
<i>Lepidomeda albivallis</i>	Spring/Lotic	1960	1960	1970	—	2,4,9	Courtenay et al., 1985; Scopettone et al., 1992; USFWS, 1994
<i>Lepidomeda altivelis</i>	Spring	1960	1930	1930	1940	2,3,4	Hubbs and Miller, 1960; Miller et al., 1989
<i>Lepidomeda mollispinis pratensis</i> (1)	Spring/Lotic	1960	1950	1950	—	2,4	Hubbs and Miller, 1960; USFWS, 1993
<i>Oncorhynchus clarki henshawi</i> (33)	Lotic	1845	1890	1930	—	1,2,3,4,7	Sumner, 1940; Behnke, 1992; USFWS, 1995b
<i>Oncorhynchus clarki seleniris</i> (4)	Lotic	1933	1920	1920	—	1,2,7	USFWS, 1985; Behnke, 1992
<i>Oncorhynchus clarki utah</i> (23)	Lotic/Lentic	1874	1870	1910	—	1,2,3,4	Kershner, 1995; Duff, 1996; Holden et al., 1996
<i>Oncorhynchus clarki</i> 'Alvord'	Lotic	1934	1890	1890	1940	1,2,3,4,7	Williams and Bond, 1983; Miller et al., 1989; Behnke, 1992
<i>Oncorhynchus clarki</i> 'Humboldt' (?)	Lotic/Lentic	1978	1890	1930	—	1,2,3,4,7	Behnke, 1992; USFWS, 1995b
<i>Prosopium abyssicola</i>	Lentic	1919	—	—	—	—	Sigler and Sigler, 1987
<i>Prosopium gemmifer</i> (1)	Lentic	1919	—	—	—	—	Sigler and Sigler, 1987
<i>Prosopium spilonotus</i>	Lentic	1919	—	—	—	—	Sigler and Sigler, 1987
<i>Relictus solitarius</i> (4)	Spring	1948	1930	1930	—	2,3	Hubbs et al., 1974; Stein and Salisbury, 1994; Haskins, 1995
<i>Rhinichthys osculus lariversi</i>	Spring	1972	—	—	—	1	Pedretti et al., 1987
<i>Rhinichthys osculus lethoporus</i>	Spring	1948	—	1970	—	2,4	Hubbs et al., 1974; Vinyard, 1984
<i>Rhinichthys osculus nevadensis</i>	Spring/Lotic	1893	1971	1970	—	2,4,5	Williams and Sada, 1985; USFWS, 1990; Scopettone et al., 1995

## APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
Fishes (continued)							
<i>Rhinichthys osculus oligoporus</i>	Spring	1948	1970	1970	—	1,2,5	Vinyard, 1984
<i>Rhinichthys osculus reliquus</i>	Spring	1948	1940	1950	1969	2	Hubbs et al., 1974; Miller et al., 1989
<i>Rhinichthys osculus robustus</i> (?)	Lotic	1903	1900	—	—	1,3,4	La Rivers, 1962
<i>Rhinichthys osculus velifer</i>	Spring	1893	1969	1969	—	2,3,4	Miller, 1984; Tuttle et al., 1990
<i>Rhinichthys osculus</i> 'Amargosa'	Lotic	1995	—	—	—	2	Williams et al., 1982; Moyle et al., 1995; Sada et al., 1995
<i>Rhinichthys osculus</i> 'Benton Valley'	Spring	1995	1940	1940	—	2,4	Sada, 1989; Sada et al., 1995; USFWS 1998a
<i>Rhinichthys osculus</i> 'Diamond Valley'	Spring/Lotic	1948	?	?	—	?	Hubbs et al., 1974
<i>Rhinichthys osculus</i> 'Foskett Spring' (1)	Spring	1948	—	—	—	1	Andreasen, 1975; Williams et al., 1990
<i>Rhinichthys osculus</i> 'Little Lake'	Spring	1995	1940	1940	1940	2	Sada, 1989; Sada et al., 1995
<i>Rhinichthys osculus</i> 'Long Valley'	Spring	1995	1960	1960	—	2	Sada, 1989; Sada et al., 1995; USFWS 1998a
<i>Rhinichthys osculus</i> 'Meadow Valley'	Lotic	1948	—	—	—	—	Hubbs and Miller, 1960; Stein, 1997
<i>Rhinichthys osculus</i> 'Monitor Valley'	Spring	1948	—	—	—	1	Heinrich, 1991; D.W. Sada, field notes, 1996
<i>Rhinichthys osculus</i> 'Oasis Valley'	Spring	1995	—	1980	—	2,4	Heinrich, 1993; Sada et al., 1995
<i>Rhinichthys osculus</i> 'Pahranagat Valley'	Spring	1984	—	1960	—	1,2	Tuttle et al., 1990
<i>Rhinichthys osculus</i> 'Upper White River'	Spring	1948	1970	1970	—	2,3,4,9	Courtenay et al., 1985; Scopettone et al., 1992
<i>Richardsonius egregius</i> (?)	Lotic/Lentic	1859	1900	—	—	1,2,3,4	La Rivers, 1962
Mollusks							
<i>Assiminea infima</i>	Spring	1947	1930	—	—	10	Pistrang and Kunkel, 1958; Hershler 1987; Sada, 2001
<i>Fluminicola dalli</i>	Spring	1884	—	—	—	—	Hershler and Frest, 1996
<i>Fluminicola modoci</i>	Spring	1912	—	—	—	—	Hershler and Frest, 1996
<i>Fluminicola turbiniformis</i>	Spring	1865	—	—	—	—	Hershler and Frest, 1996
<i>Pyrgulopsis aardahli</i>	Spring	1989	?	?	—	4	Hershler, 1989
<i>Pyrgulopsis aloba</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis amargosae</i>	Spring	1987	—	—	—	—	Hershler, 1989
<i>Pyrgulopsis anatina</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis anguina</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis augustae</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis aurata</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1996; Hershler, 1998
<i>Pyrgulopsis basiglans</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis bifurcata</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis breviloba</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis bryantwalkeri</i>	Spring	1916	?	?	—	?	D.W. Sada, field notes, 1991; Hershler, 1994
<i>Pyrgulopsis cariniata</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis chamberlini</i>	Spring	1998	?	?	—	10	Hershler, 1998
<i>Pyrgulopsis cruciglans</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis crystalis</i>	Spring	1987	—	1970	—	2,4	Sada, 1985; Hershler and Sada, 1987; D.W. Sada, field notes, 1997
<i>Pyrgulopsis dixiensis</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1991; Hershler, 1998
<i>Pyrgulopsis eremica</i>	Spring	1995	?	—	—	1	Hershler, 1995
<i>Pyrgulopsis erythropoma</i>	Spring	1893	—	1970	—	2,4	Sada, 1985; Hershler and Sada, 1987
<i>Pyrgulopsis fairbanksensis</i>	Spring	1987	—	1970	—	2,4	Hershler and Sada, 1987
<i>Pyrgulopsis fusca</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis gibba</i>	Spring	1995	?	?	—	1,4	Hershler, 1995; Hershler, 1998
<i>Pyrgulopsis gracilis</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis hamlinensis</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis hendersoni</i>	Spring	1933	?	?	—	?	Hershler, 1994; Hershler, 1998
<i>Pyrgulopsis hovinghi</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis hubbsi</i>	Spring	1998	?	?	—	4	Courtenay et al., 1985; Hershler, 1998
<i>Pyrgulopsis humboldtensis</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis imperialis</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis inopinata</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis isolata</i>	Spring	1987	—	—	—	—	Sada, 1985; Hershler and Sada, 1987
<i>Pyrgulopsis landeyi</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis lata</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis lentiglans</i>	Spring	1998	?	?	—	?	Hershler, 1998

## APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First Major			Threats	References
			loss	decline	Extinct		
Mollusks (continued)							
<i>Pyrgulopsis leporina</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis limaria</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1996; Hershler, 1998
<i>Pyrgulopsis lockensis</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis longae</i>	Spring	1995	?	?	—	4	Hershler, 1995
<i>Pyrgulopsis longiglans</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1996; Hershler, 1998
<i>Pyrgulopsis marcida</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis merriami</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis micrococcus</i>	Spring	1893	—	—	—	5	Sada, 1985; Hershler and Sada, 1987; Hershler, 1989
<i>Pyrgulopsis militaris</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1996; Hershler, 1998
<i>Pyrgulopsis millenaria</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis montana</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis nanus</i>	Spring	1987	—	—	—	2,4	Sada, 1985; Hershler and Sada, 1987
<i>Pyrgulopsis neritella</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis nevadensis</i>	Lentic	1883	1890	1890	1890	4	Galat et al., 1981; Hershler, 1994
<i>Pyrgulopsis nonaria</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis notidicola</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis orbiculata</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis owensensis</i>	Spring	1989	?	—	—	4	Hershler, 1989; Hershler and Pratt, 1990
<i>Pyrgulopsis papillata</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis peculiaris</i>	Spring	1998	?	?	—	10	Hershler, 1998
<i>Pyrgulopsis pellita</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis perturbata</i>	Spring	1989	—	?	—	4	Hershler, 1989
<i>Pyrgulopsis picilllis</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis pilcata</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis pilsbryana</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis pisteri</i>	Spring	1987	?	?	—	2,4,5	Hershler and Sada, 1987
<i>Pyrgulopsis planulata</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis ruinosa</i>	Spring	1998	1990	1990	1990	4	D.W. Sada, field notes 1991; Hershler, 1998
<i>Pyrgulopsis sathos</i>	Spring	1998	?	?	—	4	Courtenay et al., 1985; Hershler, 1998
<i>Pyrgulopsis saxatalis</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis serrata</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis sternalis</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1992; Hershler, 1998
<i>Pyrgulopsis sulcata</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis transversa</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis umbilicata</i>	Spring	1998	?	?	—	1	D.W. Sada, field notes, 1996; Hershler, 1998
<i>Pyrgulopsis variegata</i>	Spring	1998	?	?	—	1	Hershler, 1998
<i>Pyrgulopsis villacampae</i>	Spring	1998	?	?	—	4	Hershler, 1998
<i>Pyrgulopsis vinyardi</i>	Spring	1998	?	?	—	?	Hershler, 1998
<i>Pyrgulopsis wongi</i>	Spring	1989	?	—	—	5	Hershler, 1989; Hershler and Pratt, 1990
<i>Pyrgulopsis</i> 'Longstreet Spring'	Spring	1981	1970	1970	1970	5	Taylor, 1980; Sada, 1985
<i>Tryonia angulata</i>	Spring	1987	?	1970	—	2,4	Sada, 1985; Hershler and Sada, 1987
<i>Tryonia elata</i>	Spring	1987	?	1970	—	2,4	Sada, 1985; Hershler and Sada, 1987
<i>Tryonia ericae</i>	Spring	1987	?	1970	—	2,4	Hershler and Sada, 1987
<i>Tryonia margae</i>	Spring	1989	?	?	—	?	Hershler, 1989; Pratt and Hoff, 1992
<i>Tryonia robusta</i>	Spring	1989	1930	—	—	4	Hershler, 1989; Pistrang and Kunkel, 1958
<i>Tryonia rowlandsi</i>	Spring	1989	?	?	—	?	Hershler, 1989
<i>Tryonia salina</i>	Spring	1989	—	—	—	—	Hershler, 1989; Sada and Deacon, 1995
<i>Tryonia variegata</i>	Spring	1987	?	1970	—	2,4	Sada, 1985; Hershler and Sada, 1987; Hershler, 1989
Aquatic insects							
<i>Ambrysus amargosus</i>	Spring	1953	1970	1970	—	4,5	La Rivers, 1953; Scopettone et al., 1995
<i>Ambrysus funebris</i>	Spring	1948	1930	1930	—	4	La Rivers, 1948; Pratt and Hoff, 1992; Polhemus and Polhemus, 1995
<i>Ambrysus relictus</i>	Spring	1994	—	1970	—	4	Polhemus and Polhemus, 1994
<i>Belostoma saratogae</i>	Spring	1958	—	—	—	—	Pratt and Hoff, 1992; Polhemus and Polhemus, 1995
<i>Capnia lucustra</i>	Lentic	1965	1960	1960	1960	2,9	California Natural History Database (1996 unpublished data)
<i>Microcyloepus formicoideus</i>	Spring	1990	1930	1930	—	4	Shepard, 1990; Pratt and Hoff, 1992
<i>Microcyloepus moapus fraxinus</i>	Spring	1949	?	1960	—	2,4	La Rivers, 1949
<i>Stenelmis calida</i>	Spring	1949	—	1970	—	5	Chandler, 1949; Deacon and Deacon, 1979; Schmude, 1992
<i>Stenelmis lariversi</i>	Spring	1992	—	?	—	?	Schmude, 1992
Fairy shrimp							
<i>Artemia monica</i>	Lentic	1964	—	—	—	4	Jellison et al., 1993; R.S. Jellison, pers. comm., 1997

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# Late Neogene Environmental History of the Northern Bonneville Basin: A Review of Palynological Studies

Owen K. Davis

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## ABSTRACT

Pollen analysis of sediments from Great Salt Lake in the northern Bonneville Basin indicate six vegetational and pluvial stages since the deposition of Bishop volcanic ash 0.76 Ma (million years ago) and Lava Creek B volcanic ash 0.6 Ma. These analyses and other pollen diagrams from the region generally record elevated percentages of forest conifers (pine, spruce, fir, and Douglas fir) during the last two pluvials: 24–14.5 <sup>14</sup>C Ky B.P. (radiocarbon-dated, thousand years before present) and ~150–130 Ka (thousand years ago). The regional vegetation was a mosaic of cold-dry pine woodland and sagebrush steppe. This mosaic was replaced by steppe vegetation 10.8 <sup>14</sup>C Ky B.P., with xeric indicators reaching maximum percentages 7–5 <sup>14</sup>C Ky B.P. Similarly, pluvial Lake Bonneville was at about the Gilbert Lake level from 87 to 24 Ka, except for a dry interval ~70 Ka, and it was above the Gilbert level from 24 to 14.5 <sup>14</sup>C Ky B.P. It then fell below the Gilbert level (i.e., it did not occupy the Wendover Basin) except for brief periods after 11,300 ± 300 <sup>14</sup>C years B.P.

Pollen analysis of sediments provided by the Amoco Production Company indicated that the upland vegetation (nonriparian, nonlittoral) has been desert from the late Miocene to the present. Estimated temperature was highest and moisture least during the Pliocene, with temperatures cooling and moisture increasing thereafter. The late Miocene (<5 Ma) was dominated by pollen of xerophytic *Sarcobatus* and *Ephedra*, which was replaced by *Chenopodiaceae-Amaranthus* and *Artemisia* pollen during the Pliocene and early Pleistocene (5–0.75 Ma). After 0.75 Ma, percentages of *Artemisia* and *Pinus* abruptly increase.

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Three noteworthy events punctuate the gradual evolution of the desert flora: a warm–cold oscillation 3.7 Ma, a cold interval 2.6 Ma, and abrupt cooling after 0.75 Ma. Pluvial–interpluvial cycles begin after the 0.75 Ma event, each with an average length of 0.1 million years. Diversion of the Bear River into the Great Salt Lake basin is indicated by increased pollen concentration after 0.31 Ma, near the oxygen isotope stage 8–9 transition.

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## Introduction

The Great Salt Lake region within the northern Bonneville Basin has been the subject of various geological and biological studies, including many vegetation histories. Early investigations (e.g., Gilbert, 1885) shaped our understanding of Cenozoic climate as much as did studies of the glacial deposits of the midwestern United States. However, understanding of continental glaciation has steadily developed through investigation of ocean sediments, whereas the pluvial record has relied on scattered outcrops woven together by radiocarbon (and other) dates. My goals in this paper are to synthesize previously published palynological studies of the northern Bonneville Basin region, to publish for the first time pollen analyses by Harry Yokum and Paul S. Martin (University of Arizona), and to compare the shorter records of Yokum and Martin with pollen diagrams created with data from the Amoco Production Company's wells, which rival ocean cores in the data they provide.

The Great Salt Lake contains an uninterrupted accumulation of pollen and other sediments spanning millions of years. The shorter, more detailed records of Yokum and Martin confirm trends shown in the uppermost layers of the Great Salt Lake wells; and the Amoco wells unite and extend the findings of these briefer investigations.

The interpretation of pollen diagrams is based on the relationship between vegetation and pollen. For the Great Salt Lake region, the modern vegetation and pollen rain is discussed in detail by Bright (1967) and Davis (1995). Briefly, valley bottoms are covered by halophytic, shadscale, and greasewood

steppes dominated by *Chenopodiaceae-Amaranthus* (hereafter *Cheno-Ams*) and *Sarcobatus* pollen. Further upslope is sagebrush steppe dominated by *Artemisia* (sagebrush) pollen. After that is woodland characterized by *Pinus* (pine), *Juniperus* (juniper), and *Quercus* pollen; pine forest with *Pinus* and *Pseudotsuga* pollen; and subalpine forest with *Pinus*, *Abies* (fir), and *Picea* (spruce) pollen.

The palynological study of Great Salt Lake environmental history began with Bright's (1967) study of Swan Lake, in Red Rock Pass (elevation, 1453 m), the overflow for pluvial Lake Bonneville. The lowermost date,  $12,090 \pm 300$   $^{14}\text{C}$  years B.P. (radiocarbon-dated years before present; United States Geological Survey, National Center Laboratory number W-1338, ~795–805 cm), on the 955 cm core provides a limiting age for the spillover, now dated at ~14.5 Ka (thousand years ago) (O'Connor, 1993). Bright subsequently obtained additional radiocarbon dates for the Swan Lake core and for additional

cores from a nearby spillover basin that he named the "Downey Core," but these analyses were never published.

The basal pollen zones ( $12,090 \pm 300$  to  $10,190 \pm 250$   $^{14}\text{C}$  years B.P.) of the Swan Lake pollen diagram are dominated by 55%–75% *Pinus* pollen, with moderate percentages (1%–5%) of *Picea* and *Abies*. From ~7.5 to ~2.8  $^{14}\text{C}$  Ky (thousand years) B.P. the diagram is dominated by Gramineae (grass), *Artemisia*, and *Cheno-Ams* pollen. From ~2.8 to ~1.7  $^{14}\text{C}$  Ky B.P., *Pinus* increased to 30%, and thereafter *Artemisia* pollen dominates the Swan Lake diagram. The sequence in Bright's unpublished Downey Core record is very similar (Robert C. Bright, pers. comm., 1975). A third "Bonneville spillover" core, collected and analyzed by Stephen T. Jackson (pers. comm., 1985) near McCammon, Idaho, has a similar pollen stratigraphy, but its sediments also contain the Mount Mazama volcanic ash, whereas Bright's cores do not.

In many respects, David B. Madsen's pollen diagram (Figure 1) of Great Salt Lake sediments near Carrington Island (Core C;

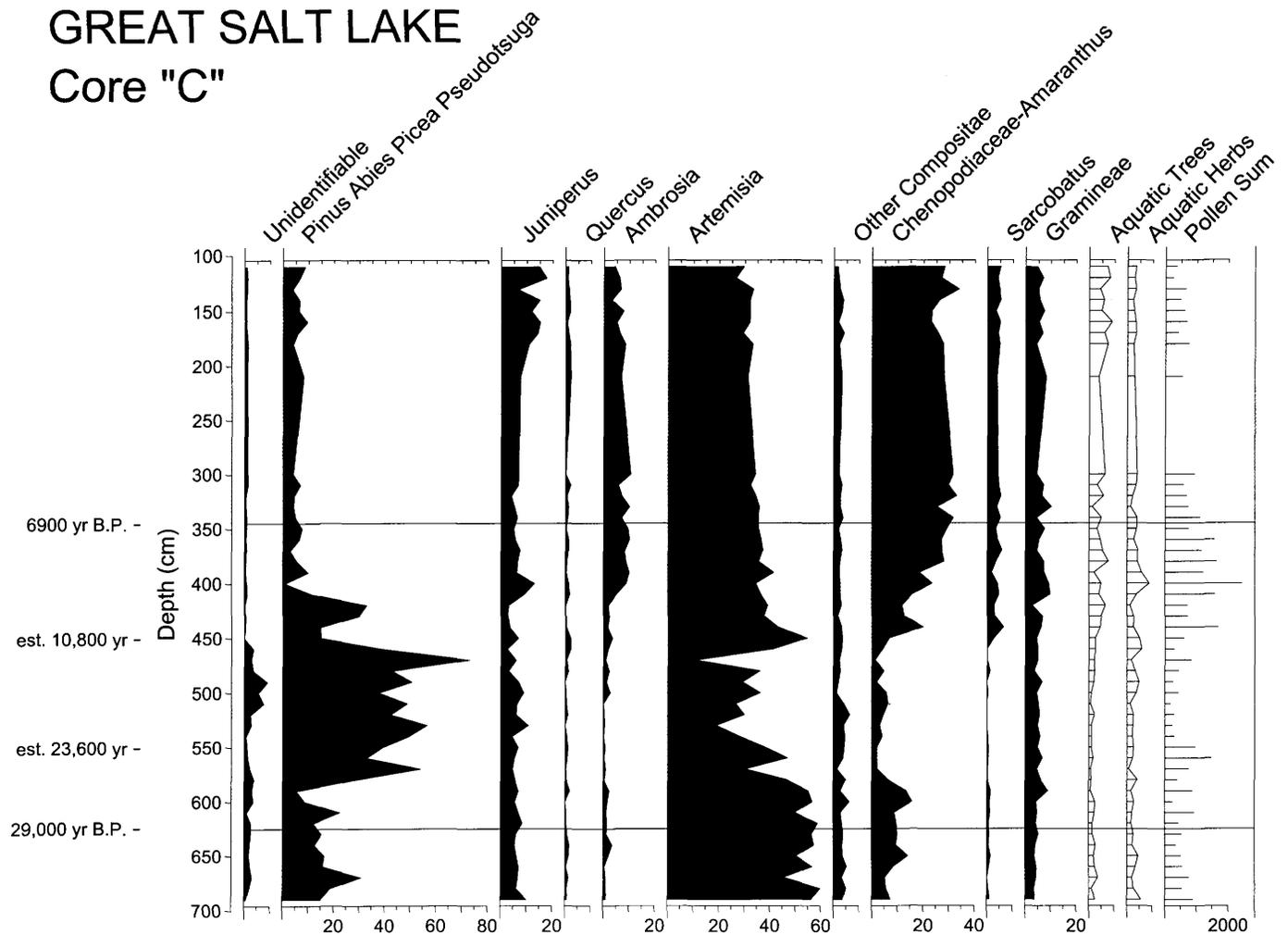


FIGURE 1.—Percentage pollen diagram for Core C, from the southern (Tooele) basin of the Great Salt Lake, selected types. Pollen of wetland trees and herbs (curves at right) are outside the pollen sum. Age estimates are based on linear interpolation between the dated horizons. (Pollen analysis by D.B. Madsen in Spencer et al., 1984.)

Spencer et al., 1984, fig. 1) is similar to Bright's Swan Lake diagram (not shown). Conifer (*Pinus*, *Abies*, *Picea*) pollen is abundant from 550 to 450 cm (~24–10.8 <sup>14</sup>C Ky B.P.). During the middle Holocene (near the position of Mt. Mazama volcanic ash, 6.7 <sup>14</sup>C Ky B.P.), the abundances of *Artemisia*, *Ambrosia* (ragweed), and *Cheno-Ams* pollen reach maxima, and *Juniperus* pollen increases after 7.5 <sup>14</sup>C Ky B.P. (Figure 1).

Two pollen diagrams from the Great Salt Lake were published by Peter J. Mehringer, Jr. (1985). A 1.7 m (~7 Ky) core taken near Bird Island (see Figure 2) records steady percentages of *Pinus* (<15%), *Artemisia* (30%), and Gramineae (5%). As in Bright's and Madsen's (Figure 1) pollen diagrams, *Ambrosia*, *Sarcobatus*, and *Cheno-Ams* pollen are most abundant during the middle Holocene ~7–5 <sup>14</sup>C Ky B.P. *Juniperus* pollen increases to a maximum of ~25% near the top of the diagram (Mehringer, 1985).

Mehringer (1985) also analyzed pollen from 4.26 to 2.66 m deep in a core from Crescent Springs, west of Great Salt Lake. Just above 3.65 m (i.e., after 26,700 ± 900 <sup>14</sup>C years B.P.), the pollen of *Picea*, *Abies*, and *Pinus* increase, as they do in Madsen's Core C diagram (Figure 1). Pollen of wetground plants—Cyperaceae (sedge) + *Triglochin* (pondweed)—reach 18% below 3.65 m, indicating an extensive marsh near Crescent Springs. Decreased percentages of these wetground types above 3.65 m probably indicate that the Crescent Springs site (elevation, 1300 m) was flooded by Lake Bonneville, with the result that no marsh vegetation existed near the core site.

Three pollen diagrams from the Wendover Basin, west of the Great Salt Lake basin, are published herein for the first time in their entirety. The pollen analyses were completed by Yokum and Martin in the early 1960s. *Pinus* curves for the Wendover and Knolls cores were published in Martin and Mehringer (1965). The "Carrozi Pit" pollen diagram (Figure 3) is based on samples collected by Paul Martin from a borrow pit near the railroad crossing of Carrozi, near Knolls, Utah. The samples were taken beneath a tufa layer dated at 11,300 ± 300 <sup>14</sup>C years B.P. by Meyer Rubin (Eardley et al., 1957:1171). In Figure 3, the sedimentation rate is assumed to be constant, and is estimated from the radiocarbon date and an age of 24 Ky at 110 cm for the *Artemisia* decrease–*Pinus* increase, based on the age of this event at Crescent Springs.

The Wendover and Knolls diagrams are from "Eardley Cores" (Williams, 1993) taken in 1960. The Knolls core is from the eastern Wendover Basin (elevation, 1289 m; 113°20'W, 40°45'N) and is 152 m in length. The Wendover core is from the western Wendover Basin (elevation, 1285 m; 115°5'W, 40°45'N) and is 171 m in length. Sediments of the upper 29 m were analyzed for the Knolls core (Figure 4), and those from the upper 30 m were analyzed for the Wendover core (Figure 5).

The chronologies for the Wendover and Knolls diagrams (Figures 4, 5) are based on the sedimentation rates derived from dated volcanic ashes by Williams (1993), including the Pahoa Ash from 160 Ka in the Wendover core (Figure 5). Approximate ages of events discussed in the text are indicated as

"est." on the left in Figures 4 and 5. For example, the beginning of the last interglacial, ~130 Ka (oxygen isotope stage (OIS) 5, Martinson et al., 1987), occurs near 2200–2400 cm in the Knolls core (Figure 4) and at about 2000 cm in the Wendover core (Figure 5).

The pollen preservation of the Wendover Basin cores (Figures 3–5) is poor in many samples, probably because of intermittent desiccation of the sediments and subsequent pollen destruction. However, similarities among these three diagrams and to the other pollen diagrams of this region permit some general statements of Late Quaternary vegetation change. The increase in *Pinus* pollen and the decrease in *Artemisia* pollen that are seen near the top of each diagram (Figures 3–5), in the Crescent Springs diagram of Mehringer (1985), and in the Core C diagram (Figure 1; Spencer et al., 1984) occurred ca. 24 Ka.

The higher *Cheno-Ams* percentages below 110 cm (estimated at 24 Ka) in the Carrozi Pit pollen diagram (Figure 3) are consistent with growth of *Atriplex* and other halophytes of the Chenopodiaceae family near the core site. This suggests exposure of the basin margin and relatively low lake depth, near the Gilbert Lake level (elevation, ~1300 m) during OIS 3. The increase of *Botryococcus* (a colonial green algae) above 110 cm in the core may indicate lower water salinity and increased water depth during OIS 2; however, the expansion of *Botryococcus* does not occur in the Knolls core during OIS 2 (above 300 cm).

In the Carrozi Pit and Knolls diagrams (Figures 3, 4), the percentages of *Picea*, *Abies*, and *Pseudotsuga* (hereafter *PAP*) indicate greater abundances of montane conifers (i.e., lower vegetation zones) during OIS 2. Increases in *PAP* during OIS 2 do not occur in the Wendover diagram (Figure 5), possibly because of poor pollen preservation; however, both the Knolls and Wendover diagrams indicate increased *PAP* percentages near the estimated depth of OIS 6—the last glacial (Knolls, 2600 cm; Wendover, 2800 cm). The low values (1%–5%) of montane conifers and high values of *Pinus* (50%–60%) are consistent with low values of *Picea* and *Abies* (1%–6%) and moderate values of *Pinus* (20%–40%) in the Crescent Springs diagram (Mehringer, 1985). They suggest that glacial (i.e., OIS 2, OIS 6) vegetation on the western and northern margins of Lake Bonneville was xeric pine woodland and sagebrush steppe. In general, *Juniperus* percentages are low during intervals with elevated montane conifer percentages, so a piñon–juniper woodland (such as may be found at low elevation today) is not indicated.

The Knolls diagram (Figure 4) contains a peak in Cyperaceae (20%–40%) and *Typha* (cattail) pollen at 1500–1100 cm (estimated at 87–64 Ka—i.e., OIS 4). The Wendover diagram (Figure 5) shows modest increases in Cyperaceae and *Typha* pollen from 1300 to 600 cm at about the same time as in the Knolls diagram, based on sediment deposition rates (Williams, 1993). A zone of no pollen preservation from 1100 to 950 cm (estimated at ~70 Ka) in the Wendover diagram suggests an interval of low water depth during which the Wendover core site was above the lake surface elevation and the Knolls site was

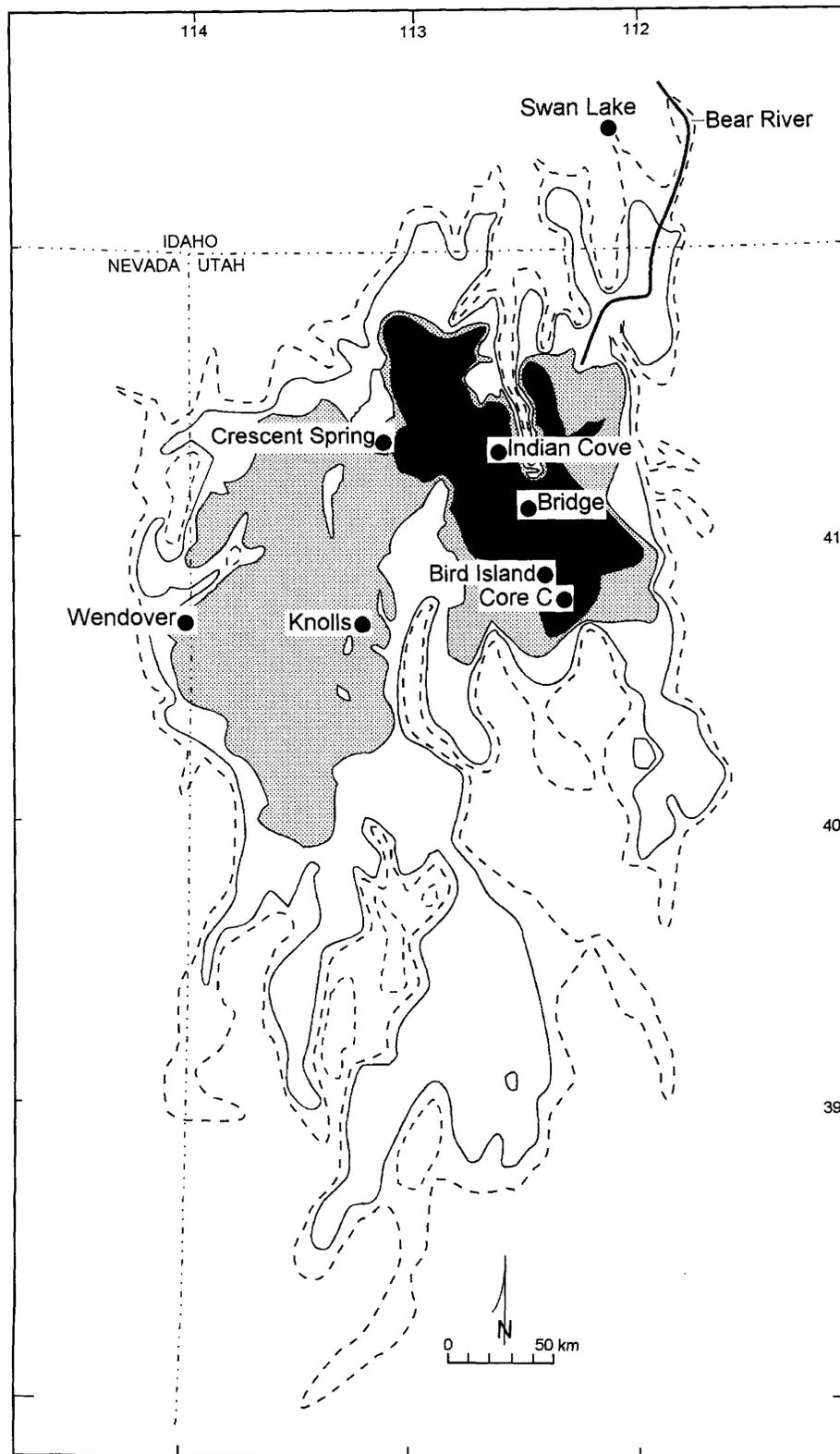


FIGURE 2.—Map of the Bonneville Basin showing location of Amoco Production Company wells and other sites of pollen analysis (bullets). The blackened area is approximately the current extent of Great Salt Lake. The shaded area is the approximate extent of the Gilbert Lake level, the solid line represents the Provo Lake level, and the dashed line represents the Lake Bonneville level.

## CARROZI PIT, UTAH

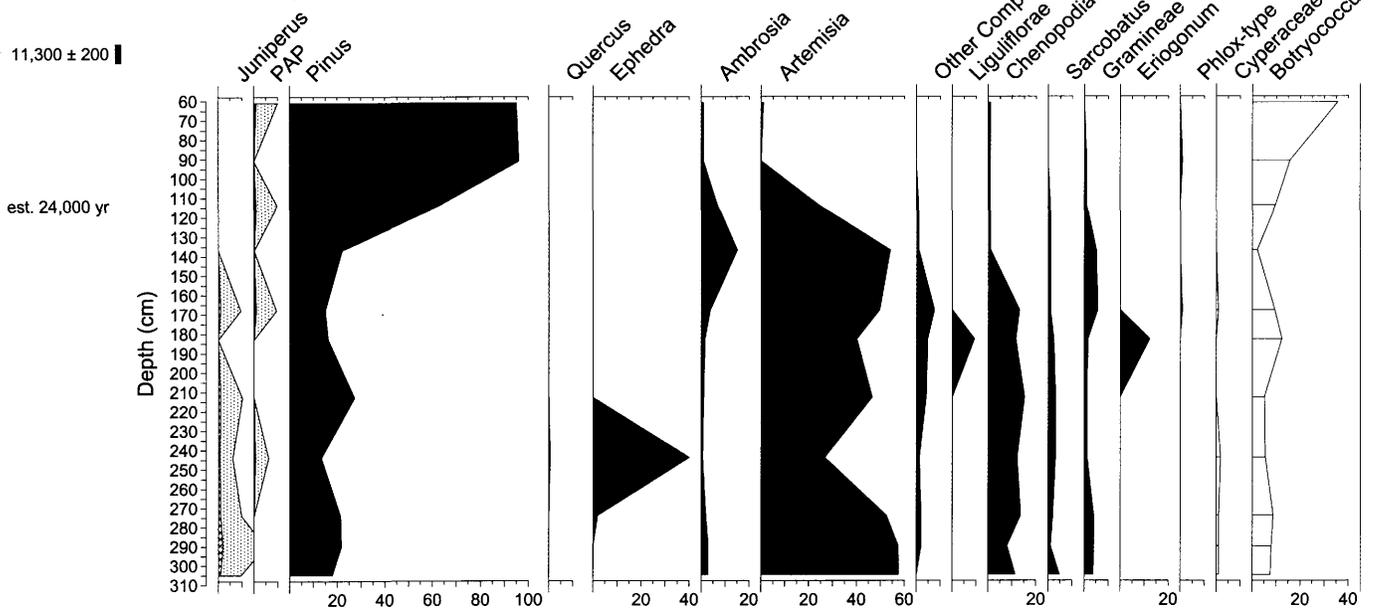


FIGURE 3.—Percentage pollen diagram for Carrozi Pit, near Knolls, Utah. Pollen of Cyperaceae and *Botryococcus* (curves at right) are outside the pollen sum, selected types. *Picea*, *Abies*, and *Pseudotsuga* (PAP) were not recorded individually in the original counts and are shown as a combined curve. Shading for *Juniperus* and PAP is a tenfold exaggeration. Black square at left is position of radiocarbon date (stratigraphically above the sediments analyzed). (Pollen analysis by H. Yokum and P. Martin, unpublished.)

below it. These elevations are near the post-pluvial Gilbert shoreline level. Isostatic depression during the Gilbert stage was about 10 m in the basin center (e.g., near the Knolls site) but less than 1 m at the basin margin (near Wendover; Currey, 1990), so the relative elevations of the Wendover and Knolls sites would have been reversed during the 70 Ka drying event.

In summary, lowering of vegetation zones during OIS 2 (~24–15 Ka) and OIS 6 (~150–130 Ka) is indicated by higher percentages of *Pinus* pollen and moderate increases of PAP pollen (Figures 4, 5). Modern analogs for these assemblages can be found 500–1500 m higher in elevation (Davis, 1981), so cooling by 3°–9° C relative to present is indicated. Modern pollen samples from closed-canopy montane forest, however, have much higher percentages of montane conifer pollen (e.g., 10%–20% PAP). Therefore, the full-glacial vegetation from 1550 to 1600 m above sea level was a mosaic of cold-dry pine woodland and sagebrush steppe rather than mesic closed-canopy forest. Steppe vegetation expanded and pine woodland contracted beginning about 10.8  $^{14}\text{C}$  Ky B.P., with maximum percentages of xeric indicators from ~7 to 5  $^{14}\text{C}$  Ky B.P.

The pluvial lake level in the Wendover Basin was near the Gilbert Lake level during OIS 4 and OIS 3 (87–24 Ka, estimated) except for an interval of drying ~70 Ka (estimated; Figures 4, 5). Lake depth was well above the Gilbert level during

OIS 2 (24–14 Ka) and presumably during OIS 6. Lake Bonneville did not permanently occupy the Wendover Basin after  $11,300 \pm 300$   $^{14}\text{C}$  years B.P. Pollen of littoral vegetation (e.g., Cyperaceae and *Typha*) is most abundant in the Knolls and Wendover cores (Figures 4, 5) during low-water (Gilbert level) phases when the lake shore is near the core sites.

### Methods

Pollen analysis of well cuttings, made available by Amoco Production Company, extend the vegetation and climatic record of the Great Salt Lake Basin into the Miocene.

THE AMOCO WELLS.—From June 1978 through December 1980, Amoco Production Company oversaw the drilling of 15 wells into the sediments of Great Salt Lake from floating platforms. Several of these wells exceeded 3 km in depth, and the cumulative thickness of sediment drilled exceeded 26 km. Sediment cuttings were collected from the wells at selected intervals of 3 m or 10 m. Several kinds of geophysical and sedimentological data were gathered for each well, and approximately 2700 line-kilometers of seismic reflection data also were collected. These data were provided to the University of Arizona, Department of Geosciences, as part of a cooperative research agreement with Amoco Production Company.

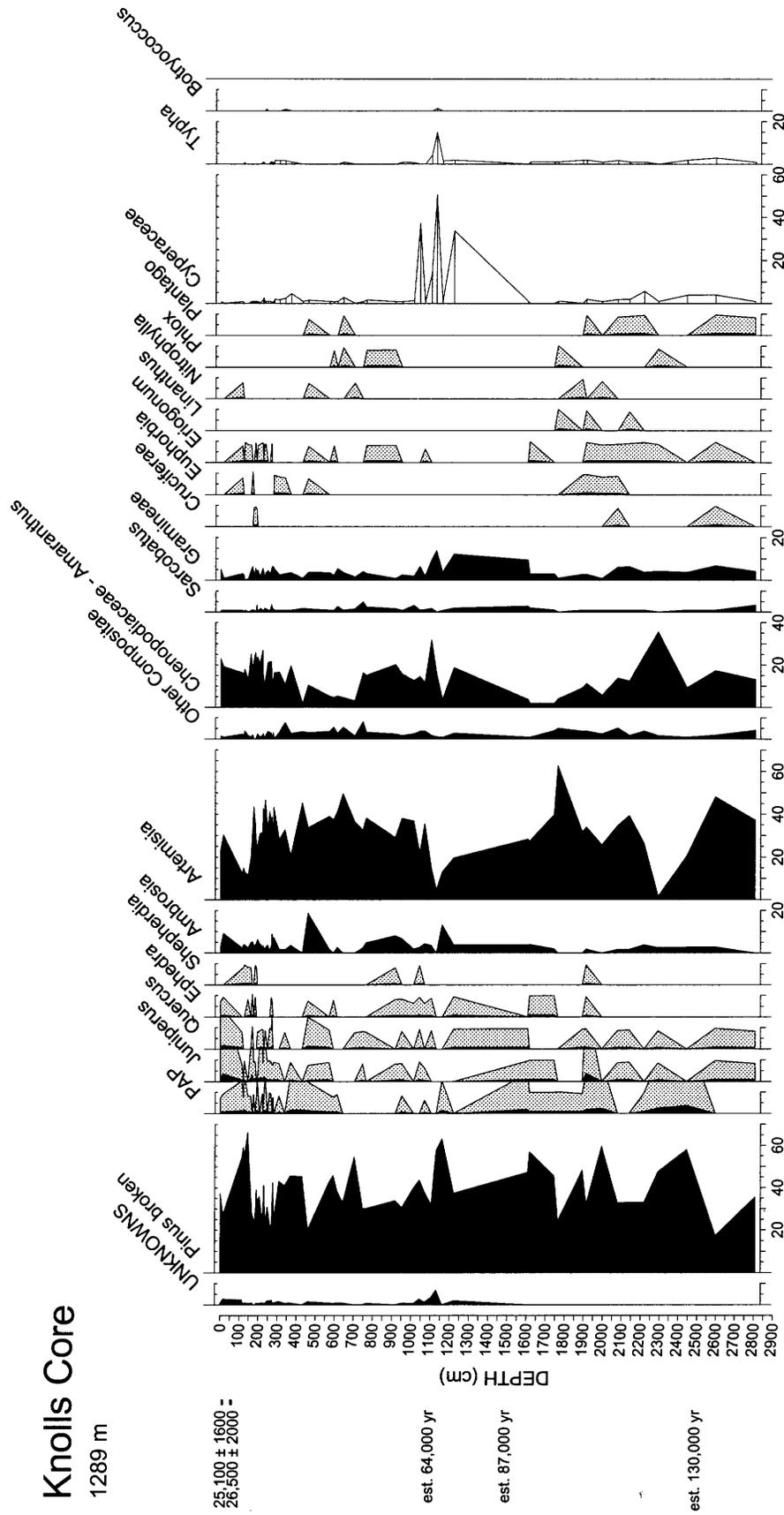


FIGURE 4.—Percentage pollen diagram for the Knolls core, eastern Wendover Basin, Utah, selected types. Pollen of Cyperaceae and *Botryococcus* (curves at right) are outside the pollen sum. Shading is a tenfold exaggeration. PAP = *Picea*, *Abies*, and *Pseudotsuga*. Ages on the far left are years B.P. (Pollen analysis by H. Yokum and P. Martin, unpublished.)

## Wendover Core

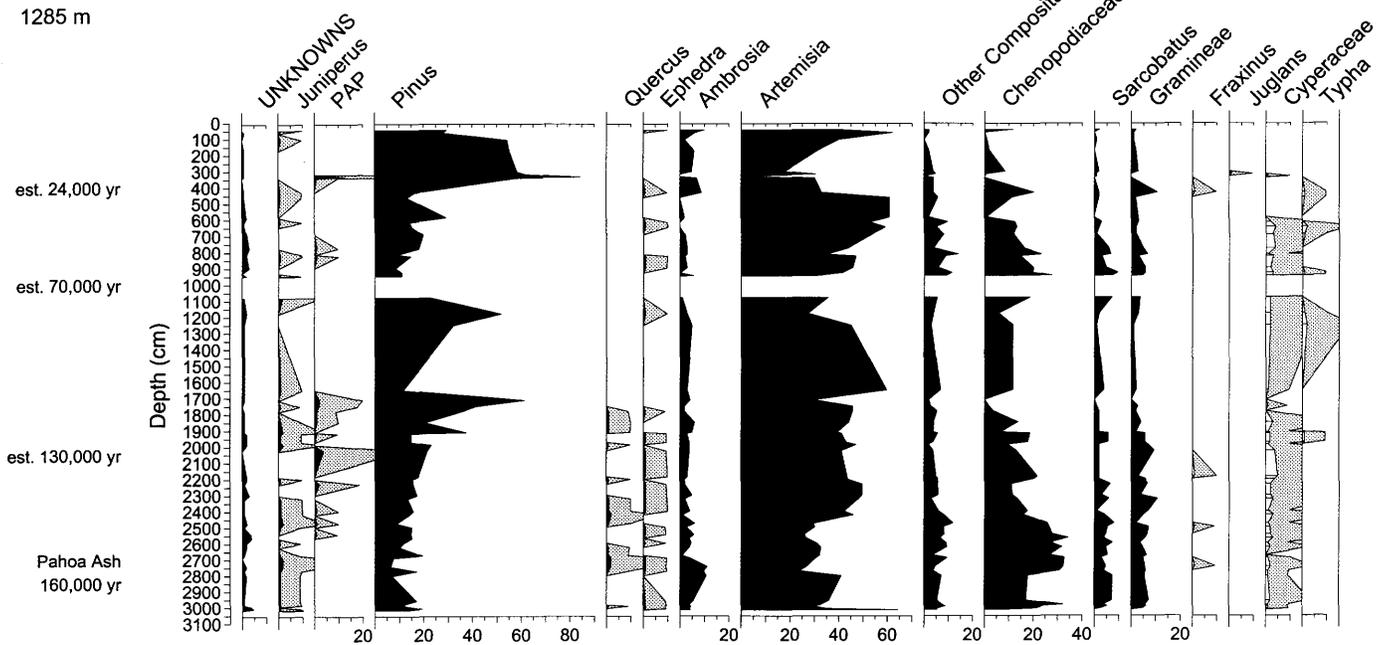


FIGURE 5.—Percentage pollen diagram for Wendover core western Wendover Basin, Utah, selected types. Pollen of Cyperaceae and *Botryococcus* (curves at right) are outside the pollen sum. Shading is a tenfold exaggeration. PAP = *Picea*, *Abies*, and *Pseudotsuga*. Ages on the far left are years B.P. (Pollen analysis by H. Yokum and P. Martin, unpublished.)

Amoco palynology laboratories processed pollen from 13 of the wells, representing about one-half of the sediment thickness drilled. Most of the samples (443/650) have been counted, and results have been published for five wells (Davis, 1996, 1998, 1999; Moutoux, 1995; Moutoux and Davis, 1995; Davis and Moutoux, 1998; Moutoux et al., in prep.). Coverage was best for the Bridge, Indian Cove, South Rozel, and Antelope Island wells. Sediment cuttings (~5 g) were prepared by Amoco personnel at 30 m intervals, with each sample incorporating equal portions from three adjacent subsamples, each 10 m apart. Some samples were screened and divided into <20 and >20  $\mu\text{m}$  fractions before being mounted on separate slides. For counting purposes, the relative pollen concentration on each slide was assumed to be equal, so equal numbers of rows were counted on each slide until a full count (300 grains) was reached. This procedure produced results very similar to undivided samples.

The Amoco samples were supplemented with samples prepared at 3 m intervals from the Indian Cove Well (Figure 2). The site is about 5 km offshore (west) from Little Valley of the Promontory Range. Well cuttings were available at 3 m (10 ft) intervals from 15 to 220 m deep (15–606 Ka) and at 9 m (30 ft) intervals from 232 to 628 m (643–1484 Ka). Given the sedimentation rate for the Indian Cove well, this sample density

gives 8 Ky resolution to 600 Ka and 23 Ky resolution from 0.6 to 1.5 Ma (million years ago).

**POLLEN COUNTING.**—Three hundred pollen grains of upland species (nonriparian, nonlittoral) were counted whenever possible. This sum—used as a divisor for calculating percentages of all types—did not include algae, fungal spores, or the pollen of wet-ground plants. Samples devoid of pollen were not included in the pollen diagrams.

Pollen extraction of 1  $\text{cm}^3$  samples of Indian Cove cuttings followed routine methods, including acid digestion of minerals with HCl and HF, removal of organic material with acetolysis, and removal of organic acids with 10% KOH. *Lycopodium* spore tablets were added to permit calculation of pollen concentration.

**VOLCANIC ASH IDENTIFICATIONS.**—Chronological control for the Amoco wells is based on the identification of volcanic ashes on known age. The methods and identifications are as published by Moutoux (1995), Moutoux and Davis (1995), Davis (1998), Davis and Moutoux (1998), and Moutoux et al. (in prep.).

**CLIMATE RECONSTRUCTIONS.**—Quantitative climatic reconstructions were made by comparing fossil pollen samples with 1367 modern pollen samples from the western United States (Davis, 1995). A PASCAL computer program calculated the

squared chord distance between each fossil sample and the 1367 modern analogs by using 28 common pollen types. Wetland plants (e.g., Cyperaceae and *Typha*) were not used. Modern samples were considered analogs if the squared chord distance was 0.15 or less. The climate estimates are the averages of annual temperature and precipitation for the analogs. Values were not calculated if modern analogs were not found.

To provide a basinwide climate reconstruction, the climate estimates for three wells—Gunnison, Indian Cove, and Bridge—were combined. Values for two other wells—South Rozell and Carrington Island—were not included because preservation was poor in some intervals. The climate estimates for the three wells were averaged after climate had been interpolated at 50 Ky intervals. The average curve was then smoothed by an 11 sample moving average.

The calculations were then made for tectonic subsidence of the eastern Great Basin during the last 5 My (million years). During the Sevier orogeny of the Cretaceous, compressional tectonics resulted in the uplift of the Great Salt Lake region to approximately 1000–2000 m above the current average elevation (DeCelles, 1994). This uplift relaxed during two intervals of Cenozoic extension: 50 to 40 Ma and ~30 Ma to the present. Wolfe et al. (1997) estimated equivalent lowering for the western Great Basin—but at a later date, ~13 Ma.

Approximately one-half of the sediment in the Great Salt Lake Basin accumulated during the last 5–10 Ma (Mohapatra, 1996). The thickness of sediment accumulation in the central Great Salt Lake basin is more than twice the lowering of surface elevation for the region, but I assumed that because both resulted from Cenozoic extension, their timing is similar; i.e., about one-half of the lowering occurred during the last 5–10 Ma. I used temperature rates intermediate to Miocene (2.0° C/km; Wolfe et al., 1997) and contemporary (6.0° C/km; Davis, 1981) values to estimate ~4° C warming and 225 mm lowering of precipitation during the last 5 Ma. These values were used to correct the analog-based climate estimates for tectonic lowering.

### Results and Interpretation

Pollen analysis of the Amoco well cuttings provided data that are readily comparable to those of routine analysis of cores and contemporary pollen samples. Modern analogs for the fossil samples were abundant from 5.5 Ma onward (Figure 6). Perhaps this was the result of “time averaging” of pollen in routine pollen samples (each packet of sediment containing pollen from several seasons of plant growth). Also, “habitat averaging” of the pollen from different vegetation zones in mountainous topography may produce assemblages similar to the “depth-averaged” cuttings. Furthermore, each cutting sample integrated sediment from a range of depths, so the procedure (followed by Amoco personnel) of combining three samples only widened the mixing range.

The regional vegetation recorded in the Amoco pollen diagrams was desert from the late Miocene onward. The pollen spectra were dominated by xerophytic *Sarcobatus* and *Ephedra* pollen during the late Miocene (>5 Ma). They were replaced by *Cheno-Ams* and *Artemisia* during the Pliocene and early Pleistocene (5–0.75 Ma) as the Chenopodiaceae and Compositae (Asteraceae) diversified and spread through the flora (Leopold and Denton, 1987; Cerling et al., 1997). *Artemisia* and *Pinus* percentages abruptly increased in the late Pleistocene (0.75 Ma). The evident antiquity of desert vegetation in the eastern Great Basin conflicts with the hypothesis that deserts expanded during the last few million years in response to uplift of the Sierra Nevada (Axelrod, 1957; Axelrod and Bailey, 1969). These reconstructions were based on leaves and other plant macrofossils, but in Great Salt Lake sediment the pollen of mesic elements—“Tertiary exotics” such as *Ulmus* (elm), *Carya* (hickory), *Ostrya-Carpinus* (hop-hornbeam)—was rare, although it persisted into the middle Pleistocene. These plants probably existed in riparian settings, as do birch, maple, ash, and other “mesic” trees today.

The differences between environmental reconstructions based on pollen and those based on macrofossils must result, in part, from the proximity of these mesic trees to the rivers, deltas, and other sedimentary environments in which the macrofossil floras are preserved (Axelrod, 1957; Axelrod and Bailey, 1969). In contrast, the recruitment area for airborne pollen encompasses a much larger area, including the xeric uplands.

MAJOR VEGETATION EVENTS.—Three noteworthy events at 3.7, 2.6, and 0.75 Ma punctuated the gradual evolution of the desert flora. The 3.7 Ma event was best represented in the Bridge and South Rozel wells, and the 2.6 Ma event was best represented in the East Gunnison and Indian Cove wells. The 3.7 Ma event was characterized in the upland (nonwetland) pollen by an abrupt increase in *Pinus* and *Artemisia* and a decline in *Cheno-Ams* (Figure 6); it was similar to the 0.75 Ma event. In the Bridge well (Figure 6), poor preservation and high *Cheno-Ams* percentages from 3980 to 3682 Ka (1698–1607 m) were followed by high percentages of *Artemisia* and *Pinus* (also *Abies* and Cupressaceae) from 3580 to 3320 Ka (1576–1454 m). In the South Rozel well, the same transition occurred between 3790 and 3580 Ka (2200–2100 m). This event matched the marine record for cooling and increased ice volume dated 3.8–3.6 Ma (Tiedmann et al., 1994).

During the 2.6 Ma event, the pollen diagrams from the East Gunnison and Indian Cove wells show reduced percentages of *Cheno-Ams* and increased *Pinus*, *Artemisia*, *Abies*, and Cupressaceae. However, the percentages of upland taxa changed less during this event than during the 3.7 or 0.75 Ka events. In all Great Salt Lake wells investigated (Moutoux, 1995; Moutoux and Davis, 1995; Moutoux et al., in prep.), the 2.6 Ma event coincided with the beginning of high percentages of wetland taxa (Cyperaceae, *Typha*, and *Azolla*) and algae (*Pediastrum* and *Botryococcus*). In the marine record, this event marked the beginning of the Pleistocene, with increasing  $\delta^{18}\text{O}$  values and a

# Bridge Well, Great Salt Lake

## Pollen Percent

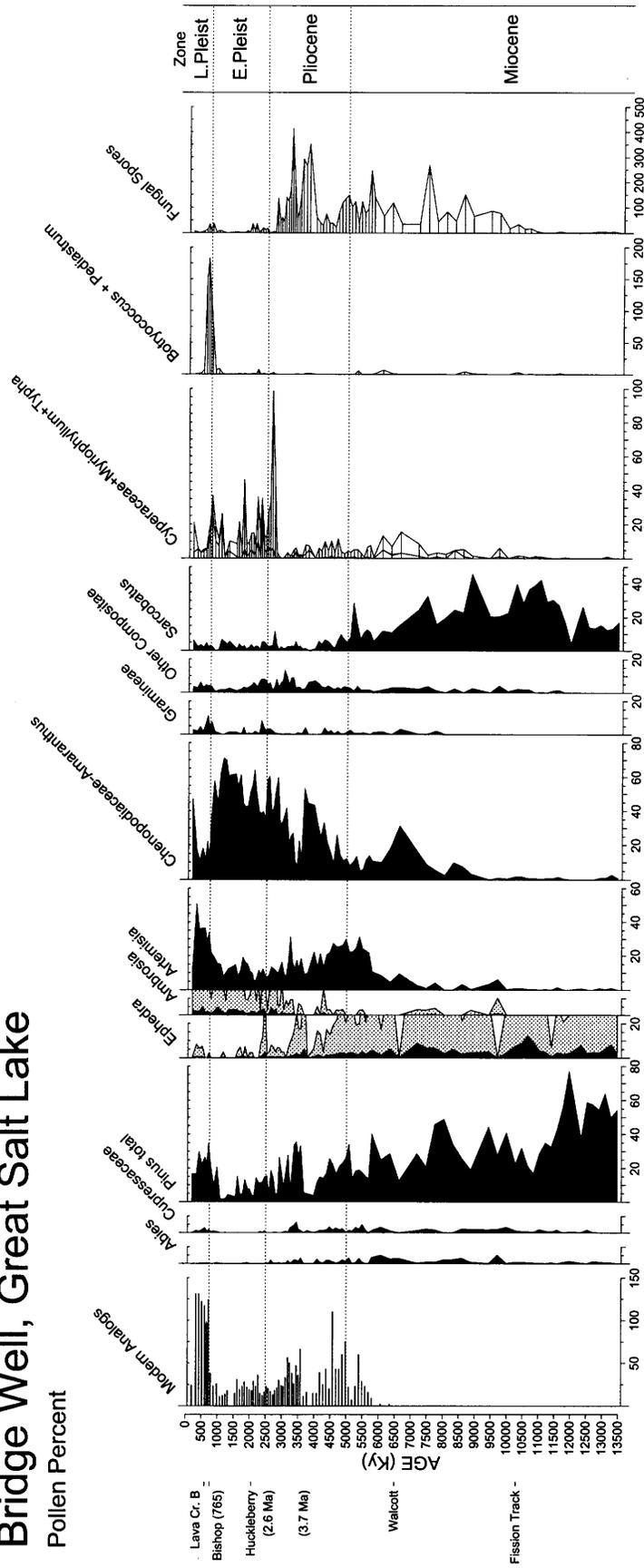


FIGURE 6.—Percentage pollen diagram for Amoco's Bridge well showing selected types. Location of chronologic control and major vegetation events (2.5 Ma, 3.7 Ma) is shown at left. The modern analog curve shows number of contemporary samples matching (squared chord distance < 0.14) each fossil sample. Curves to the right of *Sarcobatus* are not included in the pollen sum. (Pollen analysis by T.E. Moutoux.)

greater amplitude of glacial–interglacial fluctuations (Tiedmann et al., 1994).

The 0.75 Ma event was the most distinctive transition of the Great Salt Lake pollen record (Moutoux, 1995; Moutoux and Davis, 1995; Moutoux et al., in prep.). Before 750 Ka, *Cheno-Ams* pollen exceeded 50% of the pollen assemblage; thereafter, *Artemisia* and *Pinus* predominated, Cupressaceae and other Compositae increased, and Gramineae decreased (Figure 6). This event appears to be a permanent downward displacement of vegetation zones by ~500 m in elevation, in which greasewood steppe (with high percentage of *Cheno-Ams*) was replaced by sagebrush steppe in the intermountain basins. Terrestrial (versus marine) pollen records indicate significant changes occurred during the late Pleistocene, such as the general increase of steppe vegetation (*Artemisia* and Gramineae) after 620 Ka in northern California (Adam et al., 1989) and the expansion of *Quercus* after 900 Ka in Colombia (Hoogheemstra, 1984); however, no other terrestrial record indicated a 750 Ka event that was of greater magnitude than the 2.6 Ma one. Marine records showed increased amplitude of 100 Ky periodicity after 750 Ka (Raymo et al., 1987; Ruddiman et al., 1987) but indicated no change in average conditions.

**CLIMATE RECORD.**—The climate reconstruction for Great Salt Lake wells indicated maximum temperature and minimum moisture during the Pliocene, with cooling and increasing moisture thereafter. This trend differs from that of earlier Great Salt Lake publications (Moutoux, 1995; Moutoux and Davis, 1995) because of the incorporation of tectonic subsidence in the climate estimates. A pronounced temperature peak (5° C greater than modern values) at 3.8 Ma coincided with the *Cheno-Ams* maximum preceding the 3.7 Ma event (Figure 7). The peak itself should be considered tentative because the climate reconstruction for that time included only the Bridge well data. The peak was followed by oscillations leading to a decline in temperature ~3.0 Ma that was reflected in a decline of polar temperatures (Funder et al., 1985; Webb and Harwood, 1991) and a lowering of eustatic sea levels by 35 m (Krantz, 1991).

The 2.6 Ma event (2° C cooling; Figure 7) appears in the Bridge well pollen diagram (Figure 6) as decreased *Cheno-Ams* and increased conifer pollen. Thereafter, temperatures gradually declined and precipitation increased until 0.75 Ka, when the overall (average of glacial + interglacial) temperature dropped 3° C and annual precipitation increased by 100 mm. The uppermost samples provided estimates of temperature at 10.8° C and precipitation at 310 mm, which are equivalent to present-day values (Figure 7).

**PLUVIAL CYCLES.**—The relationships between glacial indicators, interglacial indicators, wetland types, and algae were used to produce the water depth reconstruction in Figure 8. Six pluvial–interpluvial cycles followed the deposition of Lava Creek B ash, with an average cycle length of ~100 Ky (Figure 8). Water depth minima coincided with low values of wetland plants and high values of glacial indicators; water depth maxima also coincided with low values of wetland plants but high

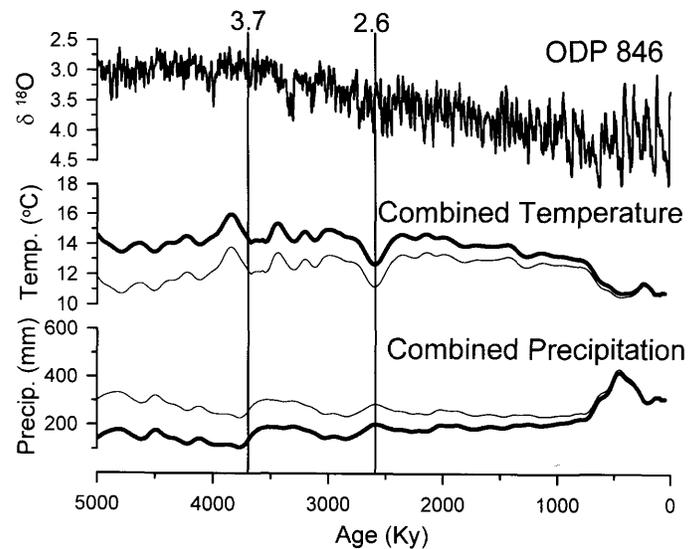


FIGURE 7.—Comparison of Great Salt Lake climate estimates with global records of climate change (bold lines). Climate reconstruction for Great Salt Lake wells was based on modern analogs (squared chord distance <0.14) in a database of 1367 contemporary samples from western North America. Average annual temperature (Temp.) and precipitation (Precip.) curves are smoothed 11-point averages of estimates for the Gunnison, Indian Cove, and Bridge wells. Dashed lines are the temperature and precipitation estimates that have not been corrected for tectonic subsidence of the region. The  $\delta^{18}\text{O}$  line is for Ocean Drilling Program (ODP) site 846 (Pisias et al., 1992).

values of interglacial indicators. The amplitude of the oscillations increased through time, with minima becoming lower and maxima becoming greater.

Evidence from core samples indicates that before 2.6 Ma pollen preservation was poor, fungal spores were abundant, and the pollen of wetland plants was scarce. Apparently, the lakes and marshes of the Great Salt Lake basin were shallow and intermittent. From 2.6 until 0.75 Ma, pollen preservation was good, and percentages of wetland plants (*Cyperaceae*, *Typha*, and *Myriophyllum*) and planktonic algae (*Pediastrum* and *Botryococcus*) were generally high (Figure 6). During this interval (early Pleistocene), shallow lakes and marshes apparently persisted in the northern basin of Great Salt Lake.

Beginning 0.75 Ma, spanning the sedimentary interval containing Bishop (0.76 Ma) and Lava Creek B (0.6 Ma) ashes (Sarna-Wojcicki et al., 1991), and contemporaneous with the cooling and moistening recorded by the upland pollen data (Figure 7), the percentages of wetland plants and algae declined (Figures 1, 4). The event was marked in the aquatic environment by a peak of *Botryococcus* or *Pediastrum* soon after the deposition of Lava Creek B ash. After the transition, the close-interval samples from the Indian Cove well (Figure 8) show a regular pattern of montane conifers (*Abies* + *Picea* + *Pseudotsuga*) during glaciations and of basin floor taxa (*Cupressaceae* + *Ambrosia* + *Sarcobatus*) during interglacials (Davis and Moutoux, 1998). Figure 8 shows that high percentages of the interglacial indicators coincided with the odd stages

## INDIAN COVE WELL

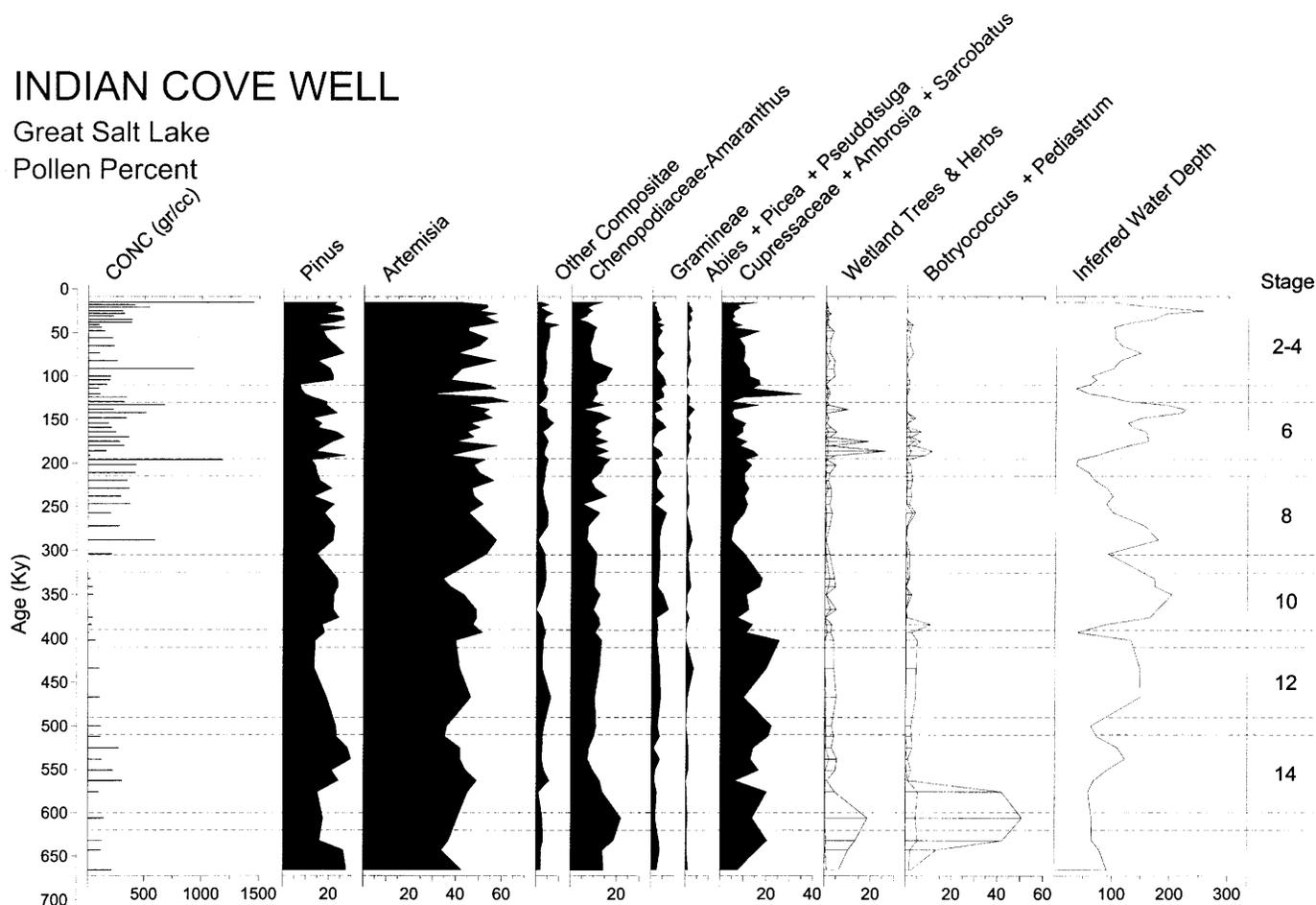
Great Salt Lake  
Pollen Percent

FIGURE 8.—Indian Cove pollen diagram showing selected types. The chronology is based on the presence of Lava Creek B and Bishop volcanic ashes, adjusted by matching the marine oxygen isotope chronology. Curves to the right of Cupressaceae + *Ambrosia* + *Sarcobatus* are not included in the pollen concentration sum. Inferred water depth is a smoothed curve of pluvial indicators (*Abies* + *Picea* + *Pseudotsuga*, weighted  $\times 10$ ) plus shallow water indicators (wetland types and *Botryococcus* + *Pediastrum*) minus interpluvial indicators (Cupressaceae + *Ambrosia* + *Sarcobatus*) expressed as percent of the pollen sum. The values are smoothed by a 3-point moving average. Correlation with the marine oxygen isotope chronology is indicated to the right, where the ages of the even-number stages are marked.

of the marine oxygen isotope chronology, and that high percentages of the glacial indicators matched the even stages.

Algae and the pollen of wetland plants was most abundant at the beginning of the even-numbered stages, shown in Figure 8; i.e. rare during interpluvials when the lake was saline and rare during pluvials when littoral vegetation was far from the core site, but common when the lake was fresh and shallow. This pattern implies global climatic control of lake cycles during the last 0.75 My.

**DIVERSION OF BEAR RIVER.**—The Indian Cove diagram (Figure 8) shows a dramatic increase in total pollen concentration (from an average of 6000 to 30,000 grains/cm<sup>3</sup>) after 310 Ka (marine OIS 9). The concentration remains high to the surface and represents a fundamental change in the pollen sedimentation of the lake. This transformation may have resulted

from the diversion of the Bear River (the largest tributary) into the Great Salt Lake basin. Before its diversion, the river had flowed northward into the Snake River drainage via Lake Thatcher. Spillover of Lake Thatcher into the Great Salt Lake may have led to the catastrophic overflow of Lake Bonneville into the Snake River plain 14.5 Ky B.P.

Bright (1967) dated the diversion from the Snake River drainage at 35 <sup>14</sup>C Ky B.P., but unpublished K/Ar dates recorded for the damming basalt are highly variable (R.C. Bright, pers. comm., 1994). Strontium isotope data of Bouchard et al. (1998) suggest that the history of Lake Thatcher and the Bear River may involve more than one diversion, with the earliest evidence for Bear River in the Thatcher Basin dating to marine OIS 6. Regardless of whether the proposed diversion dates to OIS 9 or OIS 6, it appears not to have permanently increased

the lake's depth. Figure 8 suggests that the amplitude of the pluvial-interpluvial oscillations steadily increased through the late Pleistocene, culminating in the catastrophic overflow through Red Rock Pass.

### Conclusions

Although the time resolution of the Amoco well pollen samples is comparatively low, they permit, for the first time, the reconstruction of Late Cenozoic vegetation change for the Great Basin at a single locality. Furthermore, the pollen diagrams from the Amoco 30 m amalgam samples are comparable to the higher resolution 10 m unmixed samples (Figure 8), which are in turn consistent with the data from core sediments (Figure 1). Long cores from the Great Salt Lake are needed to produce a detailed reconstruction of Late Cenozoic vegetation and climate, but the Amoco cuttings have produced an unparalleled record of long-term change of terrestrial vegetation.

The pollen diagrams trace the development of the Great Basin desert during the Late Cenozoic, produce a climatic reconstruction comparable to that obtained from marine sediments,

and afford an indication of Lake Bonneville pluvial cycles of increasing amplitude, beginning 620 Ka. The cooling and transformation of the vegetation and pluvial cycles 0.75 Ma are a unique feature of this study. It is a robust conclusion, recorded in all wells and in both terrestrial and aquatic indicators. The transformation is different from the increased amplitude of oscillations of the marine record and should be thoroughly investigated in Great Salt Lake cores and in other long terrestrial records.

**ACKNOWLEDGMENTS.**—The sediments used in this study were provided by Amoco Production Company. Analyses were supported by National Science Foundation grants EAR-9219505 and EAR-9205065. Data for pollen analysis of Core C near Bird Island were provided by David P. Madsen. Data for the Carrozi Pit, Knolls, and Wendover cores were provided by Paul S. Martin. Nicholas Piasias generously provided data for Ocean Drilling Program (ODP) site 846 (Piasias et al., 1992), and Ralf Tiedman provided the ODP site 659 data (Tiedmann et al., 1994). Tom Moutoux counted the pollen for the Bridge well and identified the volcanic ashes with the generous assistance of Michael Perkins and William P. Nash.

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# Great Basin Vegetation History and Aquatic Systems: The Last 150,000 Years

*Peter E. Wigand and David Rhode*

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## ABSTRACT

The Great Basin was seen by early settlers as a terrifying barrier to be crossed on the way to the golden promise that was California. Although the region was visited by fur trappers and mountain men in the 1820s and 1830s, it was not until the 1840s that the European pathfinders and empire builders tarried to explore the woodland-covered mountains and playa-bottomed valleys of the Great Basin. Mormon farmers and spirited miners settled this wild land, uprooting the native people who had lived there for millennia. As the region opened to European settlement, evidence of a long and complex environmental history was discovered and explored. But as recently as 50 years ago our knowledge of Late Quaternary lake histories and climates was minimal, and our knowledge of the dynamics of Pleistocene and Holocene vegetation was virtually nonexistent. Our understanding has advanced dramatically in the last half century, with advances in analyses of pollen, woodrat middens, and tree rings. A substantial pollen and plant macrofossil database has been assembled, spanning tens of thousands to hundreds of thousands of years, such that our knowledge of Late Quaternary vegetation history in the Great Basin rivals that of any other region in the world. These data, coupled with the long-term lake histories deduced from the basins of the Lahontan, Bonneville, Chewaucan, and Owens-to-Death Valley lake systems, permit detailed examination of late Pleistocene vegetation dynamics in relation to aquatic system history. By examining proxy records from the various subregions of the Great Basin and the northern Mojave Desert, we have compiled a compelling picture of past climate and the vegetation and hydrologic responses during the last 50,000–150,000 years.

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## Introduction

Our understanding of Late Quaternary biological history in the Great Basin, particularly its vegetation history, has advanced substantially in the half century since the publication of works by Antevs (1948) and by Hubbs and Miller (1948). By that time evidence derived from the interpretation of modern biogeographic indicators such as disjunct taxa and isolated hybrid populations had led to the recognition that Pleistocene glaciopluvial episodes and mid-Holocene warming wrought substantial shifts in vegetation zones, but even the barest outlines of these shifts remained uncertain. In 1948 the number of Late Quaternary fossil plant localities studied in the Great Basin was negligible (Deevey, 1949). Laudermilk and Munz (1934, 1938) had analyzed late Pleistocene pollen and plant fragments from dung balls of the Shasta ground sloth (*Nothrotheriops shastensis*), found in Gypsum and Rampart Caves along the lower Colorado River just outside the southern margins of the Great Basin. Plant remains had been recovered from other cave sites (e.g., Smith Creek Cave; Thompson, 1984) but these were as yet unstudied. Only two Late Quaternary pollen sequences from within the Great Basin—Chewaucan and Warner marshes in south-central Oregon—had been analyzed by Ernst Antevs' colleague Henry Hansen (Hansen, 1947). These pollen records, in combination with knowledge of the northern European climatic sequence (Blytt-Sernander) (Iversen, 1973:13–14), were instrumental in Antevs' formulation of his tripartite Neothermal climatic scheme (Antevs, 1948). Another early pollen locality, Tsegi Canyon in northeastern Arizona (Sears, 1937), lay well beyond the Great Basin's southeastern edge. Use of tree ring analysis to provide clues of the Holocene climates driving vegetation changes was still in its descriptive stage, and chronologies were still relatively limited in length (Hardman and Reil, 1936; Antevs, 1938; Schulman, 1956). The revolution in reconstruction of vegetation and climate history of arid areas, brought about by the recognition of the potential of packrat middens as a fossil record (Betancourt et al., 1990), was still nearly a decade and a half in the future. Indeed, a half century ago, we had more direct information about Tertiary floras in the

Great Basin and adjacent regions than we did about Late Quaternary vegetation history (La Motte, 1936; Axelrod, 1939, 1944, 1948; Brown, 1949).

Today our much-improved understanding of late Pleistocene terrestrial vegetation history can be usefully compared with the history of Great Basin aquatic and landscape systems, with detailed human and faunal records, and, most fundamentally, with global and regional climate reconstructions. The advances in our understanding of Great Basin vegetation history come from three main sources: (1) millennia-long tree ring records, (2) pollen and plant macrofossils recovered from lake, marsh, and

dry cave settings, and (3) plant materials obtained from ancient woodrat nests (Figure 1). In addition, studies of plant macrofossils and tree ring series provide information regarding plant physiology through study of anatomical features (e.g., Van de Water et al., 1994) and stable isotopic signatures (Siegal, 1983; Feng and Epstein, 1994; Van de Water et al., 1994; Wigand, 1995; Jahren, 1996). The potential of future molecular and genetic studies of these remains (e.g., Hamrick et al., 1994; Poinar et al., 1998) will offer additional information regarding phylogeography and the response of plant populations to changes in past climate.

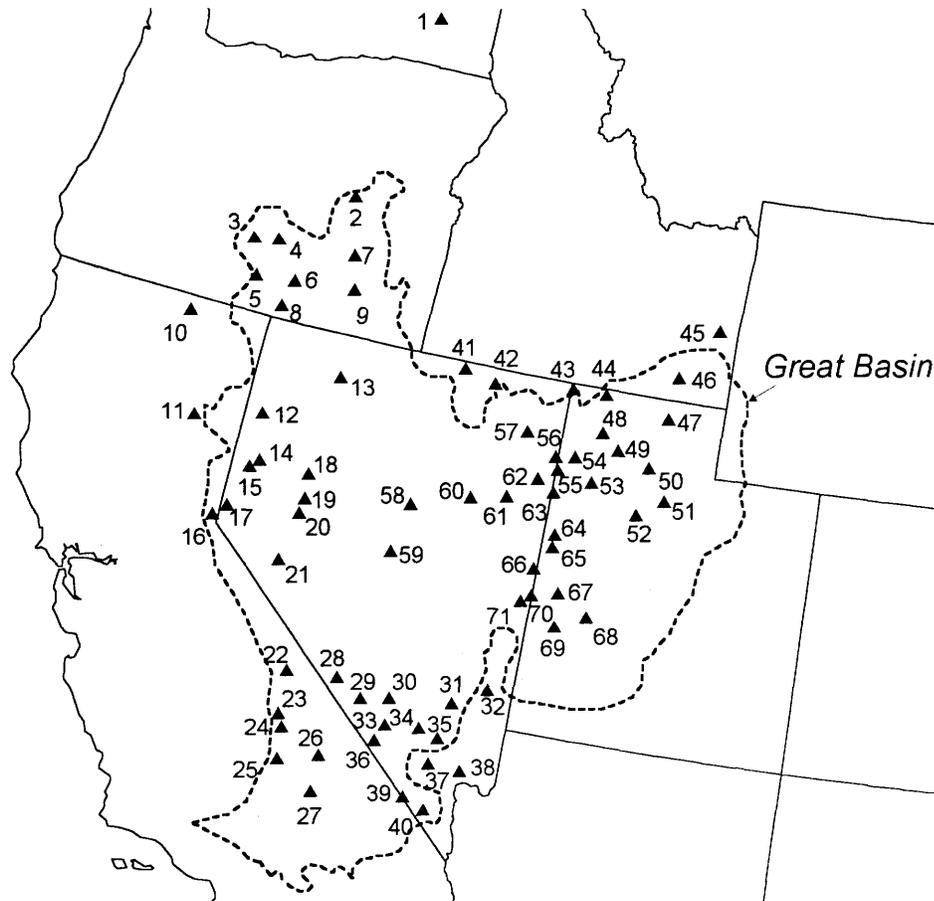


FIGURE 1.—Map of the western United States showing the Great Basin and localities, as discussed in the text, from which tree ring records, pollen and plant macrofossils, and plant materials from ancient woodrat nests were obtained. 1, Wildcat Lake; 2, Craddock Meadow; 3, Summer Lake (Ana River, Bed and Breakfast); 4, Alkali Lake Valley; 5, Chewaucan marsh; 6, Bicycle Pond; 7, Diamond Pond; 8, Warner Lake; 9, Steens Mountain (Fish Lake, Wildhorse Lake); 10, Lava Beds; 11, McCoy Flat; 12, Smoke Creek Desert; 13, Jackson Range; 14, Pyramid Lake; 15, Painted Hills; 16, Lake Tahoe; 17, Little Valley; 18, Lovelock Cave; 19, Carson Sink (Lead Lake); 20, Hidden Cave; 21, Walker Lake; 22, White Mountains (Methusaleh Walk); 23, Alabama Hills; 24, Owens Lake; 25, Little Lake; 26, Warm Sulphur Springs; 27, Searles Lake; 28, Eureka Valley; 29, Cofer Spring; 30, Eleana Range; 31, Lower Pahrnanagat Lake/Pahrnanagat Range; 32, Meadow Valley Wash; 33, Specter Range/Spotted Range/Little Skull Mountain; 34, Pintwater Range (Pintwater Cave); 35, Sheep Range; 36, Ash Meadows/Owl Canyon; 37, Tule Springs; 38, Gypsum

Cave; 39, Sandy Valley; 40, McCullough Range; 41, Owyhee River Valley; 42, Jarbidge Mountains (Mission Cross Bog); 43, Grouse Creek Range (Swallow Shelter); 44, Raft River Mountains (Curelom Cirque); 45, Grays Lake; 46, Swan Lake; 47, Bear River (Cutler Dam formation); 48, Crescent Spring/Hogup Cave; 49, Lakeside Range (Homestead Cave, Gillespie Hills); 50, Great Salt Lake; 51, Snowbird Bog; 52, Onaqui Range (Devils Gate); 53, Knolls; 54, Silver Island Canyon; 55, Wendover (Danger Cave, Leppy Overhang, Triple Barrel); 56, Pilot Range (Raven Cave); 57, Pequoop Range (Icicle Cave); 58, Potato Canyon Bog; 59, Gatecliff Shelter; 60, Ruby Marsh; 61, Cherry Creek Range; 62, Goshute/Toano Range (Top of the Terrace, Marblehead Mine); 63, West Bonneville Basin (Bonneville Estates, Twin Peaks, Pristine Shelter); 64, Indian Farm Canyon; 65, Granite Canyon; 66, Northern Snake Range (Council Hall Cave, Smith Creek Cave, Arch Cave, Ladder Cave, Old Man Cave); 67, Confusion Range; 68, Cricket Mountains; 69, Wah Wah Range; 70, Garrison; 71, Southern Snake Range.

Our intention in this paper is not to summarize everything that we currently know about vegetation history in the region, but rather to highlight major vegetation patterns and changes that reveal underlying climate trends and variability throughout the Great Basin.

#### ENVIRONMENTAL SETTING

The Great Basin of western North America is a region of dramatic topographic relief and striking vegetation transitions over short distances. Lying between the Sierra Nevada/Cascade mountain chain on the west and the Wasatch Front on the east, the Great Basin comprises a great mosaic of diverse habitats. Great Basin climate reflects the effects of both the heterogeneous topography and the varying impact of three major air mass systems that intersect over it (Houghton, 1969; Houghton et al., 1975).

*Pacific: a regime dominated by maritime polar air masses.* These moist cool air masses from the Pacific Ocean produce cool, wet winters, and their absence in summer makes the growing season hot and dry. Plant species such as Sierran white fir (*Abies concolor* var. *lowiana* (Gordon) Lemmon) and whitebark pine (*Pinus albicaulis* Engelm.) depend upon the reliable winter rainfall that this air mass provides. These species extend into the Great Basin from the west and northwest, dotting mountain tops that lie in the path of the Pacific storm tracks.

*Gulf: a regime dominated by maritime and continental tropical air masses.* These warm, moist air masses entering the southwestern United States from either the Gulf of Mexico or the Gulf of California produce hot, moist summers with midsummer torrential rainfall (originating during convective storms) and warm, dry winters. Plants, such as creosote bush (*Larrea tridentata* (Sessé & Moc. ex DC.) Cov.), and perhaps singleleaf piñon pine (*Pinus monophylla* Torr. & Fremont), that favor warmer winter temperatures and summer rainfall extend into this area from the southern desert, except in places where winter or summer temperatures are too harsh.

*Polar: a regime dominated by continental polar and arctic air masses.* These cold, dry continental air masses from the North American interior extend into the Great Basin from the northeast during the winter. Such air mass system "outbreaks" restrict the plant species able to grow within the area of greatest influence to those with physiological limits tolerant of cold, dry winters coupled with periodic drought (e.g., limber pine, *Pinus flexilis* James).

Movements of these air systems, and their effects on local and regional climate, are reflected in changes in hydrology, erosion/deposition processes, and vegetation. Displacement of winter and summer storm tracks and the variations in penetration of the summer monsoon are all affected by the realignment of these pressure systems through time. Because movements of these three large air masses reflect changes in global circulation and are potentially revealed in the climatic proxy data of the Great Basin, changes in a large portion of the earth's climate system may be monitored through time.

In addition to the effects of these air masses, Great Basin climates and vegetation are further complicated by topography. The effect of topographic diversity in the Great Basin on the distribution of precipitation has resulted in the formation of a multiplicity of habitats within close proximity, thus fostering rich biotic diversity (Billings, 1951). Elevational changes in plant distributions can be dramatic in response to the orographic effect of north-south-trending mountain chains that lie across the paths of Pacific storms or, conversely, that funnel summer monsoonal rainstorms northward. Finally, the overriding rain shadow effect of the Sierra Nevada mountains to the west exerts a massive impact upon rainfall distribution in the Great Basin. The rising of these mountains that began during the Pliocene and accelerated during the course of the Pleistocene accentuated this effect (Axelrod and Raven, 1985; Axelrod, 1990; Thompson, 1991).

#### VEGETATION RESPONSE TO CLIMATE CHANGE

During the Late Quaternary most changes in vegetation communities occurred in response to climate change. Vegetation changes observed in the Great Basin have included large-scale latitudinal shifts of plant taxa that typically occurred in the south and east as well as the primarily altitudinal shifts that characterized the central and northwestern Great Basin. Smaller scale shifts in abundance of major taxa within plant associations have characterized the entire region during both low- and high-magnitude climate changes. Differences in the response of vegetation to variation in climate result from several factors. Primary among these factors are the magnitude and duration of the new climatic regime to which individual plant species are adjusting. Secondary are the variable effects of topographic relief in the formation of microhabitats, each with its own microclimate. Third in importance is the distance to source areas from which plant species would have to expand during climatic transitions.

The climatic sensitivity of vegetation in the Great Basin lies in the physiological characteristics of its species. As a result of millions of years of adaptation to arid and semiarid conditions—even before the Great Basin was formed (Tidwell et al., 1972)—many of the plants that grow in this region are opportunistic. They have evolved to quickly take advantage of increased precipitation. Many species respond to wetter conditions through increased pollen and seed production and rapid vegetative growth. Because the annual production of biomass is linearly related to effective annual precipitation (Walter, 1954), biomass production in arid and semiarid environments is a sensitive indicator of changing climate. Such changes can be measured directly today through satellite imagery and historically through repeat photography (Hastings and Turner, 1965). Increased productivity is evidenced in the fossil record by wider tree and shrub growth rings, greater needle and leaf size, and copious production of pollen. Therefore, even relatively brief episodes of greater rainfall that resulted in increased pollen

production may be evidenced in high-frequency pollen records as sudden rises in pollen influx.

Plant adaptations favoring rapid migration are aided by Great Basin topography. Many plants disperse their pollen and seeds with the wind, favoring rapid dispersal of propagules. Seeds of some plants are ingested or held in specialized organs by certain animals, then carried great distances to favorable locations where they may germinate and grow (e.g., Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine). Because of the steep relief of Great Basin mountain ranges, species can move the equivalent of several degrees of latitude by moving vertically only a few hundred meters. The north-south-aligned mountain ranges of the Great Basin also serve as corridors (at various elevations) that facilitate the north-south movement of plant and animal species in response to the vagaries of climate. (Intervening valleys may impede east-west movement between mountain ranges, however.) As a consequence, the potential lag time between climatic input and plant response to reach a new equilibrium may be much less in the Great Basin than it is in areas of reduced topographic relief, where plants must move hundreds of kilometers latitudinally to reach a new environmental equilibrium.

#### VEGETATION CHANGE, THE HYDROLOGIC RECORD, AND CYCLES OF EROSION AND DEPOSITION

In the Great Basin, rates of erosion and deposition are usually closely tied to climate. The low rainfall and high evaporation rates that characterize much of the Great Basin today support a relatively sparse vegetation cover that leaves much of the ground surface exposed to the erosive effects of rainfall. Areas with greater rainfall have relatively greater ground cover offering more protection against erosive processes. Great Basin plant communities respond to increased rainfall through greater foliage production by extant plants and through establishment of extra local plant species. Eventually, increased biomass provides a better buffer to increases in rainfall and reduces the amount of water reaching streams and lakes. Sudden increases in rainfall (either during a single event or during the course of a year) can overwhelm the ability of relatively sparse vegetation cover to assimilate the excess. This is almost immediately reflected in increased runoff and accumulation of water in the playa lakes, the sinks of Great Basin fluvial systems. If increased effective precipitation continues, the increase in the biomass of existing plants and the establishment of new plants providing cover (or protection) for previously exposed ground will eventually reduce the rate of sediment movement. A return to sparser vegetation cover will mark the return to lower effective precipitation and greater erosion potential. Thus, monitoring changes in sediment deposition rates in streams and lakes, directly through historical records and prehistorically through paleoecological studies, can provide excellent proxy data of climate-induced vegetation change.

#### THE NATURE OF THE DATA

The natural distribution of paleobotanical data sets is constrained to a large degree by moisture differences within the Great Basin. Low amounts of effective precipitation have favored the preservation of certain kinds of proxy data. Plant macrofossils preserved in dry cave deposits and woodrat middens provide intermittent records of local vegetation spanning tens of thousands of years. Wood from long-dead trees, preserved by the dry conditions that often characterize upper tree lines in the Great Basin, provides continuous evidence of climatic variation spanning the Holocene. A few lakes and desert springs provide long and often complex sedimentary records that can span thousands to hundreds of thousands of years. High organic production in some of these areas has resulted in rapid rates of deposition, and the records are particularly valuable for the examination of high-frequency pollen and the macrofossils of local aquatic plants. These records can be compared with tree ring data to generate longer, more detailed records of regional climate and vegetation response.

In general, the number of well-preserved palynological records decreases to the south (reflecting the greater rarity of lakes and marshes), and the number of woodrat midden localities decreases to the north (reflecting increasingly wetter conditions that favor dissolution of the protective urine coating of the nests). Tree ring series are taken mainly from near the tree line in the higher mountains of the margins of the Great Basin, most commonly in the southern half of the Basin. Fortunately, recent field studies are alleviating some of these problems of data scarcity.

Integration of currently available paleobotanical proxy data reveals Great Basin vegetation dynamics in great detail for the last 4 Ka (thousand years ago) and more coarsely for the last 35 Ka. Earlier than 40 Ka, only a few pollen or midden records are available (e.g., from the Summer Lake/Chewaucan Lake basin in the northwest, Owens Lake in the west, Searles Lake in the south, and the Bonneville Basin in the east). For the period after 40 Ka, data obtained from pollen records are supplemented by evidence obtained from ancient radiocarbon-dated woodrat middens. Several high-resolution pollen records in the northwestern Great Basin and the northern Mojave Desert provide excellent coverage of both terrestrial and aquatic vegetation history from 6 Ka to the present. Ostracodes and diatoms from the northern Mojave Desert record are being used to reconstruct regional groundwater histories as well. In the Lahontan and Bonneville Basins, vegetation history inferred from middens and pollen records can be correlated with well-dated Late Quaternary lake histories.

In general, evidence of the relocation of semiarid and subalpine woodlands is most obvious for the late Pleistocene/early Holocene transition, especially in the woodrat midden record of the Great Basin and northern Mojave Desert mountain ranges (Van Devender et al., 1987). These records show that during the Pleistocene, woodland species often grew as much as 1000 m (and in a few instances >1000 m) below their

present-day elevation. Substantial shifts in woodland species, however, have occurred during the Holocene as well. During the middle Holocene, some tree species were displaced by perhaps as much as 500 m above where they are found today, especially in the western and northwestern Great Basin. Downward displacement of semiarid woodland by as much as 150 m appears to have occurred several times late Holocene.

Changes in the distribution of individual shrub species and changes in the composition of shrub communities have also been dramatic during the late Holocene. This is most obvious in the southern Great Basin and the northern Mojave Desert but also has occurred in the northern Great Basin. Changes are most obvious in woodrat midden records of lowland and intermediate elevations, but some less obvious changes in shrub communities are also apparent in the few pollen records of the Great Basin. Because the plant communities of the northern and northwestern Great Basin are situated well away from major vegetation formation boundaries, they do not appear to be as dynamic as do those of southern Nevada that currently lie on the boundary between the Great Basin and the Mojave Desert. However, as the paleobotanical evidence described below will show, this perception is more apparent than real.

These various factors have differentially shaped the vegetation history of three broad regions of the Great Basin: (1) the northwest (Lahontan Basin and adjacent mountain ranges), (2) the south (southern Great Basin and northern Mojave Desert), and (3) the northeast (Bonneville Basin and adjacent mountain ranges). Late Quaternary vegetation histories of these three regions are discussed separately below. In these discussions, chronological estimates are based on uncalibrated radiocarbon years, unless otherwise noted. Chronological divisions (e.g., the Wisconsin/Holocene break) follow general vegetation and geomorphic patterns within each separate region.

### Northern and Western Great Basin

#### LATE PLEISTOCENE (~250 TO 12.5 KA)

Mifflin and Wheat (1979) indicated that the Great Basin rivaled the Minnesota of today as a land of lakes during the Pleistocene. The Holocene remnants of these Pleistocene lakes in the northern and western Great Basin were visited by European fur trappers, including Peter Skene Ogden, as early as the 1820s (Davies et al., 1961). Several lakes, including Pyramid Lake, were described by J.C. Frémont during his explorations of the West during the 1840s (Frémont, 1845). The first study of pluvial Lake Lahontan was made by I.C. Russell (1885), who described two lake phases indicated by lower and upper lacustral clays. Morrison (1964, 1965, 1991) and Morrison and Frye (1965) further defined the lake's history using such picturesque formation names as the Eezta (early Wisconsin or earlier), the Sehoo (late Wisconsin), and the Fallon (Holocene). They correlated these lakes with stades of the Wisconsin glaciation or other Late Quaternary episodes of cooler, wetter climate. Since then, Davis (1978) and Benson et al. (1987, 1990,

1992, 1997) have further narrowed the chronology and details of lake history. These understandings serve as a backdrop for reconstruction of the vegetation history of the region.

PRE-LATE WISCONSIN (>35 KA).—A growing body of research in the northern and western Great Basin is clarifying the relationships among past climate history, lake and marsh history, and vegetation change (Mehring, 1985, 1986). Two long pollen records that include more than just the Holocene—Summer and Owens Lakes (respectively: Cohen et al., 2000; Smith and Bischoff, 1997)—are available from the region, not including a series of pollen cores from the southern Cascades near Klamath Lake (Adam et al., 1995). Although the proxy record of past climate is far from complete, the general pattern suggests that high lakes may be more closely linked to the onsets and declines of glacial episodes in the region than to the glacial maxima.

The Summer Lake basin of south-central Oregon currently lies on the transition between the pine woodlands of the eastern slope of the Cascades and the sagebrush (*Artemisia* spp.) steppe of the northern Great Basin. Three pollen localities from the Summer Lake basin span much of the last 250 Ka (Cohen et al., 2000). The Summer Lake records include the lower two-thirds of oxygen isotope stage (OIS) 6, all of OIS 4 and OIS 3, and the lower portion of OIS 2 as defined by Pisias et al. (1984) and Shackleton and Opdyke (1973). There also seem to be a few samples from the top dating to OIS 1. Shifts in the dominance of mixed montane conifers, cold steppe shrubs, and desert scrub species record the varying effects of precipitation and temperature and their changing seasonal influence. Greater abundance of fir (*Abies* spp.) and spruce (*Picea* spp.) pollen in a sediment column taken from the Ana River Canyon indicates that climate in the northern Great Basin was more mesic during the OIS 6 section (~170–220 Ka) than during OIS 4 and OIS 2 (Cohen et al., 2000). Unfortunately, an erosional episode (or episodes) removed much of the sediment that accumulated during the end of OIS 6 and much of OIS 5. Therefore, we do not have a good indication of the nature of vegetation and lake history in the Summer Lake basin during the latter portion of OIS 6 or at the beginning of OIS 5. Indices of drought (based upon a ratio of the pollen of dry- to that of wet-loving plant species) and temperature (based upon spore abundance) reflect much greater climatic variability during OIS 6 than in later stages (Figure 2). After the relatively brief cool, wet episode of OIS 4 (about 70 Ka), OIS 3 climates were relatively cool and dry and apparently comparably stable. The dominance of sagebrush and saltbush (*Atriplex* spp.) shrub communities during this stage suggests that plant communities on the valley floors were not much different than they are today. The Summer Lake paleoenvironmental records (Ana River, Wetlands Levee, and Bed and Breakfast localities; see Negrini et al., 2000; Negrini, 2002 (this volume)) are all truncated at about 22 Ka just as conditions were becoming cooler and wetter (the beginning of OIS 2 conditions). The nature of effectively wetter climatic episodes differs throughout the record.

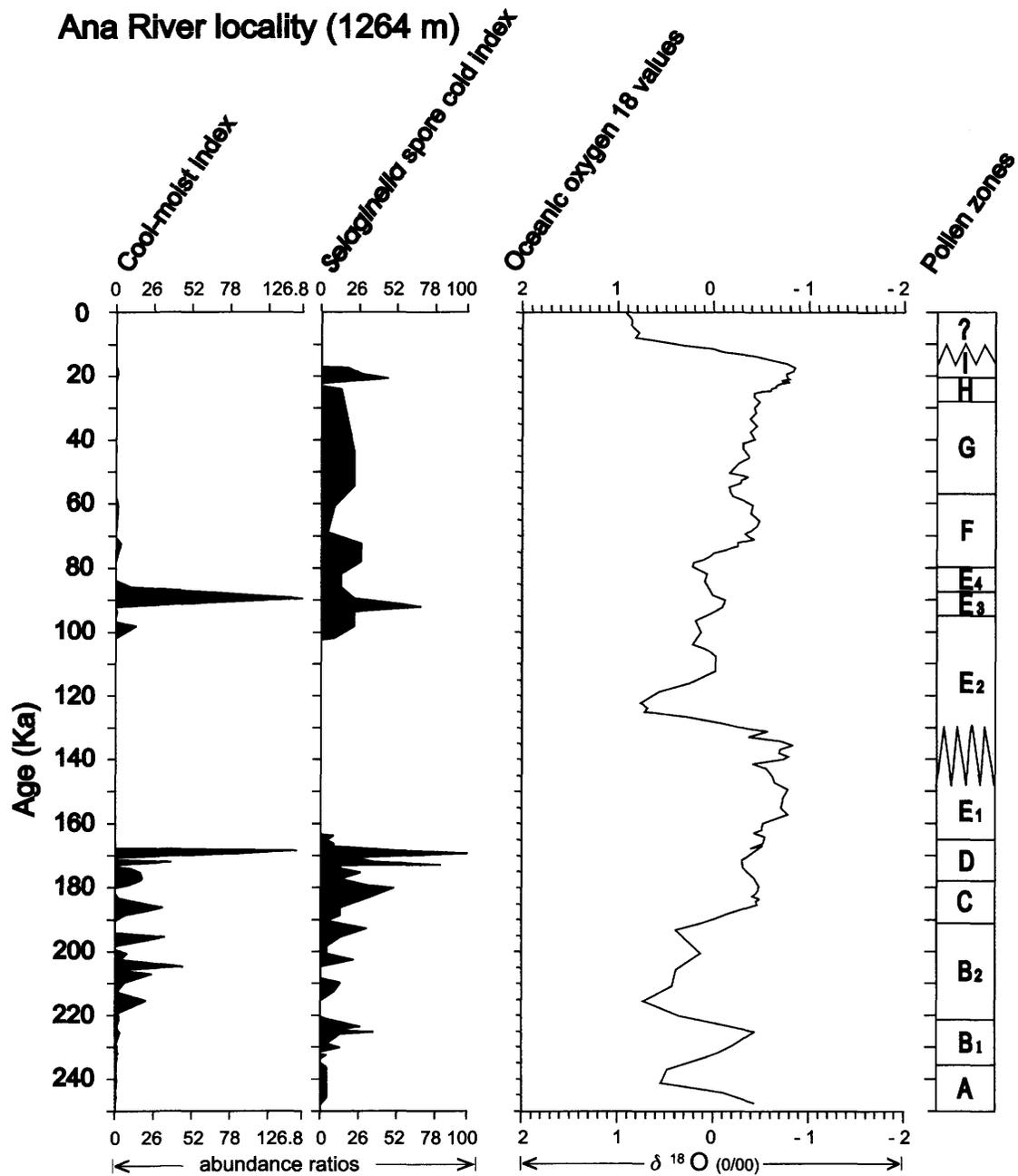


FIGURE 2.—Comparison of moisture and temperature indices from the Ana River in Summer Lake basin, south-central Oregon (elevation, 1264 m), with the oceanic  $^{18}\text{O}$  curve (Martinson et al., 1987). The cool-moist index (or rather, “drought” index) was generated by setting relative abundances of conifer pollen against those of salt-bush and greasewood pollen; values represent a ratio of pollen from the dry-loving species to that of the wet-loving species (moister is to the right on the x-axis). The temperature index is a measurement of the relative abundance of spike moss (*Selaginella densa*) spores (to the right is colder). A combination of radiocarbon and paleomagnetic dating techniques was used to obtain ages (Ka = thousands of years ago).

Glacial maxima appear to have been characterized by extremely cold temperatures and relatively little rainfall. The maxima of the interstades seem to have been typified by warmer temperatures and, in some cases, by substantial drought. The

transitions generally were typified by moister conditions and varied only in whether they were warmer or cooler. Records for both Summer Lake and Owens Lake indicate that cool, wet periods resulted in the regional expansion of conifers, but these

expansions occurred during the initial and terminal (transitional) stages of glacial stades. Once the glacial stage approached its climax, temperature (extremely cold conditions) became more important than moisture as a control for vegetation. Therefore, the transitional periods between warm, dry climates and cool, dry climates were the most amenable for the expansion of forests and woodlands. Marsh expansion and algae productivity also was greatest during these periods. When lake levels were high, the extent of marsh area in the Summer Lake basin was restricted by the steep gradients of the mountains on the north, west, and south margins. Marsh expansion was most extensive at the shallow north end of the basin during periods of intermediate-depth lakes, when the water table would have been close to the surface. Today the northern fringing marsh is artificially maintained by levees constructed by the U.S. Fish and Wildlife Service. The levees result in high water table conditions in the northern part of the Summer Lake basin—conditions that mimic those of the intermediate-depth lakes found locally during the Pleistocene and the moist periods of the Holocene. Marsh areas during shallow-lake periods would have been severely restricted to areas immediately surrounding stream entries at lake edges or around spring seeps.

This climatic pattern also appears to be reflected in the Owens Lake pollen record (Woolfenden, 1993, 1997). A ratio of juniper (*Juniperus* sp.) pollen to *Ambrosia*-type pollen reflects the effect of Late Quaternary climatic conditions on vegetation; this ratio clearly indicates that periods of greater juniper pollen were warmer and periods of *Ambrosia*-type pollen were cooler (Woolfenden, 1997, fig. 17). Although wetter than those of today, Owens Lake climates >35 Ka were relatively dry. More closely spaced samples at Owens Lake revealed greater detail in the record, but major transitions to a warmer, drier climate at 120 Ka, and to a cooler, wetter climate at 70 Ka are clear in the records from Owens Lake and the Summer Lake basin. Dugas (1998) recorded a highstand of pluvial Lake Malheur northeast of Summer Lake between 80 and 70 Ka based on the occurrence of water-deposited Pumice Castle tephra. Gehr (1980) dated mollusk shells from a beach ridge indicating a highstand of pluvial Lake Malheur at 32 Ka, and Dugas (1998) presented additional dates that Gehr obtained on shells that confirm this age from other beach ridge positions. In addition, the occurrences of indicator species reflect the warm conditions of the interglacial and even, to some extent, the interstades for the last 150 Ka. At Owens Lake, oak (*Quercus* sp.) and walnut (*Juglans* sp.) pollen were more common during the last interglacial and the interstades (Woolfenden, 1997, fig. 8). In the record from the Ana River, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is the indicator.

PRE-FULL GLACIAL (35 TO 26 KA).—Terrestrial conifer pollen evidence from the Bed and Breakfast and Wetlands Levee localities at Summer Lake (Figure 3) and from woodrat midden strata west of Pyramid Lake indicates that cooler, wetter conditions prevailed from 34 to 30 Ka. Haploxyton pines in this area primarily prefer a cooler and/or wetter climate pines

whereas diploxyton pines generally prefer a warmer and/or drier climate. This shift was heralded by an expansion of juniper (Figure 2) and sagebrush. Increased regional abundance of grass together with retreat of saltbush and greasewood (*Sarcobatus* sp.) are indicated (Figure 3). Slight differences between the Wetlands Levee and the Bed and Breakfast records may reflect differences in both sample spacing and distance from shore within the basin. Dramatically reduced productivity of the eutrophically adapted algae *Botryococcus* at the Bed and Breakfast locality, indicates colder water temperatures during this period (Figure 3). A return to drier conditions at ca. 29.6 Ka is indicated by a decrease in fir and spruce and an increase in saltbush (Cohen et al., 2000). A major drought from 28 to 26 Ka is flanked by regionally correlatable grass expansions in the woodrat midden pollen record at Pyramid Lake as well as in the sediments of Summer Lake (Figures 3, 4). This drought is evidenced by saltbush expansion and is reflected in lowered lake levels throughout the northwestern Great Basin (Negrini and Davis, 1992).

In the north-central Great Basin, subalpine and/or tundra species of juniper (prostrate or creeping juniper, *Juniperus horizontalis* Moench, and common juniper, *J. communis* L.) appear in a woodrat midden from the Owyhee River Valley, dating from about 27 Ka (Wells, 1983). Their appearance in a woodrat midden dating to this period of drought (Benson et al., 1990; Negrini and Davis, 1992) suggests that the period may have been not only dry but cold as well.

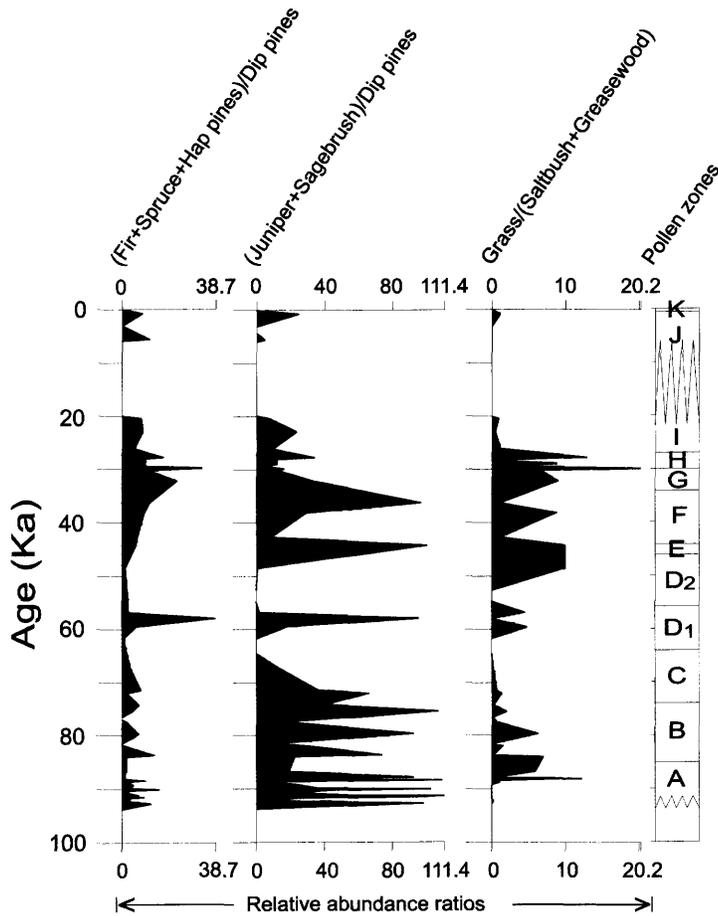
The pollen records from Summer Lake and McCoy Flat (a valley floor site along Pine Creek, west of Eagle Lake on the eastern fringe of northern California's Modoc Plateau), and the woodrat midden records from around the pluvial Lake Lahontan basin, indicate that juniper occasionally was locally abundant between 50 and 12 Ka in the northwestern Great Basin (Figures 5, 6). This occasional juniper pollen, which differs somewhat in appearance from juniper pollen typically found in the sediments of Summer Lake and McCoy Flat during most of the Late Quaternary, might be that of common and/or prostrate juniper. This might indicate colder, more tundra-like or alpine-like conditions.

Woodlands dominated by Utah juniper (*J. osteosperma* (Torr.) Little), as evidenced by the presence of Utah juniper twiglets dating to ~34 Ka in woodrat middens, were growing at least as far north as the shores of pluvial Lake Lahontan (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). Comparison of juniper with other species in the pollen and macrofossil records from the region indicates that juniper expansions occurred during cool, moist periods of climate before and after the glacial maxima.

LAST GLACIAL CYCLE (26 TO 12.5 KA).—Effectively moister climate after 24.5 Ka, coincident with renewed growth of pluvial Lake Lahontan, encouraged the spread of Utah juniper woodlands and allowed whitebark pine to intrude into scattered localities as low as 1380 m in elevation (Wigand and Nowak, 1992). Slopes currently dominated by saltbush scrub were

Wetlands Levee locality

west-central Summer Lake basin



Bed and Breakfast locality

southwestern Summer Lake basin

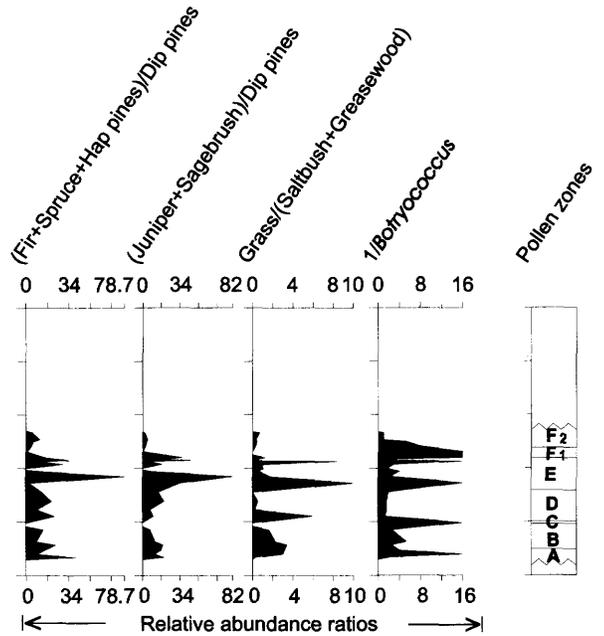


FIGURE 3.—Ratios of the abundances (x-axis) of selected major pollen types from the Wetlands Levee and Bed and Breakfast localities in the Summer Lake basin, south-central Oregon, by date (years before present, B.P.). Increases in the ratio of (fir + spruce + haploxyton (Hap) pine)/diploxyton (Dip) pine indicates cooler, moister conditions. Increases in the ratio of (juniper + sagebrush)/Dip pine herald the expansion of juniper woodland. Increased regional moisture is indicated with increases in the ratio of grass/(saltbush + greasewood). Dramatically reduced productivity of the algae *Botryococcus* is revealed by plotting the inverse of its abundance,  $1/Botryococcus$ . All ratios indicate moister conditions to the right and drier conditions to the left.

characterized then by sagebrush steppe and by occasional perennial seeps lush with fewflower spikerush (*Eleocharis quinqueflora* (F.X. Hartmann) Schwarz) (Wigand and Nowak, 1992). Utah juniper macrofossils that were found in a woodrat midden dating to  $20,460 \pm 990$  years B.P. (before present; laboratory no. Beta-41919), located just above the highest shoreline of pluvial Lake Lahontan on the western margin of the Carson Sink, reflect the peak of pre-glacial maximum expansion of juniper well beyond its current limits (Wigand and Nowak, 1992). This period corresponds to the rapid rise of pluvial Lake Lahon-

tan at the beginning of the last glacial cycle (Benson et al., 1997, fig. 4). By 20 Ka the onset of much cooler, drier glacial maximum conditions led to a decline in Utah juniper, disappearance of whitebark pine from the midden record, and expansion of mixed sagebrush and shadscale (*Atriplex confertifolia* Torr. & Fremont) desert scrub communities (Nowak et al., 1994a). Approximately 23 and 12 Ka, during the wetter periods leading up to and following but not during the glacial maximum, whitebark pine occurred along the western margin of the Lahontan Basin, more than 1000 m lower than its current eleva-

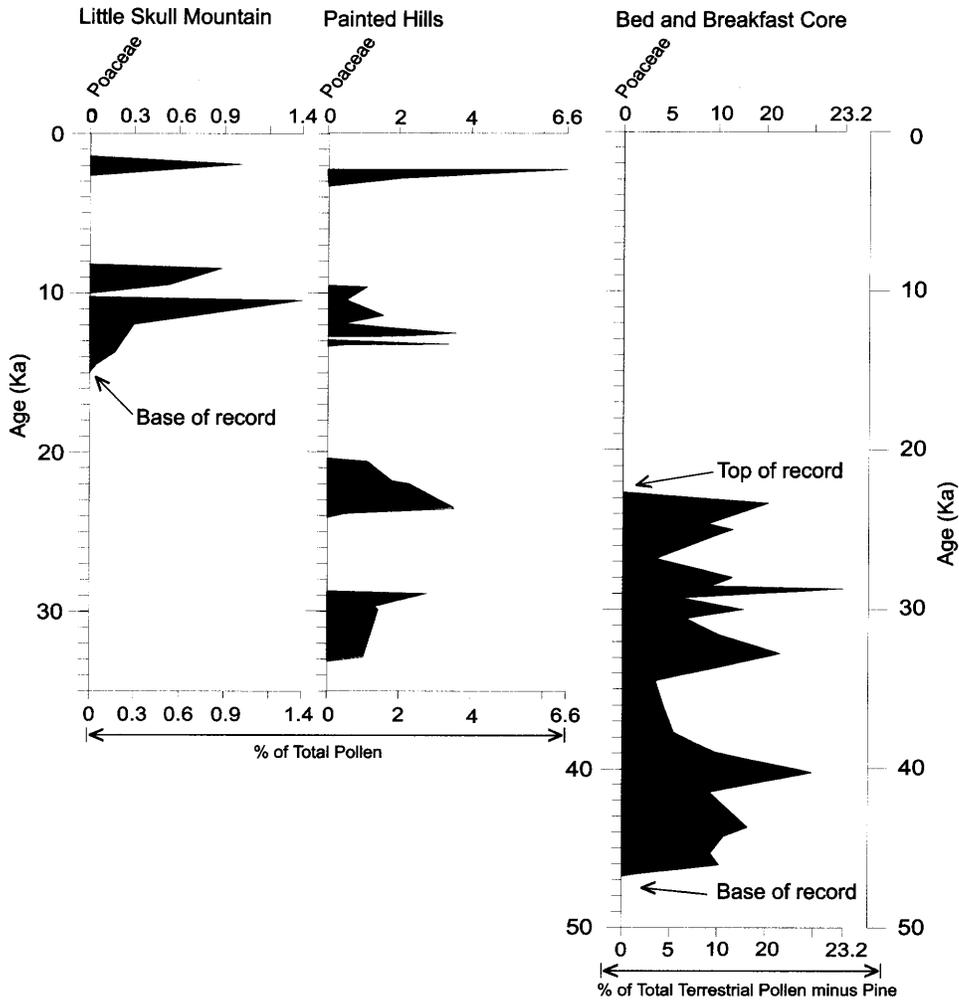


FIGURE 4.—Comparison of Late Quaternary relative abundances (as percentages) of grasses (Poaceae) in lacustrine core sediment from the Bed and Breakfast locality in Summer Lake basin, Oregon, with the relative grass percentages from the woodrat midden pollen records obtained from Painted Hills west of Pyramid Lake, west-central Nevada, and from Little Skull Mountain in the northern Mojave Desert, southern Nevada, by date (years before present, B.P.). The pollen record from Pyramid Lake was obtained from a single stratified woodrat midden, whereas the Little Skull Mountain record was from several adjacent woodrat middens.

tion (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). This provides an indication of just how cold the glacial maximum may have been in northwestern Nevada. Estimates of the temperature difference for the onset and decline of the glacial maximum, based upon the current temperature limits of white-bark pine in the area today, indicate that the mean annual temperature (MAT) was at least 7° C colder during the onset and decline of the glacial maximum. Considering that woodland in this region disappeared during the glacial maximum because conditions were so cold, the MAT may have been 1°–2° C colder still.

The harsh (much colder and drier) conditions during the glacial maximum around 18 Ka also may have severely restricted

semiarid woodland. Juniper even may have been locally or regionally extinct in the northwestern Great Basin. Utah juniper appears to have been present before and after the glacial maximum along the western shore of pluvial Lake Lahontan (Wigand and Nowak, 1992; Nowak et al., 1994a, 1994b). After the glacial maximum, woodrat midden data indicate that western juniper (*Juniperus occidentalis* Hook.) was present in places along the shores downwind of pluvial Lake Lahontan, where it may benefitted from “lake effect” (Thompson et al., 1986). Absence of woodrat midden strata and the scarcity of pollen records dating to the glacial maximum preclude making definite inferences regarding the distribution of juniper on the landscape. Greater shrub dominance, however, in both the

Bed and Breakfast locality (1264 m)

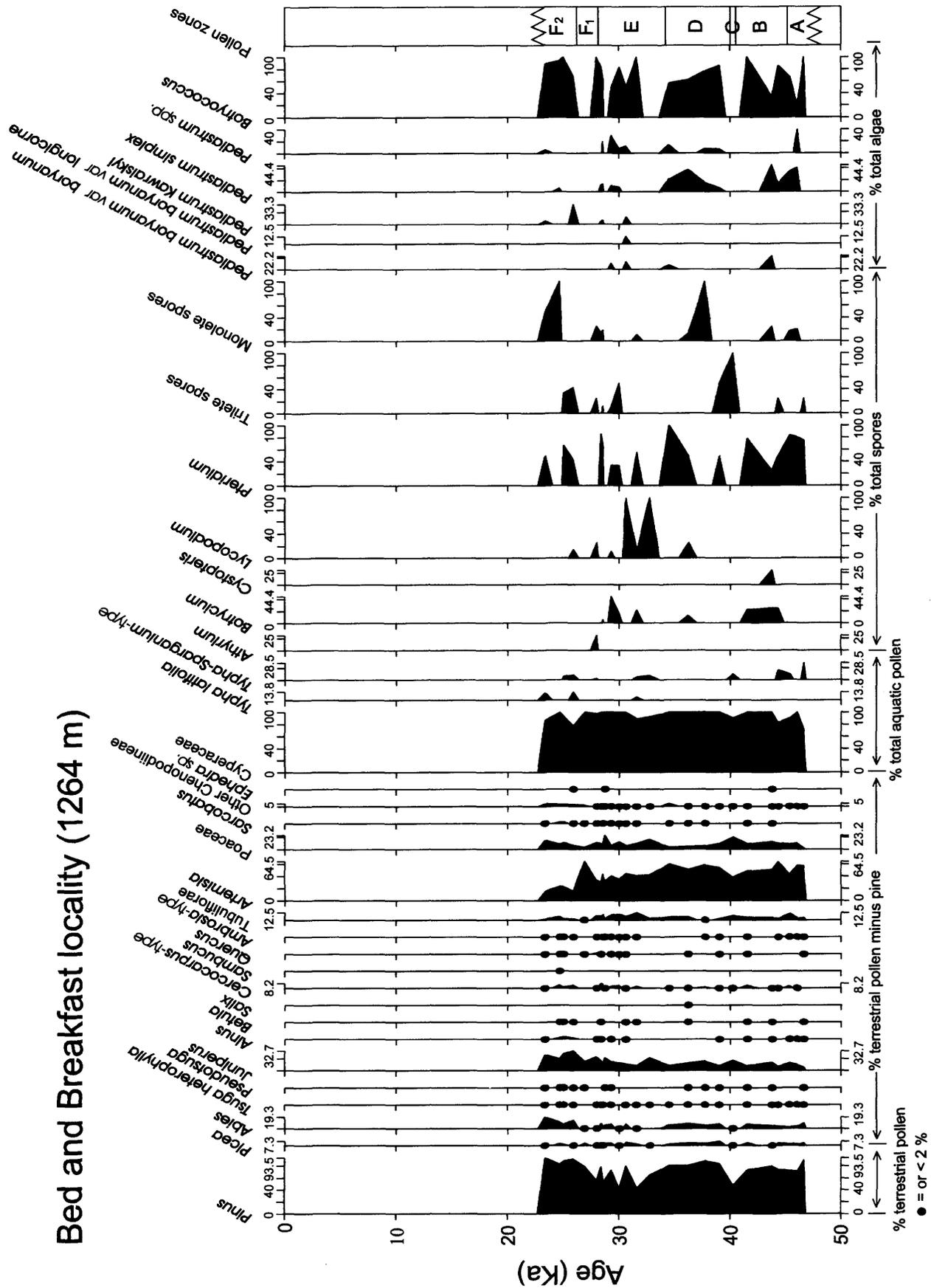


FIGURE 5.—Relative percentage diagram of major pollen, spore, and algae types from the Bed and Breakfast locality, Summer Lake basin, Oregon (elevation, 1264 m). Dates are based upon paleomagnetic age assignments. A bullet (●) on a line indicates a constituent value of  $\leq 2\%$ . Pollen zones are from Cohen et al., 2000.



pollen and macrofossil samples from woodrat midden strata immediately before and after the glacial maximum suggests that juniper may have been relatively scarce, probably occupying protected locations. On the other hand, shrub communities dominated by sagebrush, and at times saltbush, characterized extensive portions of the northwestern Great Basin (Wigand and Nowak, 1992). These data suggest that it was either too dry or too cold (or both) for juniper woodland to survive in the northern Great Basin during the last glacial maximum.

Relatively warmer, wetter conditions after the glacial maximum led to dramatic increases in sagebrush-dominated communities, and limited reexpansion of whitebark pine as well (Wigand and Nowak, 1992; Nowak et al., 1994a). Findings of Utah juniper in woodrat middens dated to 12,260 ± 140 years B.P. (Beta-47203) and 11,980 ± 110 years B.P. (Beta-47204) at the highest strandline on the eastern shore of the Carson Sink reflect reexpansion of semiarid woodland after the glacial maximum. By 12.5 Ka (concurrent with the final late-Pleistocene high-

stands of pluvial Lake Lahontan (Benson et al., 1990, 1992); see Negrini, 2002) mesic plant communities, reflecting lake effect and orographic forcing of rainfall along the eastern shore of pluvial Lake Lahontan, contrasted sharply with more xeric plant communities to the west (Wigand and Nowak, 1992).

The pollen record from a large woodrat midden west of Pyramid Lake that spans the last 34 Ky (thousand years) suggests substantial differences between climates at the onset (~24 Ka) and at the end (~12 Ka) of the last glacial cycle (Wigand and Nowak, 1992; Figure 7). Despite the expansion of whitebark pine during both periods (evidenced by the presence of macrofossils in the midden), the substantially greater abundance of sagebrush pollen and the appearance of mountain mahogany (*Cercocarpus* sp.) in the macrofossil record of the latter period suggest cooler temperatures and less precipitation 12.5 Ka than ~24 Ka. In part this could also reflect greater variability in climate, as suggested by the deep-water tufa record from Pyramid Lake (Pelican Point) (Benson et al., 1995; Benson et al., 1996).

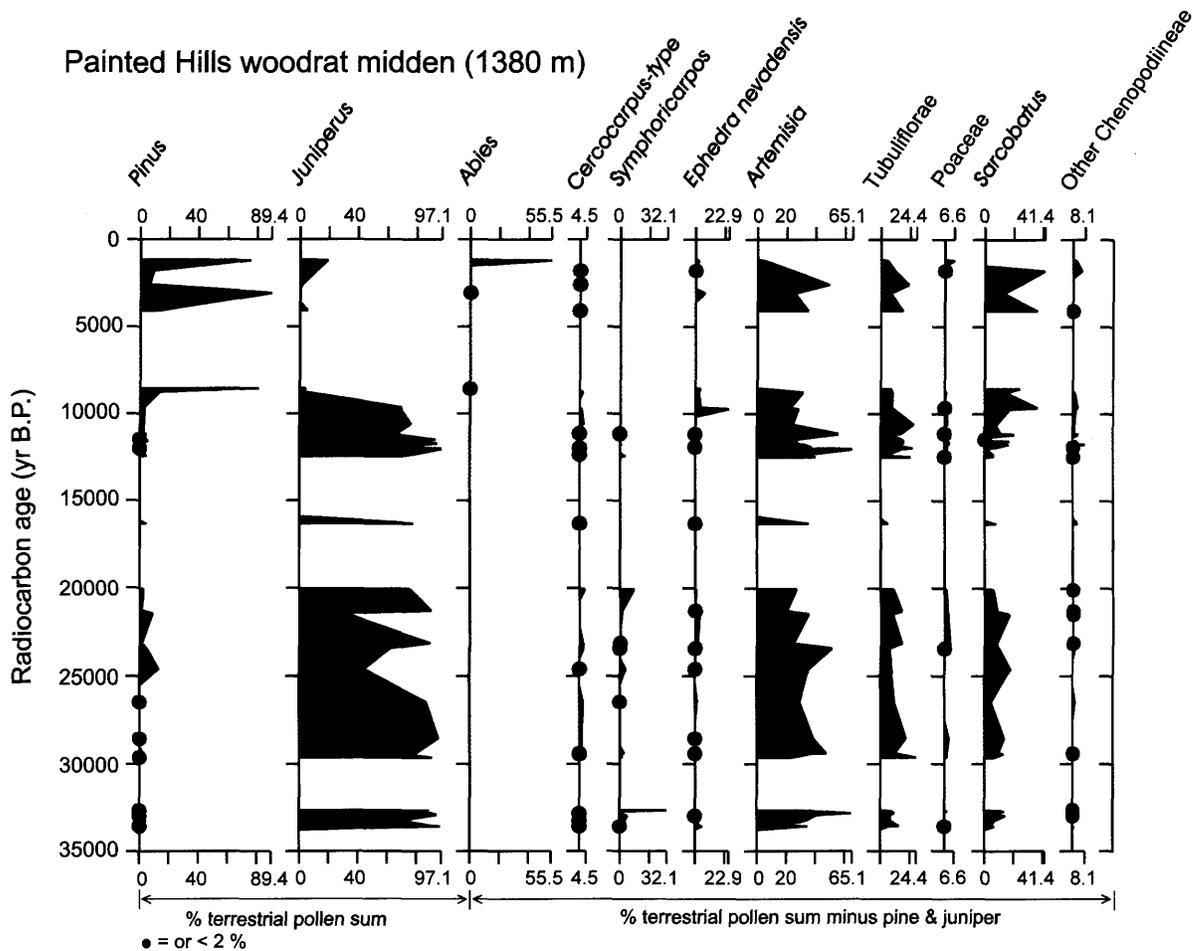


FIGURE 7.—Relative percentage diagram of major pollen types from a single stratified woodrat midden near Pyramid Lake, western Nevada (elevation, 1380 m). Dates are radiocarbon-based. A bullet (•) indicates a value of ≤2%.

## LATEST PLEISTOCENE/EARLY HOLOCENE (12.5 TO 8 KA)

This period is characterized by often incredibly diverse plant communities that contained species typical of the cooler conditions of the glacial period along with pioneering plant species that heralded the Holocene. Mehringer (1985) noted several characteristics that tied many of these plant communities together during this time, especially at the higher elevations and in the more xeric areas of the northern Great Basin. This includes (1) a treeless sagebrush steppe, often with abundant grass; (2) common occurrence of russet buffaloberry (*Shepherdia canadensis* (L.) Nutt.), occasionally juniper (probably common juniper), and more rarely spruce and fir; (3) combinations of pollen types such as *Rumex-Oxyria*, *Bistorta*, *Polemonium*, *Eriogonum*, and *Koenigia* that indicate subalpine or alpine plant communities; and (4) abundance of the spores of cold-climate plants such as *Selaginella densa*, *S. selaginoides*, *Botrychium*, and *Lycopodium*. For example, the pollen record from 2250 m at Fish Lake near Steens Mountain, Oregon, reflects the substantially colder conditions of the transition from the late Pleistocene to the early Holocene. The pollen record is dominated by sagebrush (*Artemisia*) and grass (Poaceae), which are representative of a cool, moist steppe (Mehringer, 1985). It also contains juniper pollen, which may signal the movement of common juniper from its lower elevation distribution during the Pleistocene to its new Holocene position high atop the mountain (Mehringer, 1985). By 9.7 Ka the last glacial ice remnants disappeared from the high, southeast-facing cirque basin near the top of Steens Mountain that became Wildhorse Lake (2560 m). Common juniper was probably established in the surrounding subalpine grassland that had replaced the snow and ice of the Pleistocene (Mehringer, 1985, 1986). The departure of ice from this basin and initiation of the lake may record, in part, the impact of the early Holocene thermal maximum.

The 9000-year-long pollen record from Bicycle Pond in the Warner Valley, south-central Oregon, indicates that the current lower limit of western juniper on the west-facing slope of Hart Mountain was probably dominated by a grassy, sagebrush steppe 9 Ka (Figure 8). Juniper, though present then, was less abundant than today. Although scattered pine trees may have occurred in nearby canyons, pine woodland probably lay where it does today: around the tops of the mountains lying west of the Warner Valley and in the west-facing canyons and on the east slope of Hart Mountain. The aquatic pollen record suggests that throughout the Pleistocene, Bicycle Pond was fed by a seasonal stream and springs that flowed from the layered basalts that composed the mountain above it. Bicycle Pond is cradled by a steep-sided, Pleistocene landslide basin that restricts littoral plant growth to a narrow margin. The well-drained slopes behind the littoral margin support a grassy, sagebrush steppe, which extends a couple of hundred meters to the floor of the Warner Valley. Grass pollen values that were higher in the early Holocene than today reflect a wetter environment then; and abundant sedge pollen (Cyperaceae) from that period

indicates that the marsh around Bicycle Pond was much more extensive than it is today and reflects substantial early Holocene spring activity.

At lower elevations, the early Holocene expansion of sagebrush steppe vegetation is matched by expansion of saltbush-dominated desert scrub vegetation before the fall of Mazama ash (see Chenopodiaceae values in Figure 8). The climax of saltbush scrub vegetation before and after the fall of Mazama ash is clearly evident in the pollen records from the Warner and Chewaucan valleys analyzed by Hansen (1947). Analysis of pollen from sediments in the Alkali Lake Valley in south-central Oregon, undertaken by one of the authors (Wigand), indicates that marshes (abundant sedge pollen) were present in the valley floor until ~9.5 Ka but disappeared soon after to be replaced by saltbush-dominated shrub communities. Gehr (1980) and Dugas (1998) recorded a series of radiocarbon dates between 9.6 and 7.4 Ka on mollusks from beach ridges and charcoal that indicated multiple pluvial highstands of Lake Malheur including some within five meters of its overflow into the Snake River drainage at Malheur Gap. The latter of these lakes may have been considerably lower. Mehringer and Cannon (1994) recorded a wet episode in the Fort Rock Basin, dating to around the fall of Mazama ash. In any case, generally drier conditions resulted in the establishment of saltbush communities by the time that Mazama volcanic ash fell in the region.

The pollen record from Fish Lake indicates that sagebrush steppe had expanded, becoming denser during the climatic warming of the early Holocene on Steens Mountain (Mehringer, 1985, 1986). This climaxed shortly before the fall of Mazama volcanic ash.

Further south in northwestern Nevada, the persistence of Utah juniper during the early Holocene at lower elevations (below where it occurs today) ended ~9.5 Ka. Radiocarbon ( $^{14}\text{C}$ ) dates for Utah juniper of  $9640 \pm 110$  years B.P. (Beta-46256) and  $9700 \pm 90$  years B.P. (Beta-46255) record the last time that it appeared during the early Holocene beyond its current distribution west of the Lahontan Basin. These dates correspond directly with the last dates on lithoid tufa that Benson et al. (1995) obtained from Pyramid Lake (Pelican Point), suggesting that retreat of juniper and dramatically lowered lake levels are contemporaneous and coincide with high northern hemisphere solar radiation during the early Holocene (Kutzbach and Guetter, 1986; Kutzbach et al., 1993). In areas more distant from the current margin of the semiarid woodland, juniper may have disappeared as much as a thousand years earlier.

Radiocarbon dates for Utah juniper from woodrat middens on the southwest margin of the Smoke Creek Desert, northwestern Lahontan Basin, suggest that it disappeared from that area by 10.3 Ka. A cluster of these dates ranging from  $10,830 \pm 100$  years B.P. (Beta-47200) to  $10,340 \pm 210$  years B.P. (Beta-35814) are the last from that area until a late-Holocene reexpansion of juniper.

As juniper was disappearing from areas it occupied during the Pleistocene, it was expanding northward into new areas. The

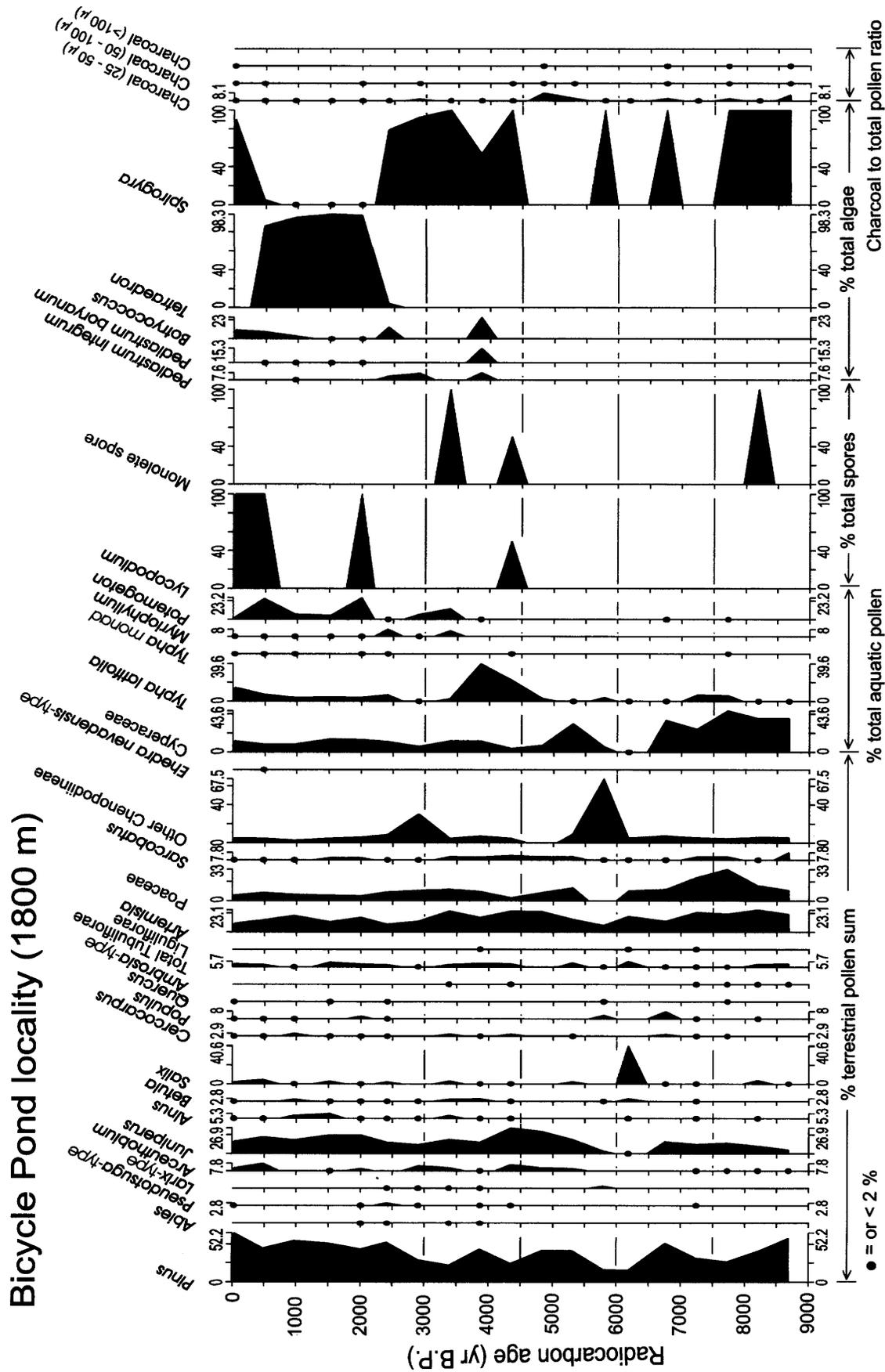


FIGURE 8.—Relative percentage diagram of major pollen, spore, and algae types and charcoal from Bicycle Pond, Warner Valley, south-central Oregon (elevation, 1800 m). Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates. A bullet (●) indicates a value of  $\leq 2\%$ .

presence of semiarid juniper woodland in the northwestern Great Basin by ~8.5 Ka is evidenced by juniper pollen values in pollen records from McCoy Flat in northern California and from Bicycle Pond on the west slope of Hart Mountain in the Warner Valley, south-central Oregon (Figures 6, 8). This is further corroborated by directly dated Utah juniper twigs from woodrat middens in the Jackson Range of northern Nevada with a date of  $8490 \pm 90$   $^{14}\text{C}$  years B.P. (Beta-64360). Although we know from the pollen records mentioned above that juniper occurred in south-central Oregon, no macrofossils have been recovered that indicate the species. This is the earliest species identification for the area.

The pollen record from Hidden Cave in the Carson Sink also reflects the early Holocene decline of woodland and expansion of desert shrub vegetation at the expense of sagebrush steppe (Wigand and Mehringer, 1985). Although the high lakes had disappeared from the Lahontan Basin by 11.0 Ka, cattail (*Typha*) pollen in Hidden Cave sediments indicates that extensive marshes remained until about 9.6 Ka (Wigand and Meh-

ringer, 1985, fig. 36). The pollen record indicates that dramatic regional decline in pine and sagebrush and equally dramatic increases in greasewood characterized this period. The ongoing effects of regional drought at low elevations are reflected in the fourfold increase in Chenopodiineae (primarily saltbush) pollen in Hidden Cave sediments by ~9.0–8.0 Ka, levels that would characterize the remainder of the Holocene. Additional evidence of desiccation of the lake basin is indicated in analysis of the sediments from the cave.

Statistical parameters of grain size analysis of Hidden Cave sediments conducted by P.J. Mehringer, Jr. (see Wigand and Mehringer, 1985), in the late 1970s indicate that between 7.5 and 5.5 Ka the energy of colluvial processes was declining as the energy of early Holocene storms was waning (Figure 9). However, eolian processes (indicated by more-positive skewness of sediments) were increasingly more active during this period of transition in the Lahontan Basin (Figure 9). Although the colluvial contribution to transportable sediment was declining during this transitional period, the regional reduction in plant cover

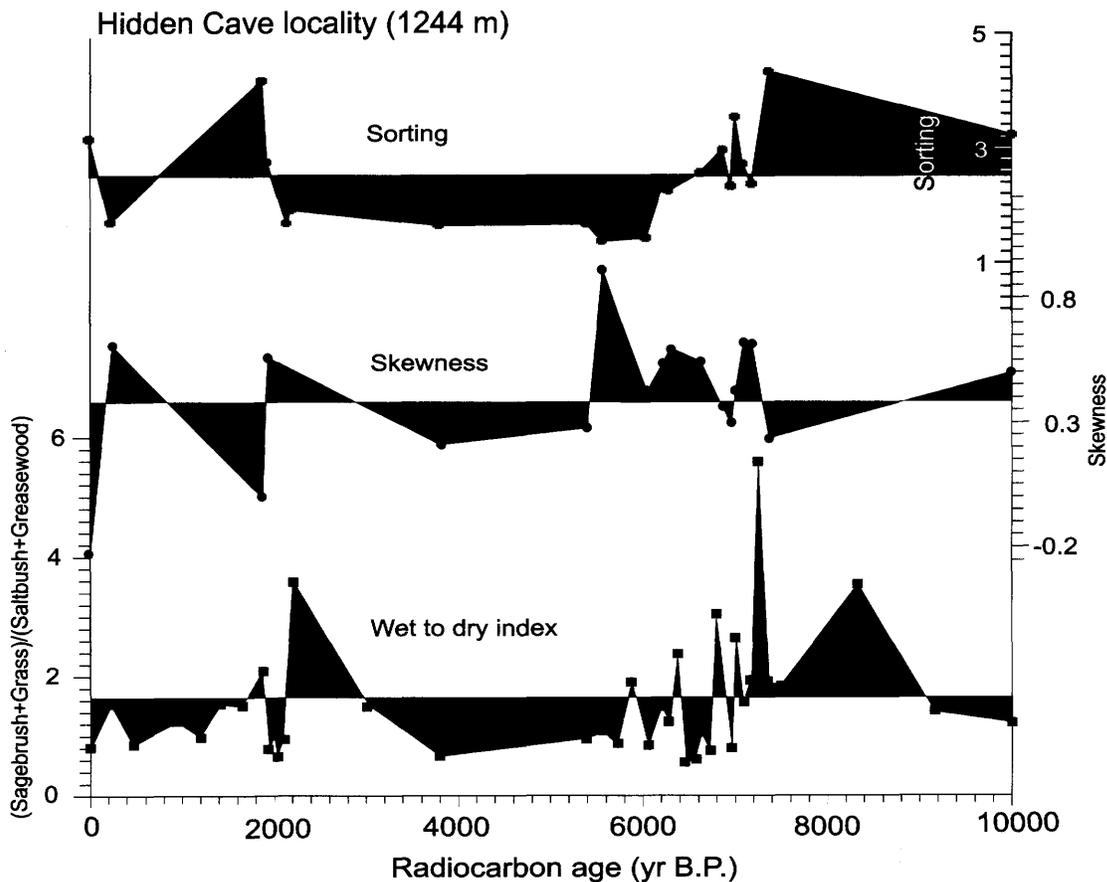


FIGURE 9.—Wet-to-dry index, (sagebrush + grass pollen)/(saltbush + greasewood pollen), generated with sediment pollen data from Hidden Cave in the Carson Sink, Nevada, compared with the skewness and sorting of Hidden Cave sediments; the latter two are statistical parameters derived from grain-size analysis and can be related to understandings of erosional and depositional processes. Skewness is used as a measure of eolian activity, and sorting is used as a measure of the amount of energy in the medium that moved sediment. “Up” on the drought index indicates wetter climate, up on the skewness index indicates greater eolian activity, and up on the sorting index indicates greater energy in the medium that was moving sediment. Sample dates were based on deposition rates extrapolated from radiocarbon dates (Davis, 1985).

density in response to drought was exposing large areas to eolian erosion (Figure 9). The pollen record from Lovelock Cave (Byrne et al., 1979) corroborates these trends. The general correspondence between the Hidden Cave and Lovelock Cave pollen records is close.

Preliminary pollen analyses of human fecal material, removed from the 9400-year-old Spirit Cave burial site in the Carson Sink of west-central Nevada, corroborate the environmental reconstruction (Wigand, 1997a). (The cave contained the partially mummified body of a man, the Spirit Cave Man, 5'2" tall and about 40–50 years old.) The fecal material was composed almost entirely of the remains of small fish (Eiselt, 1997). However, a very low pollen background in the samples may have mirrored the regional pollen rain. The pollen may have found its way into the fecal material through residues present on plants eaten by the early Nevadan or may have entered through the stomachs of the fingerlings that were ingested. Fish may have eaten the pollen as it floated on the wa-

ter surface of the marsh during flowering time (suggested by P.J. Mehringer, Jr.). This pollen record is statistically identical to pollen of the same age recovered from nearby Hidden Cave (Wigand, 1997a). It reflects a saltbush-dominated environment with evidence for persistent marshes and eolian habitats. Comparison of the drought index from Hidden Cave with one produced from the Hogup Cave pollen record analyzed by Kelso (1970) indicates that this was a regional pattern at low elevations across the northern Great Basin (Figure 10).

Today the McCoy Flat area comprises a mosaic of mixed-conifer-forested, Late-Tertiary/early Pleistocene volcanic cones that rise above a lattice of wide, low-grade stream valleys dominated by sagebrush steppe. The pollen record from McCoy Flat indicates that by the early Holocene a regional decline in pine and juniper woodland corresponded to an increase in steppe dominated by sagebrush and rabbitbrush (*Chrysothamnus*-type pollen) (Figure 6). An increase in grass values at this time, corresponding to the increase seen at Bicycle Pond and in

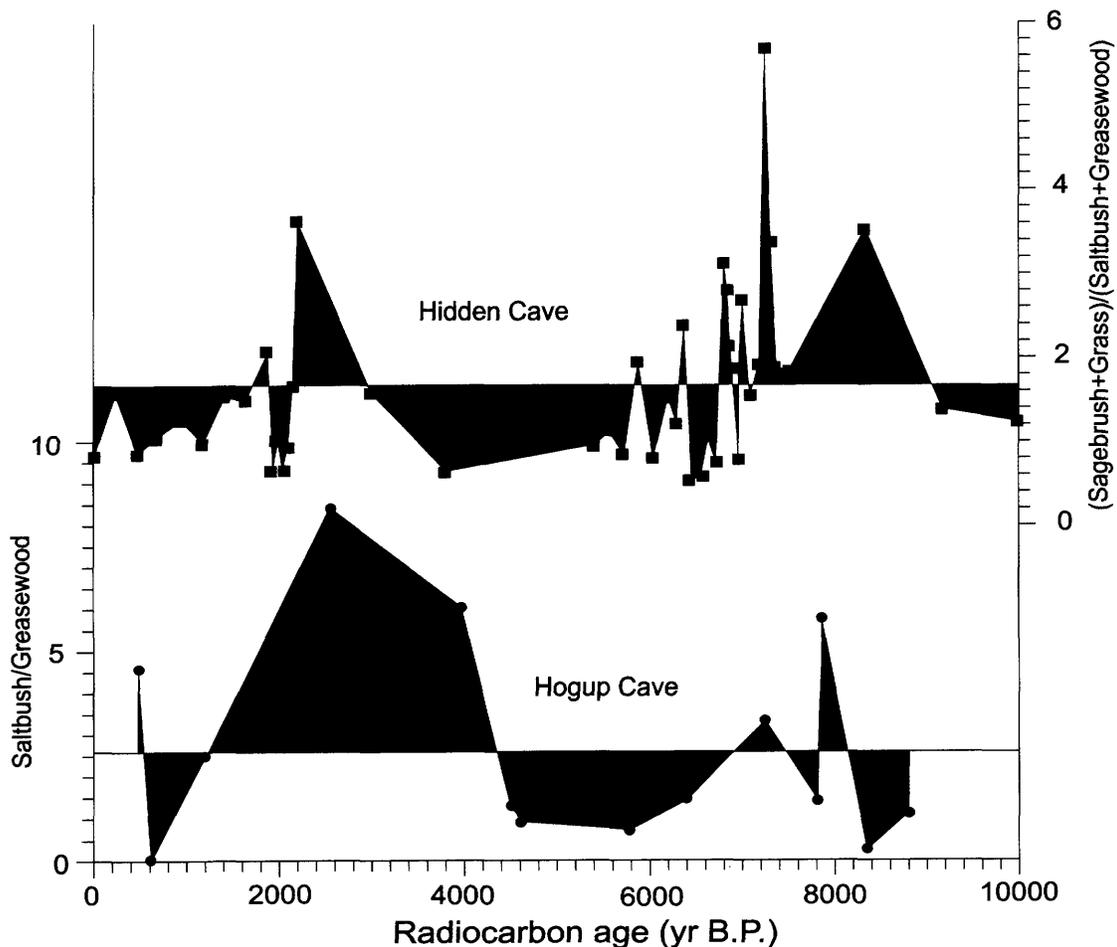


FIGURE 10.—A comparison of two drought indices generated from pollen analyses of sediments obtained from Hidden Cave in the Lahontan Basin, Nevada (Wigand and Mehringer, 1985), and Hogup Cave in the Bonneville Basin, Utah (Kelso, 1970). Up indicates wetter climate. Differences between the two records primarily reflect sample spacing and error introduced through extrapolation of sample ages from radiocarbon-based dates.

the midden pollen record from Pyramid Lake, may reflect a regional response to increased rainfall in late spring or early summer, an increase also hinted at in vegetation records further south and east in the Great Basin. Increased cattail pollen in the record may simply reflect decreased competence of the local stream, which was now filling the deep channel cut that had characterized Pine Creek during the Pleistocene.

#### MIDDLE HOLOCENE (8 TO 5.5 KA)

The McCoy Flat and Bicycle Pond records indicate that by the beginning of the middle Holocene the retreat of juniper woodland and the expansion of sagebrush steppe had reached a climax (Figures 6, 8). Both of these records also indicate that saltbushes (*Chenopodiineae* pollen) were regionally more important than they had been before. The decline of grass in the McCoy Flat record reflects the middle-Holocene drought.

At Steens Mountain, the Fish Lake pollen record indicates that sagebrush steppe became the dominant vegetation at elevations lying above the juniper woodland zone (Mehring, 1985). Sagebrush pollen to grass pollen ratios from Fish Lake indicate that the climate that typified the period between 8.8 and 5.6 Ka was the driest to occur there during the Holocene (Mehring, 1986). The Wildhorse Lake record evidences the arrival of sagebrush steppe by ~8 Ka (Mehring, 1986). It was to remain dominant at these elevations until about 3.8 Ka. In southern Oregon, dry pluvial lake basins are indicated by dune deposits dated to this period, including ones in the Catlow Valley at Skull Creek (Mehring and Wigand, 1986), Fort Rock Valley (Mehring and Cannon, 1994), and the Malheur Valley (Dugas, 1998).

The all-pervasive drought of the middle Holocene is reflected in the dearth of paleobotanical records throughout the northern Great Basin at low elevations and especially around the Lahontan Basin. The almost continuous midden record that exists in the Painted Hills on the west shore of Pyramid Lake is interrupted for almost 4000 years, from ~8 to 4 Ka (Wigand and Nowak, 1992). Juniper macrofossils disappear from woodrat middens lying 200 m above the early and late-Holocene lower elevational limits of juniper evidenced in the woodrat midden record. This suggests that juniper retreated upward in elevation by at least 200 m or more above its current distribution during the middle Holocene.

The Hidden Cave pollen record indicates dominance of saltbush shrub communities in the margins of the Lahontan Basin (Wigand and Mehring, 1985). Statistical parameters generated from the grain size analysis of Hidden Cave sediments indicate that transport of sediment through eolian (less positive skewness) and colluvial (better sorting) processes in the Carson Sink had declined substantially (Figure 9). The near absence of evidence of high-energy colluvial transport may have resulted from the rarity of high-energy storms in the Lahontan Basin. Reduced colluvial transport despite the reduced vegetation cover indicates that rainfall was at a minimum, especially dur-

ing the summer. The dramatic reduction in eolian activity may be attributable to the depletion of transportable materials in the basin. Because colluvial and fluvial activity was at a minimum, there was a reduction in the material that would have been available for eolian transport. A comparison of the Hidden Cave drought index with one generated from the pollen record of Kelso (1970) from Hogup Cave in northwestern Utah suggests that widespread drought characterized much of the northern Great Basin (Figure 10). Pyramid Lake may have reached its lowest level at this time (Born, 1972).

Woodrat midden evidence from the White Mountains on the California–Nevada border indicates that middle-Holocene drought displaced semiarid woodlands upward in elevation by as much as 300–500 m (Jennings and Elliot-Fisk, 1993). Taken together with the evidence from the Lahontan Basin, it appears that this displacement may have characterized large portions of the western Great Basin (Wigand and Nowak, 1992).

Upward woodland displacement in this area coincides with the age of drowned trees found 10–15 m below the modern surface of Lake Tahoe. These trees became established in the Tahoe Basin during periods of intense, long-duration drought ~6.5 Ka (Lindström, 1990). Throughout the northern Great Basin lakes and marshes desiccated and pollen of drought-tolerant salt desert species increased substantially (Wigand, 1987; Mehring and Wigand, 1990). At Diamond Pond south of Lake Malheur in south-central Oregon, greasewood pollen reached levels of 80% of the terrestrial pollen, whereas currently it makes up less than ~20% of the modern pollen record. These changes coincided with dramatically reduced evidence of the activities of Native American populations (Grayson, 1993). This is consistent with a decline in foraging resources and corroborates the severity of this drought (Aikens, 1986).

#### EARLY LATE HOLOCENE (5.5 TO 2 KA)

Beginning ~5.4 Ka, the extreme drought of the middle Holocene came to an end. Temperatures remained warm, but pollen and macrofossil data indicate gradually increasing annual precipitation punctuated by periodic increases in rainfall abundance (Davis, 1982; Mehring, 1986; Wigand, 1987). A brief, extremely dramatic climatic event that can be correlated from the Columbia Plateau of eastern Washington to the spring deposits of Ash Meadows in the northern Mojave Desert effectively signals the end of the middle Holocene in the intermountain West.

Evidence for this panregional event begins in the north at Wildcat Lake in eastern Washington. At 5.4 Ka, the deposition of reworked Mazama ash in the lake sediments suddenly ended (Peter J. Mehring, Jr., pers. comm. to Wigand, 1978). This indicates that vegetation density on the landscape became great enough to prevent the resuspension of the volcanic ash either by wind or water. This increase in vegetation density probably directly reflects a dramatic shift toward greater rainfall.

At Diamond Pond in south-central Oregon there was a shift from dry-climate pollen assemblages to much more mesic assemblages (Wigand, 1987). Just after 5.4 Ka, pollen spectra that previously had been dominated by as much as 80% greasewood pollen were instead characterized within a few decades by as much as 40% sagebrush pollen. Although a shift back toward drier climate occurred during the next 1400 years, the conditions that characterized the period before 5.4 Ka never occur.

This event is also noted in the Tahoe Basin on the west-central margin of the Great Basin, where montane forests were so rapidly submerged beneath the cold waters of Lake Tahoe at 5.5 Ka that they had no opportunity to decay (Martin Rose, pers. comm. to Wigand, 1995). An 8000-year-long tree ring record of a bristlecone pine (*Pinus longaeva* D.K. Bailey) from Methuseloh Walk in the White Mountains reveals this same rapid shift in climate that ended a period of drought that may have lasted as long as 1500 years (Graybill et al., 1994). The paleolimnological record from Walker Lake, the southernmost subbasin of ancient pluvial Lake Lahontan, indicates that the Walker Lake basin, which had been a dry playa, was refilled by ~4.7 Ka (Bradbury et al., 1989). This probably resulted from wetter conditions at this time, but it also may have been caused by a shift in the course of the Walker River from the Carson Basin to the Walker Basin. This shift, however, also may have resulted from changes in the Walker River alluvial process precipitated by a change in climate.

The shift to wetter conditions at ~5.5 Ka had other ramifications as well. It initiated the reexpansion of woodlands and montane forests. The earliest evidence of western juniper reported in its historic range of northeastern California and eastern Oregon are twigs from ancient woodrat middens at Lava Beds, California (5.4 Ka), and Diamond Craters, Oregon (4 Ka) (Mehringer and Wigand, 1987, 1990).

Just east of the Tahoe Basin, a 3.5 meter core (unpublished) recovered from a bog north of Little Valley, Nevada, revealed responses of both local montane forest and regional semiarid woodland and sagebrush steppe to climate change since ~6.3 Ka, when the pond formed (Figure 11). Little Valley is on the east slope of the Sierra Nevada near the lower edge of the montane forest. Across the valley to the east lie the piñon- and juniper-dominated ranges of the Great Basin. Cluster analysis of the Little Valley core pollen reflects the shift from dry middle-Holocene conditions to more mesic late-Holocene conditions. Local sagebrush predominance between 6.3 and 5.6 Ka (Zone I) indicates relatively more xeric conditions than any of the succeeding periods. A retreat of sagebrush and an increase in pine and juniper initiated a period of more mesic climate between 5.6 and 4 Ka (Zone II) (Figure 11). Sedges probably dominated the margins of the pond during both periods. Two more mesic periods occurred between 5.6 and 4 Ka, when fir may have first expanded into the valley from above. This period corresponds with the drowning of low-lying trees in the Tahoe Basin by rising lake levels. Between 4 and 1.9 Ka (Zone III), major downward expansions of fir (both red fir, *Abies*

*magnifica* A. Murr., and white fir, *A. concolor* (Gordon & Glend.) Lindl. ex Hildebr.) into Little Valley occurred (Figure 11). Abundant sedge pollen at this time records filling of the pond and generation of sedge peat. In addition, alder (*Alnus*), birch (*Betula*), and willow (*Salix*) pollen evidences the establishment of these taxa in mesic communities in Little Valley. This period was clearly cooler and more mesic than those that preceded or followed it. Local fire severity seems to have increased substantially between 5.6 and 4 Ka, perhaps in response to the greater availability of fuel. After 3 Ka, fire severity appears to have declined substantially.

Expansions of juniper woodland into areas at elevations lower than where it is currently found in the northern Great Basin are recorded in the Diamond Pond juniper pollen record and by western juniper macrofossils from woodrat middens in Diamond Craters east of Diamond Pond (Wigand, 1987; Mehringer and Wigand, 1990). Expansion of western juniper woodland into the lower elevation sagebrush steppe began about 4.5 Ka (Wigand, 1987). The rate of juniper woodland expansion increased dramatically ~3.7 Ka and again 2.7 and 2.3 Ka. Except for two lapses, western juniper woodland remained near this lower elevational limit (~150 m below its current extent) until about 1.9 Ka (Wigand, 1987; Mehringer and Wigand, 1990). Broad Neoplacial expansion of pine in the woodlands on the northernmost boundary of the Great Basin is recorded in the Craddock Meadow, Oregon, pollen record (Wigand, 1989). Further south a pollen record from Potato Canyon Bog in Grass Valley, central Nevada, also shows evidence of expansion of semiarid woodland during this period (Madsen, 1985). Three episodes (~3.7, 2.7, and ~2.3 Ka) of fir expansion at Little Valley (Figure 11) mirror the episodes of moister climate revealed at Diamond Pond as well. Together these data reflect a pattern of forest and woodland expansion that occurred throughout the entire northern and western Great Basin.

These episodes are characterized not only by the expansion of both forests and woodlands, but also by a regional rise in the water table and a reexpansion of lakes and marshes (Wigand, 1987; Grayson, 1993). Even the record from Walker Lake indicates deep lake levels between 4 and 2.9 Ka (Bradbury et al., 1989, fig. 11). Although lake levels had fallen by 2.2 Ka, the absence of dated samples between 2.9 and 2.2 Ka leaves lake level elevation during that period in question. In general, climates in the northern Great Basin during the Neoglacial or Neoplacial from 4 to 2 Ka were cooler and substantially wetter, with winter precipitation dramatically increased relative to summer precipitation (Davis, 1982; Wigand, 1987).

Although macrofossils indicate the presence of western juniper at lower elevations than its current distribution, juniper pollen values from Diamond Pond indicate that juniper woodlands at the lower elevations during this Neoplacial expansion were less dense than those currently found in the area (Wigand, 1987). Recent analyses of  $\delta^{13}\text{C}$  in western juniper twigs and Utah juniper twigs from ancient woodrat middens indicated that water stress—either as a result of drought or frequent freezing

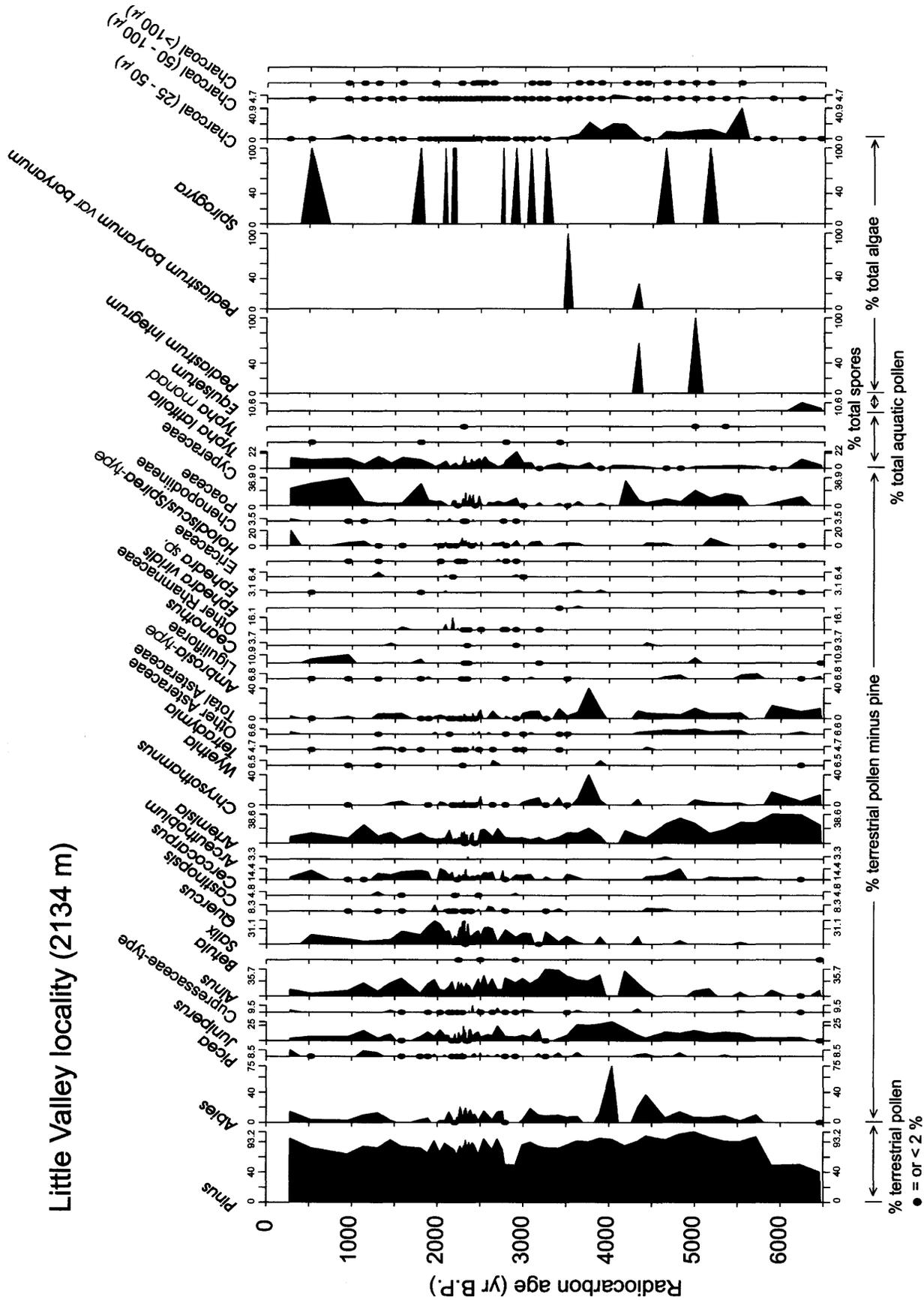


FIGURE 11.—Relative percentage diagram of major pollen, spore, and algae types and charcoal from Little Valley, Nevada (elevation, 2134 m), on the east slope of the Sierra Nevada east of Lake Tahoe. Samples were dated based on a deposition rate curve generated from a polynomial fit on seven radiocarbon-based dates. A bullet (●) indicates a value of  $\leq 2\%$ .

during the growing season—typically affected the condition of juniper during the Neopluvial (Wigand, 1995).

Intermediate-elevation juniper woodland was at least as thick or thicker than it is today (Davis, 1981). Based upon modern studies, the more mesic conditions of the Neopluvial brought on by a combination of increased rainfall and lowered summer temperatures probably resulted in closer spacing of trees and more foliage near the middle elevational distribution of juniper (Fritts and Xiangdig, 1986; Miller and Wigand, 1994).

Juniper pollen values at Fish Lake on Steens Mountain indicate that although a late middle-Holocene upward elevational shift in juniper occurred when conditions were still warm but increasingly wet, lower juniper pollen values during the succeeding Neopluvial period suggest that the upper tree line of juniper dropped in elevation (Mehring, 1985, 1987; Mehring and Wigand, 1987). The colder temperatures that seem to have characterized this period probably limited juniper expansion at higher elevations.

Periodic increased abundance of grasses relative to sagebrush and saltbushes during this period indicate that the broad areas lying around Diamond Craters, which today are dominated by desert scrub vegetation, may have been characterized by a grassy, sagebrush steppe. A dramatic reduction in desert shrub vegetation was also caused by marshland expansion into areas previously dominated by greasewood and saltbushes (Wigand, 1987; Mehring and Wigand, 1990). This pattern probably characterized much of the northern and western Great Basin.

Increased abundance of grass pollen coincident with woodland expansion also mirrors the presence of a vigorous herbaceous understory and of occasional fire episodes. Three very pronounced grass pollen increases at Diamond Pond are closely tied to preceding charcoal events between 4 and 2 Ka and are evidence of dramatic local grass expansion after fire (Miller and Wigand, 1994). Although climatic conditions favored juniper growth at middle elevations and expansion at lower elevations during this period, the charcoal recovered from Diamond Pond cores evidences frequent drought-driven local and regional fires. The fuels that accumulated from the abundant herbaceous understory promoted fire and probably helped maintain the low density of the lower elevational juniper woodlands—the point in its distribution where juniper would be stressed the most when droughts occurred (Wigand, 1987; Miller and Wigand, 1994). Periodic, regional megadroughts resulted in extensive fires that characterized both the lower and middle elevational distribution of juniper woodland in the Great Basin during the Neopluvial (Wigand, 1987).

#### MIDDLE LATE HOLOCENE (2 TO ~1 KA)

After the Neoglacial ~1.9 Ka, the Great Basin climate generally became warmer and drier (Davis, 1982; Wigand, 1987; Wigand and Rose, 1990; Wigand and Nowak, 1992). Juniper

pollen values in the northwestern Great Basin declined dramatically relative to shrubs and grasses (Wigand, 1987). In addition, the shift in the ratio of coarse to fine charcoal when compared with the changes in the dominant vegetation type at Diamond Pond clearly reflect the change from juniper woodland to shrub steppe fuels (Wigand, 1987).

At Fish Lake an increase in big sagebrush pollen relative to grass pollen reflects decreased grass in response to drier conditions and was probably characteristic of the upper sagebrush zones of the northern Great Basin (Mehring, 1987). An increase in desert scrub vegetation, indicated by increasing saltbush and greasewood pollen at Diamond Pond, provides additional evidence for increasing local and regional aridity, particularly between 1.9 and 1 Ka (Wigand, 1987). Pollen and macrofossils of aquatic plant species at Diamond Pond, Oregon, indicate that water levels had dropped substantially since the Neoglacial (Wigand, 1987).

At Little Valley, the pollen record from 1.9 Ka to the present (Zone IV) exhibits local retreat of fir, alder, birch, and willow indicating more xeric conditions (Figure 11). Increased grass and retreat of juniper during this period may reflect the shift to increased summer rainfall seen elsewhere in the northern Great Basin and also in the southern Great Basin and northern Mojave Desert (see below). Pine increases may relate to the regional expansion of piñon pine evidenced in woodrat middens between 1.5 and 1.1 Ka (and again after 0.4 Ka) (Wigand, 1997b; and see below).

An unpublished pollen record from Lead Lake in the Carson Sink records terrestrial and aquatic vegetation dynamics for the central Great Basin during the last 2200 years. The major trend for the last two millennia has been the decline in greasewood while marsh species became more dominant. The decline of greasewood is matched by increases in pine, sagebrush, and grass (Figure 12). Higher values of broadleaf cattail (*Typha latifolia* L.) and narrowleaf cattail (*Typha angustifolia* L.), indicating shallow marsh conditions, occurred between ~2.2 and 1.5 Ka. The abundance of cattail (primarily broadleaf cattail) relative to sedge between 2.2 and 1.9 Ka probably reflects influxes of fresher water than before into the marshes. These episodes correspond to wetter events indicated in the Diamond Pond record as well (Wigand, 1987). Increasing pondweed (*Potamogeton* sp.) pollen values beginning ~1.9 Ka and decreasing dramatically after ~0.8 Ka reflect slightly deeper water conditions. Renewed abundance of narrowleaf cattail after 0.8 Ka indicates renewed expansion of marsh in the Carson Sink. Ratios of the more abundant pollen types reflect these trends more clearly (Figure 13). The decline of juniper relative to sagebrush probably reflects warmer, drier conditions following the end of the Neopluvial. Increasing sagebrush relative to saltbush is the result of marsh expansion into areas previously occupied by saltbush communities. The predominance of emergent aquatic plants relative to littoral plant species indicates slightly deeper water conditions in the marsh between 1.9 and

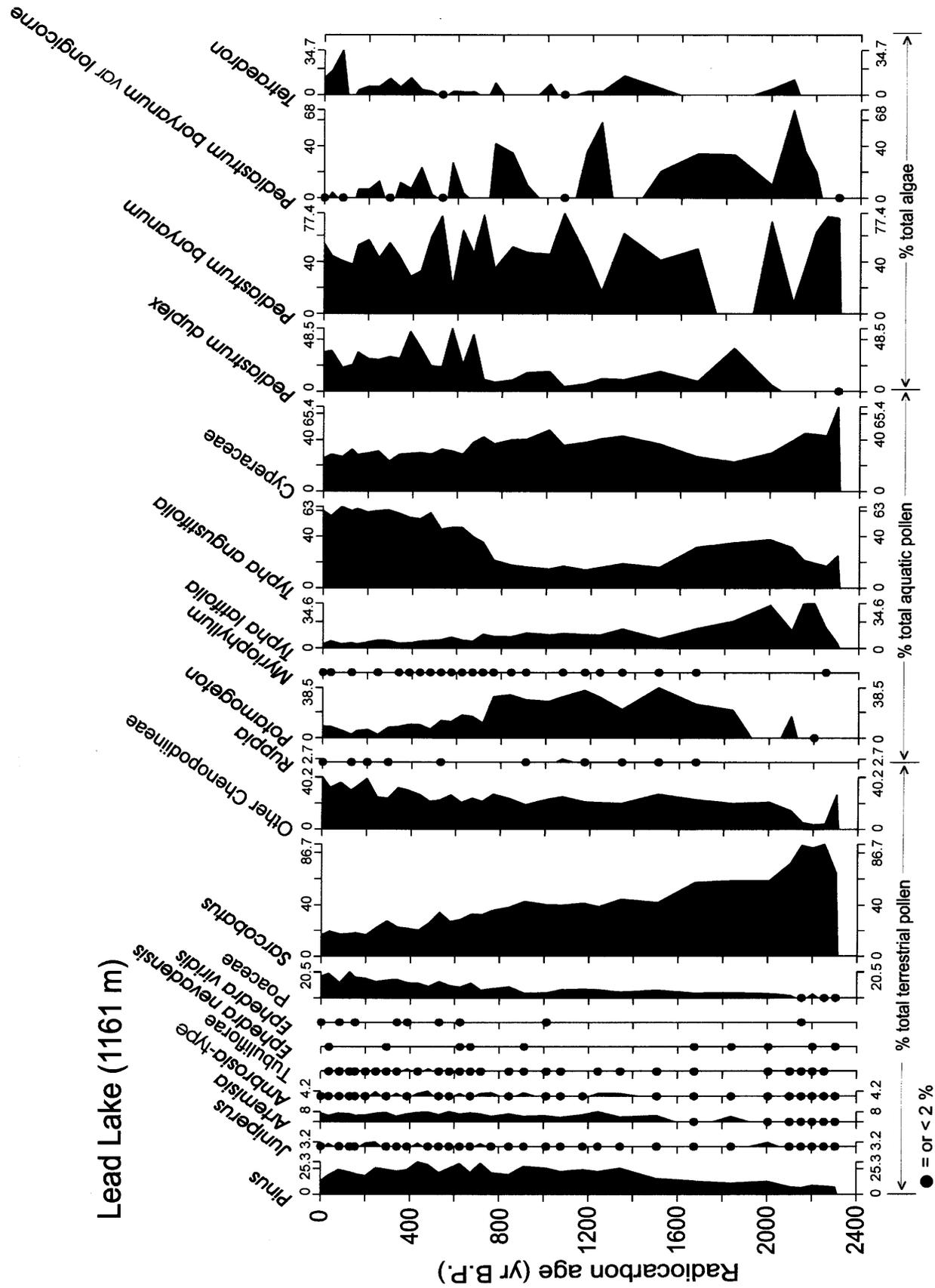


FIGURE 12.—Relative percentage diagram of major terrestrial and aquatic pollen and algae types from Lead Lake, Carson Sink, west-central Nevada. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates. A bullet (●) indicates a value of  $\leq 2\%$ .

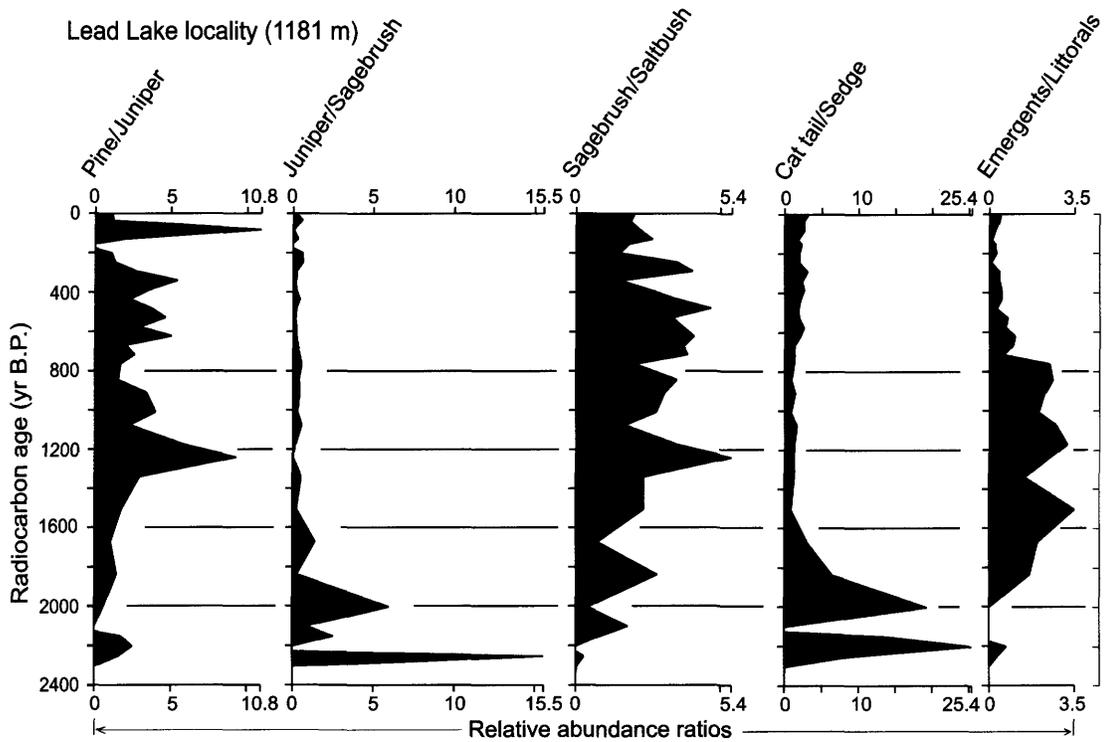


FIGURE 13.—Abundance ratios of major pollen types from Lead Lake, Carson Sink, Nevada. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates.

0.8 Ka (Figure 13). Deeper water at this time does not mean that climate was wetter. Other evidence (see below) suggests that, although annual precipitation remained relatively unchanged, a shift toward more rainfall in summer resulted in the persistence of deeper water conditions into the warm season, when high evaporation rates would normally have shrunk the marsh or dried it out. Increased abundance of pine relative to juniper between 1.4 and 0.9 Ka indicate that piñon pine became an important part of the semiarid woodland in the northwestern Great Basin at this time. Although piñon pine may have entered the area earlier, the woodrat midden evidence indicates that it became much more abundant upon the landscape. Macrofossils of piñon pine from woodrat middens throughout the Lahontan Basin indicate that it expanded both northward in latitude and downward in elevation (Wigand et al., 1995) (Figure 14).

This rapid change in piñon pine distribution was primarily triggered by increased rainfall throughout the summer, which

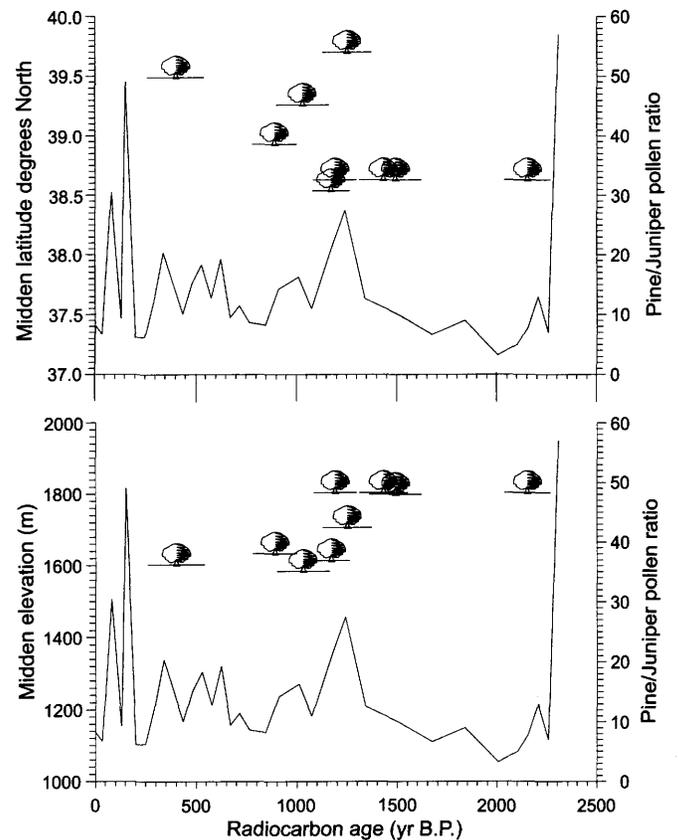


FIGURE 14.—Ratios of pine to juniper pollen (tree symbols) from Lead Lake plotted against (top) the latitudinal distribution and (bottom) the elevational distribution of directly dated juniper twigs (solid lines) from woodrat middens in the Reno, Nevada, area of the Lahontan Basin. Northward expansion of piñon pine during the last 1500 years is evident; and lower elevational distribution of juniper during the last 1500 years also is indicated. Samples were dated based on a deposition rate curve generated from a polynomial fit on three radiocarbon-based dates.

encouraged seedling establishment. However, this expansion probably would not have been possible without the milder winters that followed the end of the Neoplacial after 1.9 Ka. The pollen record from Lead Lake indicates that a contraction in semiarid woodland occurred in the area after ~1 Ka (Figure 13). This is borne out by the reduced numbers of woodrat middens in the area containing piñon pine and juniper (Figure 14).

At Diamond Pond in the Harney Basin of south-central Oregon, an early post-Neoglacial expansion of grass between 1.9 and 1.0 Ka overlaps with the piñon pine expansions seen at Lead Lake (Wigand, 1987; Wigand, 1997b). Western juniper, which during most of the record from Diamond Pond had varied in concert with grass, did not increase in abundance with grass during this period, indicating the occurrence of summer-shifted rainfall as well. That this expansion of grass was regional in nature is demonstrated by the dramatic increase of bison (*Bison* spp.) remains in archaeological sites of the northern intermountain West. Radiocarbon dates plotted with standard deviations on bison remains from archaeological sites in the northern Great Basin (Marwitt, 1973) and the plateau of eastern Washington (Schroedl, 1973) show remarkable coincidence with this period of grass expansion (Wigand, 1997b, fig. 10).

A substantial increase in juniper pollen values ~1 Ka in the northern Great Basin at Diamond Pond, coincident with local increased abundance of woodrat middens containing western juniper macrofossils, evidences a renewed expansion of woodland in the north and the end of grass abundance (Wigand, 1987; Mehringer and Wigand, 1990). This corresponds to increased large versus small charcoal values, indicating both a change in fuel type as well as more frequent fires as fuels accumulated in response to wetter climate (Wigand, 1987; Wigand et al., 1995). Dugas (1998) indicated that higher lake stands may have occurred in the Malheur Basin ~1 and ~0.8 Ka.

#### THE LAST MILLENNIUM IN THE NORTHERN AND WESTERN GREAT BASIN (<1 KA)

Evidence of severe drought and resultant fire in the northern, central, and southern Great Basin between ~0.9 and 0.5 Ka, confirmed by Sierran and Great Basin tree ring studies, coincide with a decline of the woodland (Holmes et al., 1986; Wigand, 1987; Wigand and Rose, 1990). The drought of the middle of the millennium is recorded in the expansion of salt-bushes in the northern Great Basin and in evidence that Diamond Pond reached some of its lowest levels since the middle Holocene (Wigand, 1987). Reexpansion of marsh at Lead Lake evidences regional drying of the western Great Basin after 0.8 Ka (Figures 12, 13). Charcoal evidence from the cores at Little Valley indicates that fire frequency increased considerably after about 0.6 Ka (Figure 11). Destruction of the lower margin of the woodland appears as a sudden gap in the woodrat midden evidence of northern Nevada for this period (Wigand and Nowak, 1992; Figure 14). Stine (1990) reported that extended

droughts were terminated about 0.9, 0.6, and 0.35 Ka by brief wet events.

The "Little Ice Age," a pattern of stronger winter precipitation and cooler temperatures beginning 300 to 400 years ago, terminated the droughts of the middle portion of the millennium and initiated a gradual reexpansion of juniper woodland in the northern Great Basin (Mehringer and Wigand, 1990). Further south in the central and southern Great Basin, increasing pine pollen values relative to juniper pollen values indicated that piñon pine benefited more from the shift toward mesic climate conditions (Wigand and Nowak, 1992; Wigand, 1997b). By the time Europeans first entered the area, climate-initiated reexpansion of Great Basin woodlands was well underway. In the northern Great Basin, increased occurrence of pine in the pollen record at Lead Lake during the last 0.15 Ka corresponds to the 2.5-fold increase in areal coverage of piñon pine after the Little Ice Age, as recorded in stand establishment records (Tausch et al., 1981).

The pollen record at Diamond Pond indicates increasing aridity since the end of the Little Ice Age. Juniper woodland retreated and sagebrush steppe advanced (Wigand, 1987). Grasses seem to have become less abundant throughout the region. A decrease in water depth in Diamond Pond reflects a regional drop in the water table in the Harney Basin (Wigand, 1987; Mehringer and Wigand, 1990). Lower frequency fluctuation of juniper pollen values in the early 1800s contrasts with the recent sharp increases since the middle 1900s (Mehringer, 1987; Mehringer and Wigand, 1990). Increased variability, in part, reflects a real expansion in woodland, but also it may reflect reduced sediment compaction. Fewer years are represented in each of the one-centimeter-high samples at the top of the core than in samples from lower down in the cores. As a result, interannual variability of pollen production in response to weather variation from year to year is not being averaged as much as it was lower in the record. This gives the impression of greater climatic variability when compared with earlier periods.

The post-Little Ice Age trend toward lower effective precipitation brought on by warmer mean annual temperatures combined with the spread of woodlands should have increased the potential for fire in the Great Basin. Despite increased drought stress on the trees in this semiarid region, the occurrence of fire decreased. This contradicts the prehistoric pattern of massive fires that typified periods when Great Basin woodlands were subjected to drought conditions—i.e., the end of the Neoglacial (Wigand, 1987).

Decreased fire frequency may have occurred, in part, because conditions were dry enough to keep the production of light fuels (i.e., grasses and forbs and even shrubs) low. On the other hand, Peter Skene Ogden noted abundant evidence of fires set by Native Americans in the Harney and Malheur lakes region during the middle 1820s (Davies et al., 1961). A decline in fire frequency as Native American populations declined and were displaced may have enabled the expansion of semiarid

woodlands at the time of European settlement. Livestock grazing may also have played a role in decreased fire frequency through the reduction of fine fuels (see discussion in Miller and Wigand, 1994). Grazing may also have played a role in juniper expansion through seed dissemination and encouragement of shrubs that provided nursery areas for juniper seedling establishment.

Prehistorically, climate change was the primary factor affecting the expansion of semiarid woodlands. Droughts and resultant disturbance phenomena such as insect infestations, disease, and fire all contributed to periodic retreat of these woodlands. Since the arrival of Europeans, both climate change and human action have substantially affected woodland distribution. Drier climates during this century have resulted in increased physiological stress on plant communities. Fire suppression practices and the use of insecticides have disrupted normal cycles of disturbance phenomena such as fire, insect infestation, and disease. The resulting fuel build-up has increased the potential for intense, widespread fires.

Periods of wetter climate around 1910, the early 1940s, the late 1960s to early 1970s, and the early 1980s have served to briefly revitalize juniper woodlands in the northern Great Basin (Mehringer and Wigand, 1990). However, if droughts similar to those of the early 1990s are near the climatic norm for the last millennium, as Graumlich (1993) suggested from Sierran tree ring records, we can expect continued retrenchment of semiarid woodlands to higher elevations, with a reduction in perennial grasses and expansion of sagebrush and annual grasses.

#### Southern Great Basin and Northern Mojave Desert

Paleobotanical records from the southern Great Basin and the northern Mojave Desert consist primarily of data obtained from plant macrofossils collected from ancient woodrat middens. The Tule Springs pollen record (Mehringer, 1967), however, and a record from Death Valley (undergoing analysis) promise to extend length to our record of vegetation history and to cover gaps in the Late Quaternary record not covered by woodrat midden evidence. Other sources of climatic evidence, such as the stable isotope records from Devils Hole (Winograd et al., 1988, 1992, 1997) and Death Valley (Li et al., 1996; Ku et al., 1998), provide evidence of past climates but tell us nothing of Late Quaternary vegetation dynamics. Thus far, only the record from Browns Room at Devils Hole (Szabo et al., 1994) can successfully be compared with vegetation dynamics in the northern Mojave Desert.

If pollen preservation is adequate in the Death Valley core, that record promises to extend our paleobotanical history of the northern Mojave Desert by at least 190 Ky (Li et al., 1996; Ku et al., 1998). Currently, however, a few woodrat middens and perhaps some pollen samples from Tule Springs provide our only indication of vegetation in the area from before about 35 Ka.

#### PRE-LATE WISCONSIN (>35 KA)

Profile I at Tule Springs apparently contains pollen spectra dating to before 35 Ka (Mehringer, 1967, fig. 31). The profile documents a cool, wet event dating to more than 37 Ka. This may actually be one of the two periods of wetter climate indicated in the Browns Room record dating to either ~40 or ~45 Ka, or it may be an earlier event (Szabo et al., 1994, fig. 4). The episode is characterized by both pine and fir expansion. Neither the age nor the duration of this event can be determined, but it seems to document the same kind of vegetation pattern that is seen in later pluvial episodes. The pollen record indicates that desert shrub communities dominated by saltbushes characterized low elevations. Juniper and sagebrush pollen suggests that juniper woodland, possibly mixed with pine, was also common. As cooling progressed, the contribution of pine pollen to the record became overwhelming. This resulted, in part, from the increased area that was available for pine to expand into as its habitat was displaced down the mountainsides (see Mehringer's (1967) discussion of the impact upon pollen abundance by the displacement of species along the area elevation curve). Fir pollen became more abundant than that of juniper. This may have resulted from poor preservation of juniper pollen, but values of about seven percent suggest a substantial increase in fir regionally. Pollen from juniper and sagebrush indicates that juniper woodland was still widespread. The decrease in pine and fir values and the disappearance of juniper near the top of the profile seem to signal a return to a drier climate. This pattern is repeated throughout the late Pleistocene in the northern Mojave Desert.

Unfortunately, most woodrat middens dated to before 35 Ka have multiple dates and reflect substantial mixing of materials of many ages. Typical of this problem are middens from the Eleana Range (Spaulding, 1985). This mixing may be an indication that climatic conditions since the initial formation of these woodrat middens have been wet enough to cause resolution of the crystallized urine cementing them.

#### LATE PLEISTOCENE (~35 TO 12.5 KA)

Woodrat midden studies during the last 30 years have enabled identification to the species level of the likely contributors of both pine and fir pollen from the Tule Springs pollen record. It is clear that in the southern Great Basin and the northern Mojave Desert, expansions and contractions of limber pine and white fir (possibly Rocky Mountain white fir, *Abies concolor* var. *concolor*) record periods of wetter climate during the cooler, drier spans of the late Pleistocene (Figures 15, 16). Originally recorded in the pollen record obtained from Tule Springs (Mehringer, 1967), they have been corroborated and refined by the substantial woodrat midden record that has been accumulated (Mehringer and Ferguson, 1969; Spaulding, 1977, 1981, 1985, 1994; Forester et al., 1996).

The woodrat midden record indicates that during much of the last glacial cycle between 33 and 11 Ka, limber pine formed a

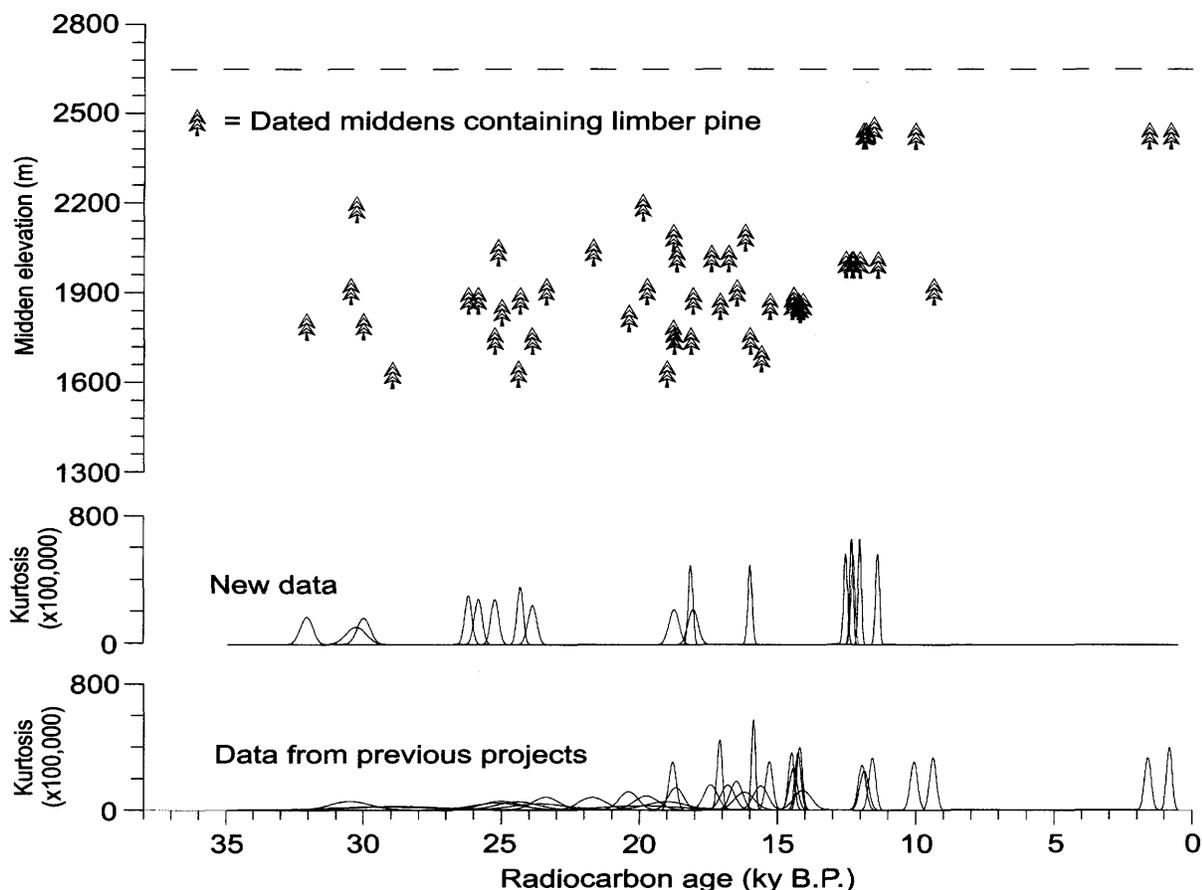


FIGURE 15.—Elevational distribution of limber pine, as ascertained with macrofossils from ancient woodrat middens in the northern Mohave Desert, by radiocarbon age. (Top) Our own and previously published data from middens containing limber pine (tree symbols) in a 200 km radius around Yucca Mountain; the dashed line is the approximate lower elevational distribution limit of limber pine in the Sheep Range today. (Middle, Bottom) Radiocarbon dates on limber pine for this study (middle) and for other studies (bottom) plotted as a normal distribution at three standard deviations around the mean. For these kurtosis plots, the normal distributions are a measure of radiocarbon date precision—i.e., the more pointed the distribution curve, the more precise the date is; and the flatter the curve, the less precise the date is.

subalpine woodland that occasionally extended down to at least 1600 m in elevation, ~1000 m below where it grows today in the Sheep and Spring Ranges of southern Nevada (Table 1; Figure 15). This is roughly equivalent to the period of highest water table in Browns Room at Devils Hole (Szabo et al., 1994). Limber pine macrofossils appear in the midden record of ~33–30 Ka, 26.5–23 Ka, 21–14 Ka, and 13–11 Ka. White fir occasionally appeared in this woodland also. At those times it certainly grew along the bases of cliffs and in canyons (where woodrat middens are preserved), but whether conditions were moist enough for it to grow on exposed slopes is uncertain. Periods of downward translocation of white fir are centered at ~35–32 Ka, 26.5–21 Ka, 16–14 Ka, and 13–12 Ka (Table 2; Figure 16). Limber pine disappears from the midden record between 35 and 33 Ka and between 23 and 21 Ka, leaving white fir as the only tree species present.

Late Pleistocene climates can be extrapolated by using modern analogue temperature and precipitation requirements for limber pine and white fir. Limber pine favors cool, dry continental conditions with rainfall distributed relatively evenly during the year; it is drought tolerant. White fir favors cool, moist conditions with a winter peak in rainfall, but it often survives in canyons where shallow groundwater is available to it. In either case, white fir expansion indicates moister conditions. Rocky Mountain white fir appears to survive under cooler and drier conditions than does Sierran white fir. The seasonal distribution of rainfall appears to vary considerably as well where Rocky Mountain white fir grows. The modern analogue climates of these two species suggest the following climatic scenario for the late Pleistocene.

The wettest periods were those when limber pine disappeared from the woodland record. These appear to coincide

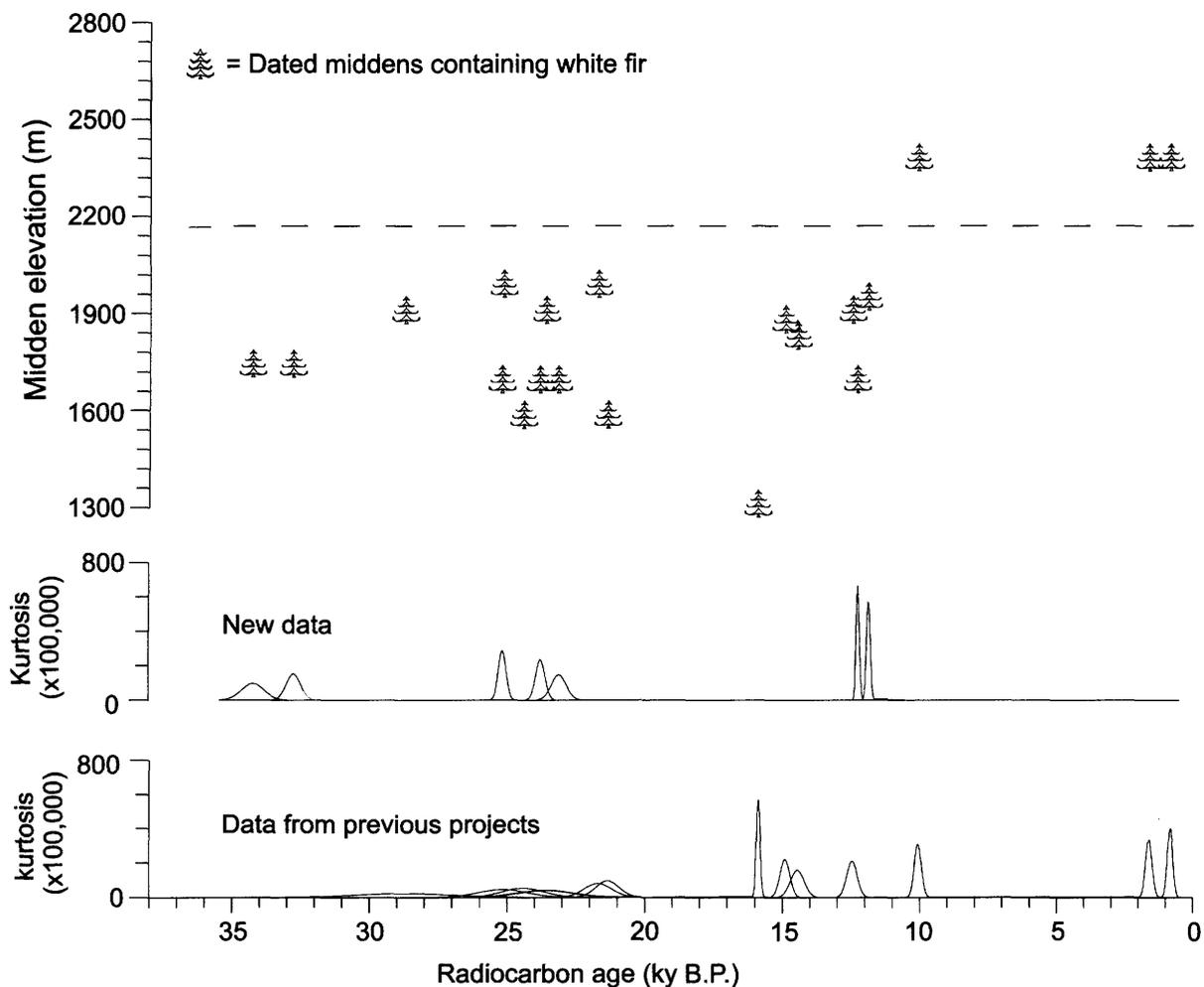


FIGURE 16.—Elevational distribution of white fir, as ascertained with macrofossils from ancient woodrat middens in the northern Mohave Desert, by radiocarbon age. (Top) Our own and previously published data from middens containing white fir (tree symbols) in a 200 km radius around Yucca Mountain; the dashed line is the approximate lower elevational distribution limit of white fir in the Sheep Range today. (Middle, Bottom) Radiocarbon dates on white fir for this study (middle) and for other studies (bottom) plotted as a normal distribution at three standard deviations around the mean. See Figure 15 caption for explanation of these kurtosis plots.

with the onset (23–21 Ka) and demise (16–14 Ka and 13–12 Ka), but not the climax, of the late glacial maximum. An earlier cold/wet period centered between ~35 and 33 Ka apparently corresponds to one noted in the pollen records from the Summer Lake basin and from the Pyramid Lake midden (see middle Holocene above in “Northern and Western Great Basin”). The pollen record from Profile II at Tule Springs records increased pine and fir corresponding with the pre-glacial maximum episodes (Mehringer, 1967, fig. 32). Such episodes suggest that Pacific air masses played a greater role in the climates of southern Nevada at that time. Conversely, periods of cold, dry continental climates (continental polar and Arctic air mass predominance) occurred from 16 to 21 Ka and from 29 to 32

Ka based on the absence of white fir in communities with abundant limber pine.

Our knowledge of the modern mean annual precipitation (MAP) requirements of key plant species together with changes in their distribution during the Pleistocene—as revealed in the plant macrofossil data from woodrat middens in southern Nevada (and northern Nevada)—indicate rapid shifts toward wetter winter precipitation patterns lasting from about one century to as long as one to two millennia. The MAP ranges for modern analogue plant species suggest a Pleistocene MAP range between 380 and 635 mm at elevations between 1500 and 2000 m (Forester et al., 1996). This is roughly an increase of 50%–90% above the current range of 200–250 mm.

TABLE 1.—Lower elevational occurrences of limber pine (*Pinus flexilis*) within a 200 km radius of Yucca Mountain, Nevada, as revealed in the current study (in **bold**), from lowest to highest elevation. Midden data analyzed by other investigators are Fortymile Canyon (Spaulding, 1994), Sheep Range (Spaulding, 1981), Eleana Range (Spaulding, 1985), Potosi Mountain (Mead et al., 1978), and Clark Mountain (Mehring and Ferguson, 1969). All sites are in Nevada unless noted otherwise (NTS = Nevada Test Site).

Locality; midden no.	Radiocarbon age (years)	Laboratory no.	Material dated	Elevation (m)
Fortymile Canyon, NTS; FMC-11A (1)	15,870 ± 70	QL-4223	Fecal pellets	1310
Sheep Range; Penthouse 2(1)	28,960 ± 2,000	A-1773	Utah juniper	1580
Sheep Range; Willow Wash 4C(1)	24,400 ± 760	A-1751	Utah juniper	1585
Sheep Range; Willow Wash 4C(2)	19,020 ± 750	UCR-729	Utah juniper	1585
Sheep Range; Basin Canyon 1	15,610 ± 260	WSU-1856	Utah juniper	1635
<b>Pahranagat Range; PR230594ARM1(1)</b>	<b>16,010 ± 80</b>	<b>BETA-74775</b>	<b>Limber pine</b>	<b>1695</b>
<b>Pahranagat Range; PR230594ARM1(1)SSIDE</b>	<b>18,160 ± 80</b>	<b>BETA-86066</b>	<b>Limber pine</b>	<b>1695</b>
<b>Pahranagat Range; PR110688PEW3(2)</b>	<b>18,765 ± 180</b>	<b>BETA-32405</b>	<b>Limber pine</b>	<b>1695</b>
<b>Pahranagat Range; PR230594ARM1(2)</b>	<b>23,890 ± 160</b>	<b>BETA-74772</b>	<b>Limber pine</b>	<b>1695</b>
<b>Pahranagat Range; PR110688PEW3(3)</b>	<b>25,250 ± 140</b>	<b>BETA-86063</b>	<b>Limber pine</b>	<b>1695</b>
<b>Double Cave, Pahroc Range; DC180595JPB1(1)</b>	<b>32,070 ± 230</b>	<b>BETA-86031</b>	<b>Limber pine</b>	<b>1743</b>
<b>Double Cave, Pahroc Range; DC180595JPB1(2)</b>	<b>30,000 ± 240</b>	<b>BETA-86105</b>	<b>Limber pine</b>	<b>1743</b>
Sheep Range; Flaherty Mesa 1	20,390 ± 340	WSU-1864	Utah juniper	1770
Sheep Range; Wagon Canyon 2	25,000 ± 710	A-1656	Utah juniper	1790
Eleana Range, NTS; ER-3(14)	14,200 ± 100	USGS-1266	Limber pine	1800
Eleana Range, NTS; ER-2(4)	14,090 ± 320	A-2927	Limber pine	1810
Eleana Range, NTS; ER-2(4)	15,300 ± 130	USGS-875	Limber pine	1810
Eleana Range, NTS; ER-2(5)	14,260 ± 110	USGS-874	Limber pine	1810
Eleana Range, NTS; ER-2(6)	14,500 ± 110	USGS-885	Limber pine	1810
Eleana Range, NTS; ER-2(10)	17,100 ± 90	USGS-1069	Limber pine	1810
<b>Ribbon Cliffs, Nellis Air Force Base; RC250588LCP11</b>	<b>18,075 ± 180</b>	<b>BETA-32407</b>	<b>Limber pine</b>	<b>1829</b>
<b>Ribbon Cliffs, Nellis AFB; RC060795PEW41A</b>	<b>24,330 ± 110</b>	<b>BETA-86080</b>	<b>Limber pine</b>	<b>1829</b>
<b>Ribbon Cliffs, Nellis AFB; RC060795PEW41B</b>	<b>26,210 ± 130</b>	<b>BETA-86082</b>	<b>Limber pine</b>	<b>1829</b>
<b>Ribbon Cliffs, Nellis AFB; RC060795PEW41C</b>	<b>25,850 ± 140</b>	<b>BETA-86084</b>	<b>Limber pine</b>	<b>1829</b>
Potosi Mountain, Spring Range; Potosi Mtn 2C2	14,430 ± 150	LJ-4005	Limber pine	1830
Sheep Range; Eyrie 3(1)	16,490 ± 220	WSU-1853	Utah juniper	1855
Sheep Range; Eyrie 1(3)1	23,380 ± 490	WSU-1864	Utah juniper	1860
Sheep Range; Eyrie 1(3)2	9,370 ± 120	WSU-1863	Utah juniper	1860
Sheep Range; Eyrie 5(2)	30,470 ± 740	WK-168	Utah juniper	1860
Sheep Range; Eyrie 5(3)	19,750 ± 450	WK-167	Fecal pellets	1860
Clark Mountain, California; CM-1	23,600 ± 980	I-3557	Twigs	1910
Clark Mountain, California; CM-2	28,720 ± 1,800	I-3648	Twigs	1910
<b>Stockade Wash, NTS; STW220594ARM113</b>	<b>11,400 ± 60</b>	<b>BETA-86123</b>	<b>Limber pine</b>	<b>1950</b>
<b>Stockade Wash, NTS; STW220594ARM114</b>	<b>12,040 ± 60</b>	<b>BETA-86088</b>	<b>Limber pine</b>	<b>1950</b>
<b>Stockade Wash, NTS; STW220594ARM111</b>	<b>12,290 ± 70</b>	<b>BETA-74777</b>	<b>Limber pine</b>	<b>1950</b>
<b>Stockade Wash, NTS; STW220594ARM112U</b>	<b>12,340 ± 60</b>	<b>BETA-86121</b>	<b>Limber pine</b>	<b>1950</b>
<b>Stockade Wash, NTS; STW220594ARM112</b>	<b>12,550 ± 70</b>	<b>BETA-74779</b>	<b>Limber pine</b>	<b>1950</b>
Sheep Range; Deadman 1(1)	17,420 ± 250	LJ-3707	Limber pine/bristlecone pine	1970
Sheep Range; Deadman 1(2)	16,800 ± 250	WSU-1860	Utah juniper	1970
Sheep Range; Deadman 1(4)	18,680 ± 280	WSU-1857	Utah juniper	1970
Sheep Range; South Crest 1(4)2	21,700 ± 500	LJ-2840	Limber pine/bristlecone pine	1990
Sheep Range; South Crest 1(3)	25,140 ± 900	A-1669	Utah juniper	1990
Sheep Range; Spires 2(1)	18,800 ± 130	USGS-199	Fecal pellets	2040
Sheep Range; Spires 2(2)	16,200 ± 350	A-1875	Limber pine/bristlecone pine	2040
<b>Cliff Springs, Belted Range, NTS; CS0909900GHH11</b>	<b>30,270 ± 360</b>	<b>BETA-64355</b>	<b>Limber pine</b>	<b>2133</b>
Clark Mountain, California; CM-2	19,900 ± 1,500	GAK-1987	Limber pine/bristlecone pine	2140
Sheep Range; Hidden Forest 3A	1,600 ± 120	A-1742	Utah juniper	2380
Sheep Range; Hidden Forest 3B	820 ± 100	WSU-2046	Rocky Mountain juniper	2380
Sheep Range; Hidden Forest 3C(1)	10,060 ± 130	LJ-3729	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 3C(2)	11,940 ± 140	LJ-3730	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 3C(3)	11,860 ± 160	LJ-3728	Limber pine/bristlecone pine	2380
Sheep Range; Hidden Forest 1	11,570 ± 120	LJ-4046	Limber pine/bristlecone pine	2400

TABLE 2.—Lower elevational occurrences of white fir (*Abies concolor*) within a 200 km radius of Yucca Mountain, Nevada, as revealed in the current study (in **bold**), from lowest to highest elevation. Midden data analyzed by other investigators are from Fortymile Canyon (Spaulding, 1994), Sheep Range (Spaulding, 1981), Potosi Mountain (Mead et al., 1978), and Clark Mountain (Mehring and Ferguson, 1969). All sites are in Nevada unless noted otherwise.

Locality; midden no.	Radiocarbon age (years)	Laboratory no.	Material dated	Elevation (m)
Fortymile Canyon, Nevada Test Site; FMC-11A (1)	15,870 ± 70	QL-4223	Fecal pellets	1310
Sheep Range; Willow Wash 4A	21,350 ± 420	WSU-1858	Utah juniper	1585
Sheep Range; Willow Wash 4C(1)	24,400 ± 760	A-1751	Utah juniper	1585
<b>Pahranagat Range; PR230594ARM1(1)</b>	<b>12,280 ± 60</b>	<b>BETA-74776</b>	<b>White fir</b>	<b>1695</b>
<b>Pahranagat Range; PR110688PEW3(2)</b>	<b>23,150 ± 270</b>	<b>BETA-32404</b>	<b>White fir</b>	<b>1695</b>
<b>Pahranagat Range; PR230594ARM1(2)</b>	<b>23,820 ± 170</b>	<b>BETA-74773</b>	<b>White fir</b>	<b>1695</b>
<b>Pahranagat Range; PR110688PEW3(3)</b>	<b>25,200 ± 140</b>	<b>BETA-86064</b>	<b>White fir</b>	<b>1695</b>
<b>Double Cave, Pahroc Range; DC180595JPB1,1</b>	<b>32,790 ± 260</b>	<b>BETA-86032</b>	<b>White fir</b>	<b>1743</b>
<b>Double Cave, Pahroc Range; DC180595JPB1(2)</b>	<b>34,260 ± 410</b>	<b>BETA-86106</b>	<b>White fir</b>	<b>1743</b>
Potosi Mountain, Spring Range; Potosi 2C L	14,450 ± 250	A-1778	White fir	1830
Potosi Mountain, Spring Range; Potosi 2A (2)	14,900 ± 180	LJ-4004	Miscellaneous	1880
Clark Mountain, California; CM-3	12,460 ± 190	I-3690	Piñon pine	1910
Clark Mountain, California; CM-1	23,600 ± 980	I-3557	Twigs	1910
Clark Mountain, California; CM-2	28,720 ± 1,800	I-3648	Twigs	1910
<b>Stockade Wash, Nevada Test Site; STW220594ARM111</b>	<b>11,890 ± 70</b>	<b>BETA-74778</b>	<b>White fir</b>	<b>1950</b>
Sheep Range; South Crest 1(4)2	21,700 ± 500	LJ-2840	Limber pine/ bristlecone pine	1990
Sheep Range; South Crest 1(3)	25,140 ± 900	A-1669	Utah juniper	1990
Sheep Range; Hidden Forest 3B	820 ± 100	WSU-2046	Rocky Mountain juniper	2380
Sheep Range; Hidden Forest 3A	1,600 ± 120	A-1742	Utah juniper	2380
Sheep Range; Hidden Forest 3C(1)	10,060 ± 130	LJ-3729	Limber pine/ bristlecone pine	2380

Shifts from the dominance of xeric climate shrub species to Utah juniper during the Pleistocene at elevations from ~700 to 1500 m record precipitation increases ranging between 33% and 66%, a gain of 50–100 mm above current values (Forester et al., 1996). Whereas today's MAP is only 150 mm, the Pleistocene MAP was at least 200 mm or as high as 255 mm at elevations between ~700 and 1500 m.

Other evidence for these wetter episodes is provided by the accumulating database of radiocarbon dates on spring deposits in the northern Mojave Desert. Dates from the Las Vegas Valley, Corn Creek Dunes, Three Lakes Valley, and Indian Springs Valley indicate several episodes of late Pleistocene and early Holocene spring activity (Quade et al., 1995, 1998). Quade et al. (1995) suggest that based upon the radiocarbon dates at Corn Creek Dunes there may be three distinct phases of discharge: an early set centered around or prior to 31 Ka, a second set from ca. 25 to 14 Ka, and a third set from 14 to 8 Ka. As more dates accumulate, these episodes may become more constrained and may match the vegetation data more closely. To the southeast in the Lake Mojave basin, a series of lakes—some lasting for as many as 2000 years and others lasting only a few hundred—span the period between ~22 and ~11.5 Ka (Brown et al., 1990, fig. 8). These may, in part, correspond to the precipitation events seen in the record from southern Nevada; however, these lakes reflect climatic conditions in transverse ranges, which may have experienced a quite different se-

quence of rainfall history because of their proximity to the Pacific Ocean.

These occasional wet episodes are set against the major portion of the Pleistocene between 35 and 12 Ka, which was dominated by more continental conditions characterized by cold-dry climate about 1.33 times wetter than today (Forester et al., 1996). Based upon a comparison of the temperature requirements of Rocky Mountain and Sierran white firs versus limber pine, the onset and decline of the late glacial maximum may have been 2°–6° C warmer than its climax.

Precipitation gradients increased substantially during the Pleistocene. The MAP was approximately 133% of what it is today at ~750 m in elevation, based upon the displacement of Utah juniper (Wells and Jorgensen, 1964; Wells and Berger, 1967; Forester et al., 1996). Limber pine displacement indicates that MAP was approximately 190% of what it is today at ~1500 m (Forester et al., 1996). If the increase in regional MAP had been regular, the percent of increase should be the same at all elevations. However, the difference in MAP between these two elevations during the Pleistocene reveals that precipitation was ~50% greater at 1500 m than it was at 750 m. Lack of woodrat midden data above 2000 m for the Pleistocene prevents extrapolation of precipitation values to higher elevations. This reconstructed rainfall gradient indicates a dramatically enhanced orographic precipitation effect during the late Pleistocene in southern Nevada.

TABLE 3.—A general sequence of climate and mean annual precipitation (MAP) for southern Nevada from ca. 35 to 12 Ka.

Radiocarbon date (Ky B.P.)	Relative climate	Estimated MAP (mm)
~35–33	Very wet, cool	560–635
33–26.5	Dry, cooler	406–457
26.5–23	Wet, cool	457–560
23–21	Very wet, cool	560–635
21–16	Dry, cold	406–457
16–14	Wet, cool	457–560
14–13	Dry, cooler	406–457
13–12	Wet, cool	457–560

By using the MAPs derived from the vegetation data summarized above, a general sequence of climate is generated for the period from ~35 to 12 Ka for southern Nevada (Table 3). This applies only for elevations around 1500 m. At elevations around 750 m, estimates should be about 50% of those at 1500 m. Above 2000 m, absence of data prevents estimation. Climate designations in Table 3 are only relative.

At lower elevations, desert shrub communities dominated by saltbushes, rabbitbrush (*Chrysothamnus* spp.), mormon tea (*Ephedra* spp.), and other shrubs appear to have prevailed through much of the late Pleistocene (Spaulding, 1985, 1990, 1994; Wells and Woodcock, 1985). Investigations in the Pintwater Cave area, north of the Spring Range in southern Nevada, revealed shrub community dominance with intermittent incursions of Utah juniper for most of the last 34 Ky. A brief appearance of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) in the area of the cave after ~34 Ka (numerous seeds in the cave sediments) suggests cooler, wetter climates at that time than later in the Pleistocene. Similar climatic conditions seem to have allowed Rocky Mountain juniper to exist on the east shore of pluvial Owens Lake between 23 and 17.5 Ka (Koehler and Anderson, 1994). The cool temperatures generated in the Owens Valley by the nearby Tioga glacial advance may have provided conditions suitable for the survival of Rocky Mountain juniper far from its current upper-elevation distributions.

#### EARLY HOLOCENE (12.5 TO 8 KA)

In southern Nevada, replacement of subalpine woodland dominated by limber pine with juniper-dominated semiarid woodland at intermediate elevations preceded the disappearance of low-elevation juniper woodland by desert scrub (Spaulding, 1977, 1981; Wigand et al., 1995). Although woodrat midden records indicate that piñon pine appeared in several areas around southern Nevada including the Pahrana-gat Range well before 8.5 Ka, it seems to have been a much less important component of early Holocene semiarid woodlands than was juniper (Spaulding, 1985, 1990; Thompson, 1990; Wigand et al., 1995). However, records from the north-central and eastern Great Basin (Thompson and Hattori, 1983; Thompson and Kautz, 1983; Wells, 1983; Madsen and Rhode,

1990; Thompson, 1990) confirm piñon pine's rapid northward expansion.

Despite evidence of warming climates in the southern Great Basin, the persistence of juniper woodland outliers after 9.5 Ka may reflect occasional wetter and/or cooler periods of climate that aided their persistence. At Little Skull Mountain on the southern edge of the Nevada Test Site, juniper persisted until 10.5 Ka but disappeared from the record by 10 Ka (Wigand, unpublished data). By 9.5 Ka, however, it reappeared in the woodrat midden macrofossil record at Little Skull Mountain. Organic mats (residues) dating primarily from 10.2 to 8.6 Ka also reflect these episodes of moister climate (Quade et al., 1998, especially fig. 5). Based upon the vegetation during this span of time, the rainfall from two different climatic regimes may have been responsible for formation of the black mats. Climates may have been considerably cooler from 11.2 to 10.2 Ka than from 12 to 11.5 Ka, resulting in reduced evaporation rates and greater effective precipitation. Climates were warmer from 10.2 to 8.6 Ka, and from 9.5 to 8.6 Ka the summer rainfall may have increased considerably.

Evidence of a shift to summer seasonal rainfall during the warm portion of the latter early Holocene between 9.5 and 9 Ka is provided by the appearance of netleaf hackberry (*Celtis laevigata* var. *reticulata* (Torr.) L. Benson) seeds in the paleobotanical record of southern Nevada. Hackberry seeds (endocarps) have been recovered from woodrat middens located on the xeric southeast slope of Little Skull Mountain (Wigand et al., 1994), from middens in the Sheep Range north of Las Vegas (Spaulding, 1990), and from the Sandy Valley (Spaulding, 1994), and several hundred seeds were recovered from the sediments of Pintwater Cave (Jahren et al., 2001). Today it occurs in canyons, seeps, and washes at elevations of 500–1700 m. Hackberry ranges from the southern Sierra Nevada foothills and the San Bernardino Mountains in the southwestern United States and northern Mexico into the southern plains to Kansas, with outliers in Washington (Benson and Darrow, 1981; Krajicek and Williams, 1990). In southern Nevada it is found associated with a spring near Pahroc Spring in the Pahroc Range, in one locality in Fortymile Canyon on the Nevada Test Site, and in canyons at the southern end of the Spring Range. The appearance of hackberry remains in middens suggests it grew at the bases of cliff faces or in arroyo bottoms, areas that are currently too dry to support it, and reveals a pattern of greater regional abundance of the tree between 9.5 and 9 Ka.

These reconstructed climatic conditions compare well with evidence of increased spring discharge found by Quade et al. (1998) that apparently may correspond to incursions of monsoon rains during the thermal maximum (Spaulding, 1985; Spaulding and Graumlich, 1986). In particular, well-developed black mats, which Quade et al. (1998) describe from the valleys surrounding the Spring Range, dating to between 9.5 and 8.6 Ka probably reflect the period of increased summer monsoon activity. Additional evidence of episodes of the incursion

of moisture during this period are the intermittent lakes that appear in the Lake Mojave basin (Silver and Soda Lake playas) at this time (Brown et al., 1990). The evidence indicates that as many as six lakes (with intervening drying) occupied the Lake Mojave basin between 11.5 and ~8.5 Ka (Brown et al., 1990, fig. 8). Therefore, during a period when other climate proxies indicate that conditions were much warmer and that mean annual rainfall was decreasing, a shift of rainfall toward the summer season coinciding with the early Holocene thermal maximum would explain the presence of perennial seeps, as evidenced by the latter period of black mat formation, the majority of which Quade et al. (1998) have dated to between 10.2 and 8.6 Ka.

In the Alabama Hills north of the Owens Lake basin, the termination of Pleistocene woodland occurred 9.5 Ka (Koehler and Anderson, 1995). This coincides with the disappearance of juniper woodland from outlier positions in the Lahontan Basin, as noted above, and also with the termination of lithoid tufa formation around the Lake Lahontan shoreline. This is also, as just noted, the beginning of the period of greater penetration of monsoon rainfall into southern Nevada. Together these data suggest a major northward displacement of regional climatic regimes at this time.

#### MIDDLE HOLOCENE (8 TO 5.5 KA)

As Spaulding (1990) indicated, the early Holocene vegetation assemblages of the northern Mojave Desert were, in most cases, unique and did not survive the middle Holocene. Pollen samples from Profile V in the Tule Springs record indicate a dramatic increase in low-spine (*Ambrosia*-type) pollen shortly after 8.5 Ka (Mehringer, 1967). This probably corresponds to the appearance of white burrobush (*Ambrosia dumosa* (Gray) Payne), one of the two codominants of the typical Mojave Desert creosote bush–white burrobush vegetation assemblage (Spaulding, 1990, fig. 9.13). According to the woodrat midden macrofossil record, creosote bush appears slightly later in the area (but see Grayson's (1993:200) discussion). Further west the appearance of these two species is even later (Spaulding, 1980). Unfortunately, pollen can not be used to document the presence or appearance of creosote bush because of its rarity in the pollen record. Both these species arrived as migrants from further south, but the climatic impetus for their arrival is unclear.

Truncation of the pollen record in Profile IV at Tule Springs sometime after 7.5 Ka corresponds with the beginning of a general absence of paleobotanic data spanning the next 2 Ka in the southern Great Basin and northern Mojave Desert (Mehringer, 1967). The dearth of vegetation data is probably a direct reflection of the impact of severe drought in the region. Springs and marshes dried and woodrats may have retreated into more favorable areas. Severe eolian erosion may have characterized parts of this period, because late-Holocene spring and marsh deposits in the northern Mojave Desert generally lie upon ero-

sion surfaces that were formed during the middle Holocene (Mehringer and Warren, 1976; Mehringer and Sheppard, 1978; Wigand, 1997b). This suggests that vegetation cover may have been very sparse.

Only a few middens are dated to this period. One collection of middens from the McCullough Range southwest of Las Vegas is dominated by thermophilic (warm-temperature) plant species (Spaulding, 1991). These reflect the warm, dry conditions of the middle Holocene. Spaulding also suggested that no evidence exists for summer seasonality of rainfall between 6.8 and 5 Ka.

LaMarche (1974) suggested that upper tree line temperatures were considerably warmer during this period and that upper tree lines extended upward. Graybill et al. (1994) indicated extended periods of drought as well. These data suggest that the middle Holocene in the Great Basin was characterized by considerable warmer and drier conditions than currently exist in the Great Basin.

#### EARLY LATE HOLOCENE (5.5 TO 2 KA)

In the northern Mojave Desert there is a dramatic change in climate at this time. It is most clearly manifested in the sudden formation of peats that overlie erosional unconformities. Peats occurred at the base of the Little Lake record in the Owens River valley (Mehringer and Sheppard, 1978), in Ash Meadows south of the Nevada Test Site (Mehringer and Warren, 1976), and at the base of the Lower Pahranaagat Lake cores in the White River valley northeast of Las Vegas (Wigand, 1997b). These peats attest to the sudden rejuvenation of springs in the region. Mesophilic plant abundance in woodrat middens of the McCullough Range began in strata dating to 5.5 Ka (Spaulding, 1991). A woodrat midden stratum in the southern Pahranaagat Range dated to 5.6 Ka reveals a brief lowering in elevation of Utah juniper below its current elevational distribution (Wigand et al., 1995).

In southern Nevada, increased abundance of woodrat middens containing Utah juniper and piñon pine macrofossils evidence a major Neoglacial reexpansion and/or increase in density of piñon–juniper woodland beginning ~3.8 Ka (Wigand et al., 1995, fig. 4). This early phase of semiarid woodland expansion culminated about 2.3 Ka.

At Lower Pahranaagat Lake, a pollen record analyzed back to 3.8 Ka with a resolution of a sample every 14 or so years provides a clear record of drought cycles for the northern Mojave Desert and the southern Great Basin (Figure 17; Wigand, 1997b). This record is correlatable with the White Mountain tree ring record of Graybill et al. (1994) (Figure 18). It provides an indication not only of relative increases in precipitation but also of shifts in seasonal distribution as well.

Wetter climate events of the Neoglacial are reflected in the record from Lower Pahranaagat Lake, but two differences from the Neoglacial wet events in the Diamond Pond record of the Great Basin are evident. First, only two of the three major wet



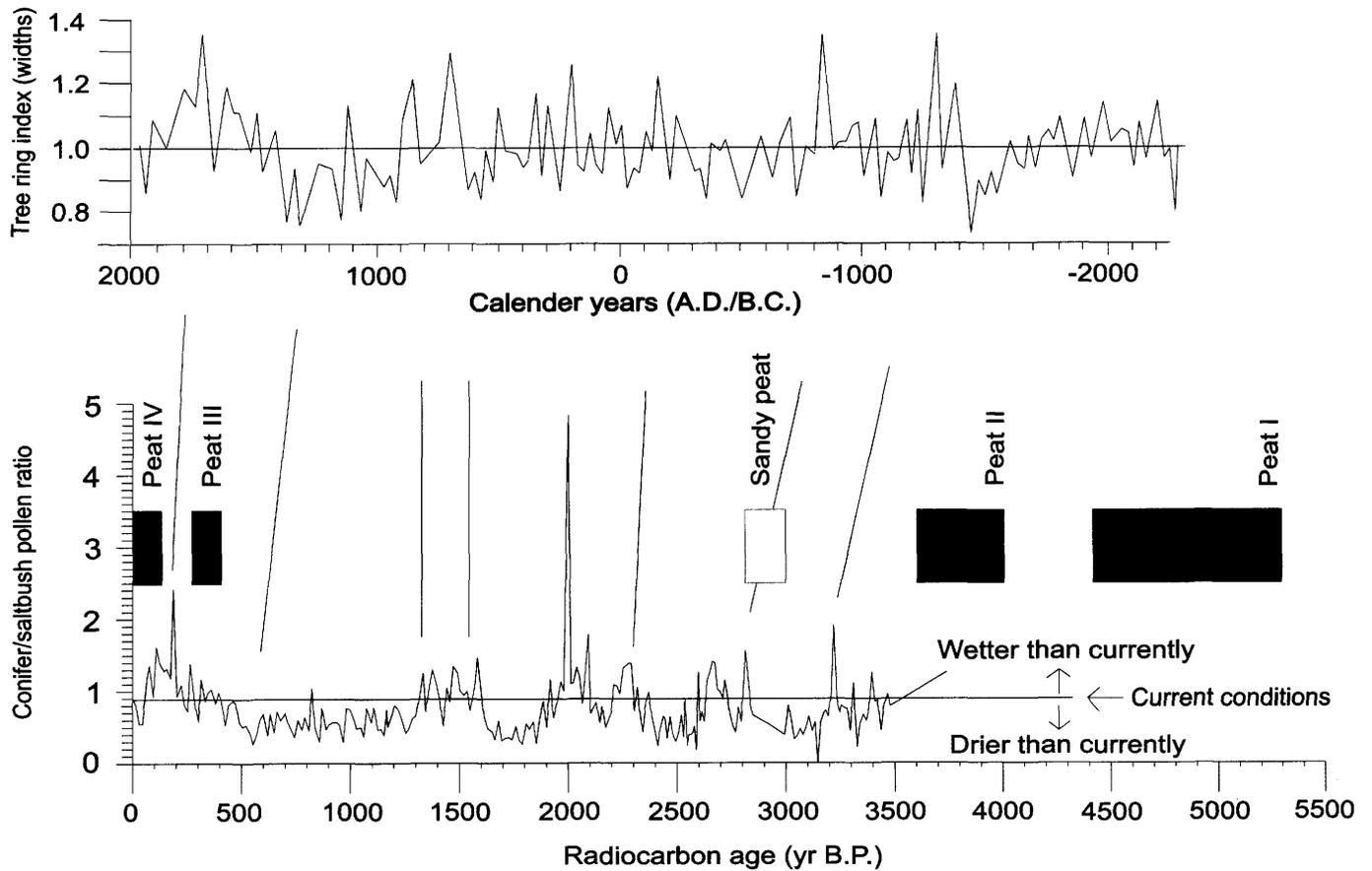


FIGURE 18.—Index of effective precipitation in the southern Great Basin and northern Mohave Desert for the last 4000 years, based on pollen, tree ring, and marsh peat proxy climate data. The conifer/saltbush pollen record of Lower Pahrnatag Lake in the southern Great Basin (bottom), by radiocarbon date, is compared with the bristlecone pine tree ring record from the White Mountains (top), by calendar date (years A.D./B.C.) (Graybill et al., 1994). Straight lines between the two graphs indicate correlations in the records. Growth of peat strata in Ash Meadows, reported by Mehringer and Warren

(1976), is also correlated with pollen ratios by radiocarbon date. The pollen ratio, (juniper + pine)/all Chenopodiineae, reflects regional precipitation. Increases in the ratio indicate wetter periods, primarily winter precipitation; decreases indicate reduced winter precipitation. The tree ring index also reflects regional precipitation, although temperature may also play a role. Wider ring widths (in millimeters) (up) correspond with greater precipitation; narrower widths (down) correspond with reduced precipitation.

periods (~3.7 and 2.7 Ka) seen in the Diamond Pond record appear in the Lower Pahrnatag Lake record (Figure 17). Second, their magnitudes (Figure 18) are considerably lesser at Lower Pahrnatag Lake than at Diamond Pond (Wigand, 1987). This may indicate that it was Pacific storm systems that were primarily responsible for these periods of wetter climate and that their impact was focused primarily upon the northern Great Basin and the Pacific Northwest, not the southern Great Basin or southwestern United States. Ely et al. (1993) indicated that, between 3.6 and 2.2 Ka, large floods are completely absent from their record of floods for the Southwest. As mentioned above, the winter-dominated storm pattern may not have been very strong in the southwestern United States, and therefore the pattern of winter storms and cyclones currently associated with heavy flooding may not have been important in the Southwest. Reduced heavy flooding episodes may also reflect the impact

of a denser vegetation cover that grew in response to heavier, winter rainfall throughout the West during the Neoglacial from 4 to 2 Ka. On the other hand, the lack of large floods could reflect a southward displacement of monsoonal systems and the resulting reduction in torrential episodes that would cause heavy floods.

Enzel et al. (1989, 1992) indicated that a shallow lake stood for a brief period in the Soda and Silver Lake basins ~3.6 Ka. This corresponds to the strongest of the wet events proposed for Diamond Pond in the northern Great Basin (Wigand, 1987). This event may have initiated late-Holocene vegetation recovery that served to buffer runoff between 4 and 2 Ka in the southwestern United States.

A terminal Neoglacial increase in pollen of juniper and several shrub species in Lower Pahrnatag Lake records a brief, though unparalleled, episode of more mesic climate (Figure

17). Because it is juniper and sagebrush that responded most dramatically, an interval of cooler, wetter climate with winter-dominated rainfall pattern seems to have occurred ~2 Ka that lasted about 150–200 years (Figure 17; Wigand, 1997b).

Reconstructed deposition rates of the Lower Pahranaagat Lake record together with dramatic changes in relative pollen values indicate that, at times, the transition to wetter, or conversely drier, conditions often took less than a decade or two (see the event 2 Ka in Figure 17). The local increase in effective precipitation needed to accomplish the observed changes in juniper abundance, based upon the difference in the minimal annual rainfall requirements between sagebrush (Mozingo, 1987) and Utah juniper (Leonard et al., 1987), must have been at least 10–20 millimeters per year at elevations around 1500 m. Reduced evaporation rates caused by reduced mean annual temperature probably played a substantial role in increasing effective precipitation.

#### LATE LATE HOLOCENE (2 KA TO PRESENT)

Severe drought marked by the expansion of saltbushes and greasewood signaled the end of the Neoglacial in southern Nevada (Figure 17). LaMarche (1974) sees a dramatic rise in tree lines at this time that lasted for the next 300 years. Increased grass abundance during this period suggests that summer-shifted rainfall characterized this episode of dry climate (Figure 17).

At Lower Pahranaagat Lake, additional increases in juniper pollen, indicating greater effective precipitation resulting from increased winter precipitation and/or reduced evaporation rates from cooler temperatures, occurred ~1.5, 0.9, 0.7, and after 0.5 Ka (Figure 17; Wigand, 1997b). In fact juniper pollen values had their last climax about 0.3 Ka (during the Little Ice Age) and have since declined.

These periods roughly coincide to times when trees were drowned in the lake basins and stream valleys in the Mono Lake area, as indicated by Stine (1990). These episodes are mirrored in the marsh pollen records from Cofer Spring north of Beatty, Nevada (Wigand and Rose, 1990), and at Warm Sulphur Springs in the Panamint Valley (Smiley and Mehringer, n.d.). They coincide more roughly with the growth of peat layers in the latest dunes from Ash Meadows (Mehringer and Warren, 1976).

Episodic peat growth in Ash Meadows is probably promoted in part by increased surface discharge from the spring mounds that dot the area (Mehringer and Warren, 1976). The movement of local sand dunes, however, could also effect the growth of peat. Dunes occasionally divert watercourses that originate at the various spring mounds and that form ponds, which serve as the areas of peat formation. Peat formation corresponding with the wet event 5.5 Ka (which Quade et al., 1998, do not report) strongly suggests that the peats occurring at Ash Meadows correlate with higher spring discharge. Additional evidence for late-Holocene spring activity is provided by a few dates that

Quade et al. (1998) reported for the Las Vegas Valley centered around 2.3, 1.4, and 0.6–0.5 Ka, periods that do not appear in the peat record at Ash Meadows.

There have been at least three substantial expansions of piñon pine as reflected in increases in pine pollen values in the Lower Pahranaagat Lake record during the last 2 Ky (Figure 17; Wigand, 1997b, fig. 3). These pollen increases and the expansions of piñon pine reflect climatic conditions of a slightly different nature than those that occurred when juniper was expanding in southern Nevada. The most revealing of these expansions occurred between ~1.6 and 1.2 Ka (Wigand, 1997b, fig. 3). This period was characterized by minimal increases in juniper pollen values and began after a distinct period of increased grass pollen values. Analysis of woodrat midden data from the Pahranaagat Range indicates that piñon pine expansion was regional. Contrasting the ecologies of juniper, piñon pine, and grass suggests that this climatic episode may have been a period of summer-shifted rainfall. Juniper, which favors winter precipitation, responded little during this period. Sagebrush, another plant favoring winter precipitation, did not respond during this period (Figure 17; Wigand, 1997b, fig. 4). The grass expansion evident just before the beginning of this period, at a time when saltbush (*Chenopodiaceae*) and greasewood pollen values signal that a drier climate was prevalent, suggested the initiation of summer-shifted rainfall (Figure 17; Wigand, 1997b, figs. 4, 5). This pattern continued into the subsequent period of increased rainfall, which would have favored the establishment of piñon pine seedlings through the more reliable supply of moisture during hot summer months. LaMarche (1974) suggested that temperatures may have been slightly cooler during this period than in the periods after the Neoglacial.

Expansion of piñon pine in the Great Basin was further favored by the reduction in harshness of winter conditions after the Neoglacial ended about 2 Ka. Piñon pine is readily susceptible to winterkill during episodes of extreme cold. Even today its distribution in the northern Great Basin is characterized by stands on lower mountain ranges sheltered behind larger chains that effectively block the direct impact of winter storms. The regional nature of the climate changes reflected in the Lower Pahranaagat Lake record is clearly documented by similar changes in contemporaneous records elsewhere in the Great Basin (see "Middle Late Holocene ..." and "The Last Millennium ..." sections, above in "Northern and Western Great Basin").

In southern Nevada, increases in saltbushes and greasewood in the pollen record of Lower Pahranaagat Lake clearly reflect the strong drought conditions of this period (Wigand, 1997b). The transition from shallow lake to marsh conditions in Lower Pahranaagat Lake about 1.2 Ka also may be linked in part to increasing drought. Three brief wet episodes ~0.9, 0.6, and 0.35 Ka correspond with those identified by Stine (1990). Pollen from the Lower Pahranaagat record indicates that woodland may have retreated in some areas (Wigand, 1997b).

The pollen record from Lower Pahranaagat Lake indicates that juniper woodland reexpanded  $\sim 0.35$  Ka (corresponding to the beginning of the European "Little Ice Age") (Figure 17; Wigand, 1997b). Some marsh expansion occurred, and there was an increase in the algae *Botryococcus*, an indicator of eutrophic conditions (Figure 17). Together these suggest that southern Nevada climates were increasingly wet. However, pine values did not increase until near the end of this period after  $\sim 0.2$  Ka. This may suggest that, although the period was characterized by wetter climates, winters may have been harsher, even in southern Nevada, thereby discouraging the establishment of piñon pine until temperatures began warming near the end of the period. Enzel et al. (1989) and Enzel et al. (1992) indicated that a shallow lake stood for a brief period in the Soda and Silver Lake basins  $\sim 0.39$  Ka. This corresponds to the record for wetter climate from Lower Pahranaagat Lake (Figure 17; Wigand, 1997b).

After the Little Ice Age, the prominence of pine in the woodlands of the southern Great Basin and northern Mojave Desert continued to grow as juniper seems to have declined (Figure 17; Wigand, 1997b, fig. 2). Saltbushes (Chenopodiaceae in Figure 17; Wigand, 1997b, fig. 2) expanded dramatically with respect to sagebrush as well. This was followed by evidence that the creosote bush/white burrobush community (represented by *Ambrosia*-type pollen) expanded as saltbush communities contracted slightly. Although it appears that no major changes occurred in the abundance of sedges, a dramatic decline in *Botryococcus* suggests that the marshes were not as eutrophic, and instead, increased salinity may have affected marsh productivity. These changes reflected the drier conditions that developed after the end of the Little Ice Age. Most recently, wetter conditions have resulted in a regional resurgence of pine and renewed activity in the marsh, signaled by renewed *Botryococcus* abundance.

### Bonneville Basin and Eastern Great Basin

The emerging picture of Late Quaternary vegetation change in the Bonneville Basin complements the well-known record of lake level fluctuations of Pleistocene Lake Bonneville and precursors (McCoy, 1981; Scott et al., 1983; Currey and Oviatt, 1985; Oviatt et al., 1987; Currey, 1990; Benson et al., 1992; Oviatt et al., 1992; Oviatt, 1997), the lesser-known Holocene history of Great Salt Lake (Currey et al., 1984), glacial records from the Wasatch Front (e.g., Richmond, 1964, 1986; Madsen and Currey, 1979; Scott, 1988), and nearby pollen localities (e.g., Bright, 1966; Beiswenger, 1991; Thompson, 1992). The Bonneville Basin provides a nearly ideal setting to examine long-term correlation between terrestrial vegetation patterns and regional aquatic history and to assess how these two systems both responded to climatic drivers. As Oviatt et al. (1992:239) sum up the situation, "by comparing chronologies from different proxy records, which show how different environmental systems responded to the same climatic factors,

we can learn a great deal about the nature of late Pleistocene climates." We can also learn much about the strengths and weaknesses of the different proxy records.

The chronological framework used in this section generally follows the Lake Bonneville sequence outlined in Oviatt et al. (1992). The interglacial Holocene is herein assumed to follow the demise of Lake Gilbert at about 10 Ka (Benson et al., 1992). Temporal divisions within the Holocene follow the venerable tripartite scheme first outlined by Antevs (1948); these divisions are made as a matter of organizational convenience of a constantly fluctuating continuum and not to characterize distinctive or unified climatic or vegetational modes.

### THE ILLINOIAN-SANGAMON GLACIAL-INTERGLACIAL CYCLE (150 TO 50 KA)

Several cores and pollen samples taken from lake sediments in the Bonneville Basin provide evidence of regional vegetation change prior to ca. 50 Ka (Eardley and Gvosdetzky, 1960; Martin and Mehringer, 1965; Eardley et al., 1973; Thompson et al., 1994; Davis, 2002 (this volume)). This period is beyond the limits of radiocarbon dating of organic materials, so dating uncertainties have prevented development of a detailed history of vegetation change. However, other dating methods (e.g., tephrochronology, paleomagnetism) allow general correlation of paleovegetation patterns with reconstructions of late Pleistocene lake history in the Bonneville Basin.

The last major deep-lake event before Lake Bonneville formed was the Little Valley lake cycle (Scott et al., 1983). Known deposits of this lake reach a maximum elevation of 1490 m,  $\sim 75$ –120 m below the maximum level of Lake Bonneville. The Little Valley cycle is broadly dated between 150 and 90 Ka, but it correlates with stage 6 of the marine oxygen isotope record (Shackleton and Opdyke, 1973; Pisias et al., 1984) as well as with the Illinoian glacial period, and it probably dates to between ca. 150 and 130 Ka (Scott et al., 1983). This lake cycle was followed by a long interglacial period during which lake levels were generally quite low. It was terminated by the Cutler Dam lake cycle, a relatively shallow lake ( $\sim 1340$  m in maximum elevation) that formed sediments called the Cutler Dam alloformation (Oviatt et al., 1987). Radiocarbon dates constrain the Cutler Dam lake to be older than 36 Ky (Oviatt et al., 1987), whereas luminescence dating places it at  $59 \pm 5$  Ka (Kaufman et al., 2001), the latter being correlative with OIS 4.

Against this backdrop, the pollen evidence for this time period (Davis, 2002) suggests that, during the Little Valley lake cycle, vegetation on the margins of the Bonneville Basin consisted of sagebrush steppe and cold-dry-adapted pine woodland generally lacking junipers. Pine and montane conifers such as spruce and fir are suggested to have occurred some 500–1500 m lower in elevation in a mosaic of open woodland and shrub steppe rather than in closed-canopy forest.

During the subsequent interglacial period, the lake basin was filled approximately to the Gilbert level, covering the Great Salt Lake Desert at least to the vicinity of Wendover (Davis, 2002). High amounts of sagebrush and moderate quantities of chenopods indicate domination of sagebrush–saltbush steppe. The continued presence of moderate quantities of pine pollen and small amounts of pollen from other montane conifers suggests that climatic conditions remained fairly cool relative to today. Littoral marsh vegetation, including sedge and cattail, is represented in modest quantities, which suggests it occurred in favorable locations. A period of lake decline is estimated to have occurred about 70 Ka, based on the absence of pollen from the Wendover core. A short but distinctive episode corresponding to the Cutler Dam lake episode may be represented by high amounts of pine, sedge, and cattail pollen and low abundance of sagebrush and *Chenopodiaceae-Amaranthus* (*Cheno-Ams*) pollen at 1100 cm deep in the Knolls core and ~1200 cm deep in the Wendover core, estimated by Davis to have occurred approximately 80–70 Ka.

#### PRE-BONNEVILLE CYCLE, EARLY AND MIDDLE WISCONSIN (~50 TO 28 KA)

During this interval, the Bonneville Basin was characterized by generally low lake levels, at or below the level of the Gilbert shoreline (Scott et al., 1983; Oviatt et al., 1992; Davis, 2002). Paleovegetation records dating to the middle-Wisconsin interstadial period are still relatively sparse, restricted to a handful of very ancient packrat middens (Wells, 1983; Thompson, 1984), to pollen from a few lake cores and from cave sites (Martin and Mehringer, 1965; Mehringer, 1977; Spencer et al., 1984; Thompson, 1984; Davis, 2002), and to occasional isolated montane peat deposits or plant fragments in lacustrine sediments (e.g., Scott et al., 1983; Oviatt et al., 1987).

Packrat middens from the southern Bonneville Basin that date between 40 and 28 Ka indicate that montane settings supported coniferous woodlands dominated by bristlecone pine, with associates including sagebrush, rabbitbrush, snowberry (*Symphoricarpos* sp.), Utah juniper, and other mesophilic shrubs (Wells, 1983; Thompson, 1984). To the north, packrat middens dating to this interval are very scarce, but one locality, Top of the Terrace (Goshute Range), yields a series of midden samples that provide evidence of changing vegetation in upland settings before 28 Ka (Rhode, 2000a; Madsen et al., 2001; see Figure 19). Samples dating from older than about 50 Ka (infinite radiocarbon dates) show evidence of abundant Utah juniper, which is gone from the record by ca. 46 Ka and does not reappear until the late Holocene. By 46 Ka, upland meadow shrubs including sagebrush, currant (*Ribes* sp.), and shrubby cinquefoil (*Potentilla fruticosa* L.) replaced juniper woodland. Limber pine began to appear by ca. 41 Ka, and it became the dominant conifer through ca. 28 Ka (with one apparent decline ca. 30 Ka). Fernbush (*Chamaebatiaria millefolium* (Torr.) Maxim.), a montane woodland shrub of drier habitats, first appeared in large quanti-

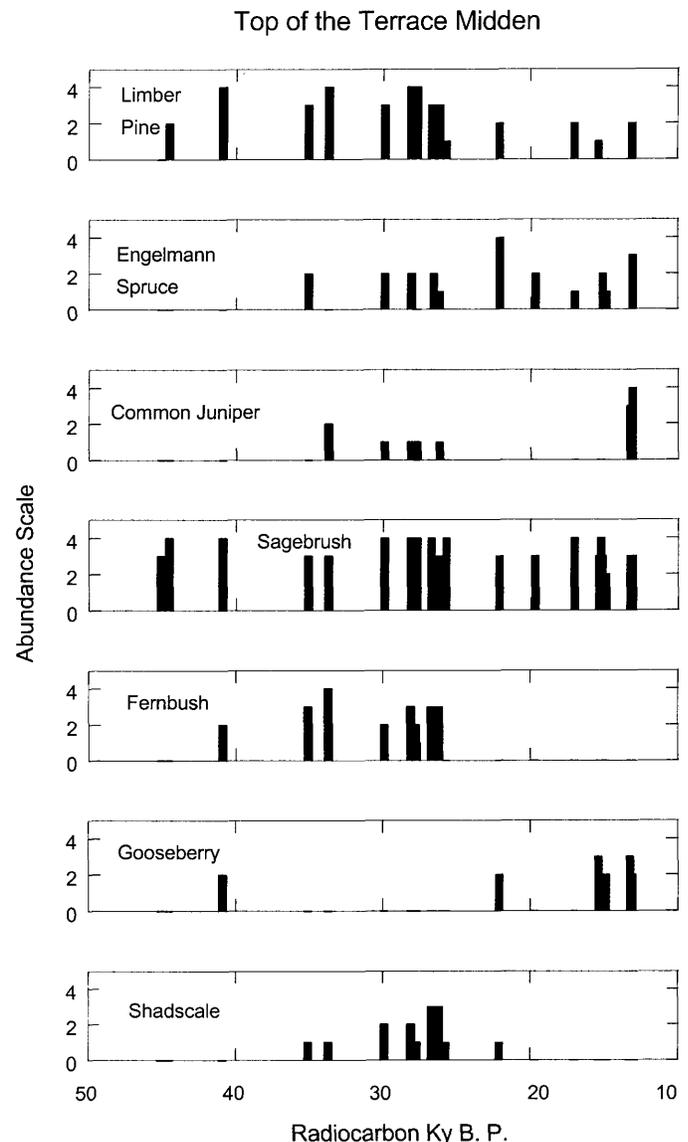


FIGURE 19.—Abundances of major plant constituents from selected radiocarbon-dated strata in the Top of the Terrace packrat midden, Goshute Range, eastern Nevada (Rhode, 1998). Radiocarbon dates are corrected for  $^{13}\text{C}/^{12}\text{C}$  but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

ties by 36 Ka, similar to the distribution of limber pine. More mesophilic shrubs, however, declined in representation: cinquefoil disappeared from the record after 40 Ka, and currant was gone by about 34 Ka. In broad terms, the dominance of subalpine conifers (bristlecone pine in the south, limber pine in the north) and abundance of relatively dry upland shrubs at the expense of mesophiles suggests cold but dry conditions from 40 to 28 Ka. The midden record hints at substantial millennial-scale variation in vegetation content along dimensions of latitude and elevation, but the existing record and available dating techniques are insufficient to document these with clarity.

Pollen records from localities in and near the Bonneville Basin help to fill out this reconstruction of middle-Wisconsin-age vegetation. Pollen in Council Hall Cave (northern Snake Range) dating from ca. 40–30 Ka reflects montane vegetation dominated by pine and steppe shrubs including sagebrush, with conifers such as juniper, spruce, and fir represented in very small quantities. The presence of pollen of xerophytic shrubs such as chenopods and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) may indicate that these taxa dominated valley floors at the time (Thompson, 1984). Pollen from the sediment cores taken from near Wendover and Knolls contain high proportions of sagebrush, moderately high proportions of *Chenopods*, and relatively low values of pine pollen prior to ca. 30 Ka (Davis, 2002). A basal date of the pollen record from Crescent Spring (Mehringner, 1977) is not available, but the sediments probably postdate ca. 28 Ka. Sediments from the Great Salt Lake Core C of Spencer et al. (1984) also postdate 30 Ka (Thompson et al., 1990). The basal units, which probably represent playa/playa edge deposits, are dominated by pollen of sagebrush and halophytic chenopods; pine pollen is lacking, although spruce, fir, and juniper pollen are present at low to moderate levels (Figure 20).

Further afield, the pollen sequence from Ruby Marsh, approximately 100 km west of the Bonneville Basin, indicates the presence of a shallow saline marsh/playa surrounded by sagebrush steppe (Thompson, 1984, 1992) from 40 to 28 Ka. Samples older than 30 Ka have the highest proportion of pine pollen of any in the 40,000-year record, but pine pollen is not abundant, indicating that pines were “probably present regionally, though not at the edge of the lake, and perhaps not in the southern Ruby Mountains” (Thompson, 1992:11). The very small amount of juniper pollen indicates that these conifers also were absent or rare.

Sagebrush steppe was the dominant lowland community on the Snake River Plain during this period, as indeed it was throughout the period from ca. 70 to 10 Ka (Bright and Davis, 1982; Mehringner, 1985; Davis et al., 1986; Beiswenger, 1991). Conifers were apparently limited to foothills and rocky terrain. Conifer pollen (mainly pine and spruce) increased slightly after 30 Ka, suggesting a slight increase in winter–spring moisture in a cold environment.

Together, these records point to cold but dry conditions before ca. 28 Ka in the eastern Great Basin. The climatic reconstruction based on vegetation data is consistent with the low lake levels that apparently characterized the Bonneville Basin prior to 28 Ka (Oviatt et al., 1992).

EARLY BONNEVILLE CYCLE,  
PRE-FULL GLACIAL (28 TO 20 KA)

Lake Bonneville began to rise about 30 Ka, slowly at first and rapidly after ca. 28 Ka; by 26 Ka the lake was roughly 100 m deep. The period from 26 to 20 Ka is marked first by continuing rise in lake level and subsequently by the Stansbury os-

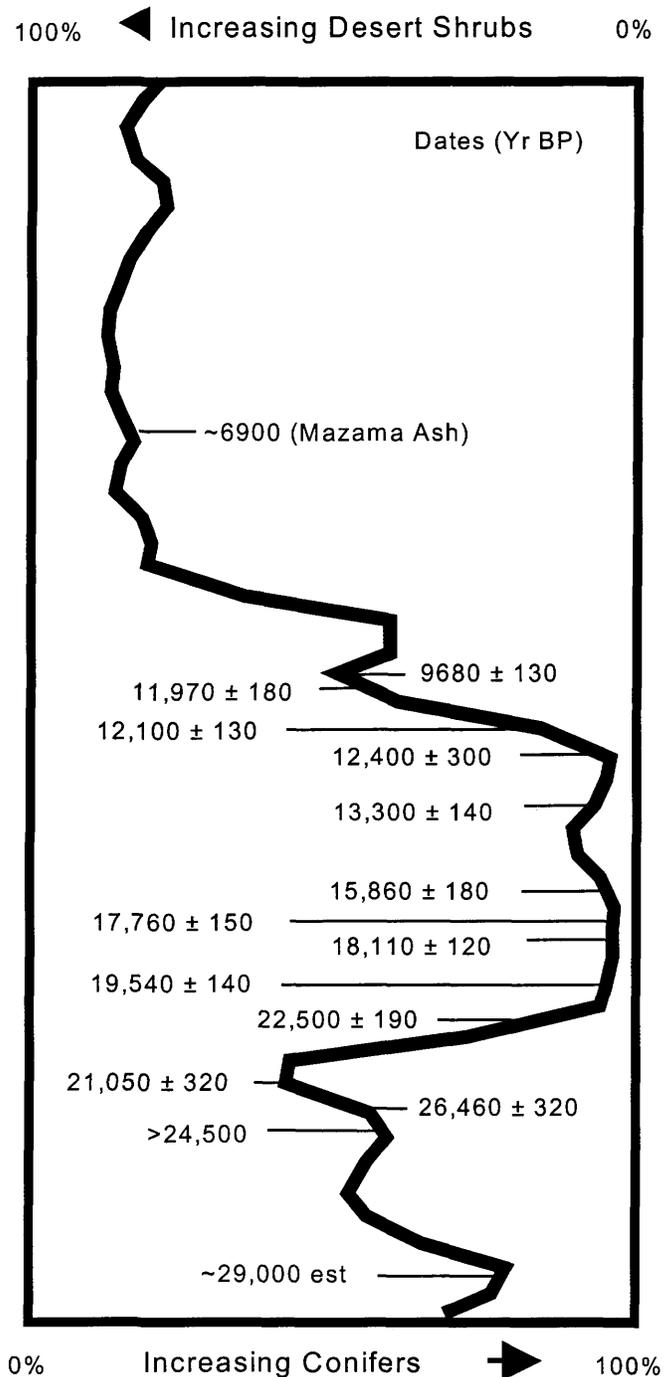


FIGURE 20.—Pollen ratios of xeric desert scrub/conifers for the last 30,000 years from Great Salt Lake Core C samples (Madsen and Kay, 1982; Spencer et al., 1984), with temporal controls in the right margin provided by Thompson et al. (1990). The curve shows relative percentages of *Chenopodiaceae-Amaranthus+Sarcobatus+Ambrosia*-type Asteraceae (scale at top) versus *Abies+Picea+Pinus+Pseudotsuga* (scale at bottom) and is smoothed by a weighted three-level moving average. (Modified from Madsen, 2000, fig. 4.)

cillation and development of the Stansbury Shoreline (Oviatt et al., 1990). According to Oviatt et al. (1990, 1992), the Stansbury oscillation represented a major change in hydrologic bud-

get, though the climatic implications are still uncertain. Oviatt (1997) correlated this event with the termination of an ice-rafting (Heinrich) event in the northern Atlantic Ocean, suggesting a global-scale climatic cause.

The vegetation record dating to the millennia after 28 Ka shows continued dominance of bristlecone pine (without spruce or Utah juniper) in the southern Bonneville Basin, based on Council Hall Cave pollen (Thompson, 1984) and a couple of packrat midden samples (Wells, 1983). However, the interval between 28 and 18 Ka is poorly represented in the existing packrat midden record in the southern Bonneville Basin. Northward, at Top of the Terrace (Figure 19), several samples document that spruce increased in abundance while limber pine declined to low amounts (Rhode, 2000a; Madsen et al., 2001). Upper montane meadow plants such as currant and cinquefoil reappeared and expanded in abundance at the expense of fern-bush; sagebrush maintained fairly consistent representation throughout. These vegetation changes suggest increasingly moist and cool conditions by ca. 22 Ka; however, the midden record for the period is more gap than record.

Fortunately, pollen and macrofossils in sediments and sediment cores provide more continuous, long-term records of vegetation change in the Bonneville Basin. The record from Crescent Spring (Mehringer, 1977) shows relatively low to moderate values of pine and spruce prior to ca. 24 Ka and relatively large values for sagebrush and Chenopodiaceae, presumably shadscale and greasewood, reflecting widespread sagebrush-shadscale associations in valley bottoms, with pine and some spruce in uplands. A transition to deep, freshwater lake conditions occurred at ca. 24 Ka (Mehringer, 1985), with large increases in pine pollen, the appearance of spruce, and the decline of chenopods. Davis (2002) shows a very similar record for pollen taken from Wendover and Knolls. Pines may not have increased much in overall abundance on the landscape, but their pollen may have been concentrated and overrepresented by large lake effects. Chenopods, on the other hand, probably lost substantial habitat as rising levels of Lake Bonneville flooded valley bottoms and margins.

The Great Salt Lake Core C (Spencer et al., 1984; Thompson et al., 1990) indicates a similar transition to a fresh, deepwater lake by ca. 22.5 Ka, with greatly increased conifer pollen at the expense of sagebrush and xerophytic chenopods (Figure 20). A similar increase in lake level after 23 Ka is indicated in the lacustrine record from Ruby Marsh (Thompson, 1992), though pollen values suggest that sagebrush steppe continued to dominate the local landscape. Pollen from Grays Lake, in the uplands adjacent to the Snake River Plain (Beiswenger, 1991) shows that a pine/spruce woodland increased in abundance by ca. 30 to 26 Ka, intruding into what had been sagebrush steppe, and suggesting increasing moisture as well as continued cold temperatures. Finally, scattered occurrences of spruce and fir wood dating between 26 and 20 Ka are found in lake deposits on the east side of the Bonneville Basin (Scott et al., 1983),

presumably indicating spruce/fir forests in the Wasatch Front. Wetter and cold conditions are indicated.

#### MIDDLE BONNEVILLE CYCLE, FULL GLACIAL (20 TO 14 KA)

During this interval Lake Bonneville rose abruptly from the Stansbury level—rapidly for the first 2000 years, then more slowly after 18 Ka—reaching the Bonneville highstand by ca. 15 Ka (Oviatt et al., 1992). Age estimates of glaciation in the Wasatch Range suggest the maximum extent of glaciation was between 20 and 18 Ka (Richmond, 1964, 1986; Madsen and Currey, 1979; Scott, 1988), at about the time Lake Bonneville was rising rapidly but a couple thousand years before the lake reached its highstand. The difference in timing between the age of the maximum extent of glaciation and the highstand of Lake Bonneville has been accounted for by the southward movement of the polar jet stream (Antevs, 1948; Benson and Thompson, 1987; COHMAP Members, 1988; Oviatt et al., 1990; Thompson et al., 1993). The rise of the lake was interrupted several times by substantial millennial-scale lake level declines (on the order of 50–100 m in depth). Oviatt (1997:155) has identified six “falling-lake events” ranging in age from 21 to 10 Ka that appear to be correlated with terminations of iceberg-rafting events in the northern Atlantic Ocean (Heinrich, 1988; Bond and Lotti, 1995). These events also appear to be correlated with glacial extent and climate changes in western North America (Allen and Anderson, 1993; Phillips et al., 1994; Clark and Bartlein, 1995). Oviatt (1997) suggested that these events may be related to latitudinal shifts in the polar jet stream that occurred several times during the late-Wisconsin interval in response to the topography of the continental ice sheet.

Vegetation records dating from the full glacial are somewhat more abundant than from the previous period. In the southern Bonneville Basin, packrat middens reveal that bristlecone pine continued to dominate, with additional representation of subalpine conifers including spruce, common juniper, Rocky Mountain juniper, and (rarely) limber pine; and shrubs including snowberry, spiny greasewood (*Glossopetalon spinescens* Gray), sagebrush, and (rarely) shadscale (Wells, 1983; Thompson, 1984). Pollen from Council Hall Cave contains large proportions of pine pollen with increasing spruce and decreasing abundance of juniper-type pollens and relatively stable amounts of sagebrush pollen. To the north, a midden sample dating to ca. 17 Ka at Top of the Terrace (Figure 19) shows an impoverished local flora, suggesting a tundra steppe dominated by sagebrush, some grass, and sparse cinquefoil, with rare occurrences of limber pine and spruce. This sample also contains several wetland plants, including bulrush (*Scirpus* sp.) and pondweed (*Potamogeton* sp.), as well as fish bones. It is highly unlikely that pondweed grew within the foraging radius of woodrats living at the midden locality. More likely is the possibility that seeds of aquatic plants were ingested by fish or waterfowl, which then became part of the diet of raptors,

regurgitated in the shelter, and subsequently collected by woodrats. The seeds imply a nearby permanent body of water, probably Lake Waring in the valley below, but possibly also Lake Bonneville, east of the Goshute Mountains. Slightly younger samples from this midden locality document the reappearance of currant and an absence of limber pine.

Pollen from the Great Salt Lake Core C (Spencer et al., 1984) shows a continued dominance of spruce and pine during this period; the relative abundance of sagebrush and especially chenopod shrubs dropped substantially after ca. 22 Ka (Figure 20). In Ruby Valley, the large, freshwater Lake Franklin deepened to ~30 m from ca. 18 Ka until after 15 Ka, drowning what had been marshland (Thompson, 1992). Pollen from these sediments, however, shows relatively little change in the composition or abundance of sagebrush steppe vegetation surrounding the lake. It is likely that the lake resulted from reduced evaporation rate in a cold but relatively dry continental climate; increased precipitation likely would have resulted in more mesophilic shrubs and conifers in the region, which is not indicated in the pollen record.

In all, increasingly cold conditions are indicated after ca. 20 Ka; whether precipitation was substantially greater is less certain. Thompson and Mead (1982) noted that a steep vegetation gradient existed between the northern and southern Bonneville Basin (above the tree line in the north, below the tree line to the south), probably reflecting the distribution of growing-season temperatures and possibly also growing-season precipitation (dry in the north, more mesic in the south). The vegetation record is not yet sufficiently detailed or well dated to distinguish vegetation changes during the several falling-lake events reported by Oviatt (1997). Rapid fluctuations of pollen values in the Great Salt Lake Core C samples (Spencer et al., 1984) suggest that certain taxa (conifers and sagebrush) varied in abundance or that tree lines may have shifted in elevation in response to global-scale climatic changes during the full glacial (Figure 20).

#### LATE BONNEVILLE CYCLE, TERMINAL WISCONSIN (14 TO 10 KA)

Dating evidence summarized by Oviatt et al. (1992) and Benson et al. (1992) suggests that, after Lake Bonneville stabilized at the Provo level after the Bonneville Flood, the lake receded precipitously after 14 Ka, falling possibly to below modern levels by ca. 12 Ka, and marking the end of the Bonneville cycle. Subsequently, a large but much shallower lake rose to the Gilbert shoreline by around 10.9 Ka (possibly as early as 12 Ka), receding again by ca. 10 Ka. As Oviatt et al. (1992) noted, however, the timing of the recession from the Provo level is one of the least-known parts of the Bonneville lake cycle; dating of the Gilbert lake phase is little better (but see Oviatt et al., 2001). Recent dating efforts (Light, 1996; D.B. Madsen and C.G. Oviatt, pers. comm. to Rhode, 1996), as well as climate reconstructions from terrestrial vegetation data (Rhode and Madsen,

1995; see below), suggest that details of both the timing and magnitude of the post-Provo recession may need to be revised. Timing of the recession of Lake Bonneville also contrasts with the pluvial Lake Lahontan record, which indicates a deepening lake between 14.5 and 12.5 Ka (Benson et al., 1992), and with the evidence from the vegetation records in the northwestern Great Basin and the northern Mojave Desert, which suggests that this period was wetter than the glacial maximum (see "Last Glacial Cycle ..." above in "Northern and Western Great Basin" and see "Late Pleistocene ..." above in "Southern Great Basin and Northern Mohave Desert").

In contrast to the poorly dated recessional lake record, the terminal Wisconsin period is one of the best represented in the entire paleovegetation record, with many packrat middens and a couple of pollen sequences available (Madsen and Currey, 1979; Wells, 1983; Thompson, 1984; Rhode and Madsen, 1995). Several substantial vegetation changes occurred after 14 Ka. In the southern Bonneville Basin (Thompson, 1990), mesophilic shrubs tended to decline in abundance, and xerophytes or thermophilous shrubs took their place. Bristlecone pine remained common until shortly before 10 Ka. Spruce is no longer found in the record of this period, and several montane shrubs also drop out at particular localities. Limber pine increased substantially in frequency, especially after 11 Ka. Utah juniper and douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) also began to appear in the south near the end of this period.

In the northern Bonneville Basin, numerous middens (Rhode and Madsen, 1995; Rhode, 2000a) document the presence of montane meadow vegetation comprising snowberry, currant, cinquefoil, sagebrush, and grass dating from ca. 14 to 13 Ka (Figure 21). From 13 to ca. 11 Ka, middens from relatively low elevations in the Bonneville Basin are dominated by limber pine, prostrate juniper, and sagebrush, and often contain remains of other montane shrubs. This evidence suggests that an extensive limber pine woodland (or mosaic of woodland and sagebrush steppe) dominated upper valley margins, while limber pine forest mixed with small numbers of spruce or fir apparently grew at higher elevations. Pollen data from Swan Lake, in the old Lake Bonneville overflow channel in southern Idaho, also show high values of limber pine and probably lodgepole pine (*Pinus contorta* Dougl. ex Loud.), along with spruce and fir, between 12 and 11 Ka (Bright, 1966). Pollen data from the Great Salt Lake Core C (Spencer et al., 1984; Thompson et al., 1990) show high relative abundance of pine and spruce until after 12.4 Ka, when sagebrush, greasewood, and Chenopodiaceae rapidly increase. Pollen from Grays Lake (Beiswenger, 1991) documents a shift by ca. 12 Ka from a pine-sagebrush parkland reflecting cold, dry glacial conditions to a woodland/steppe mosaic, including spruce, pine, and sagebrush, suggesting cool but moister conditions. Subsequent postglacial warming resulted in the upslope retreat of spruce and pine and the expansion of sagebrush and xerophytic chenopods in the Grays Lake basin.

Terminal Wisconsin-Age Packrat  
Middens, Northeast Great Basin

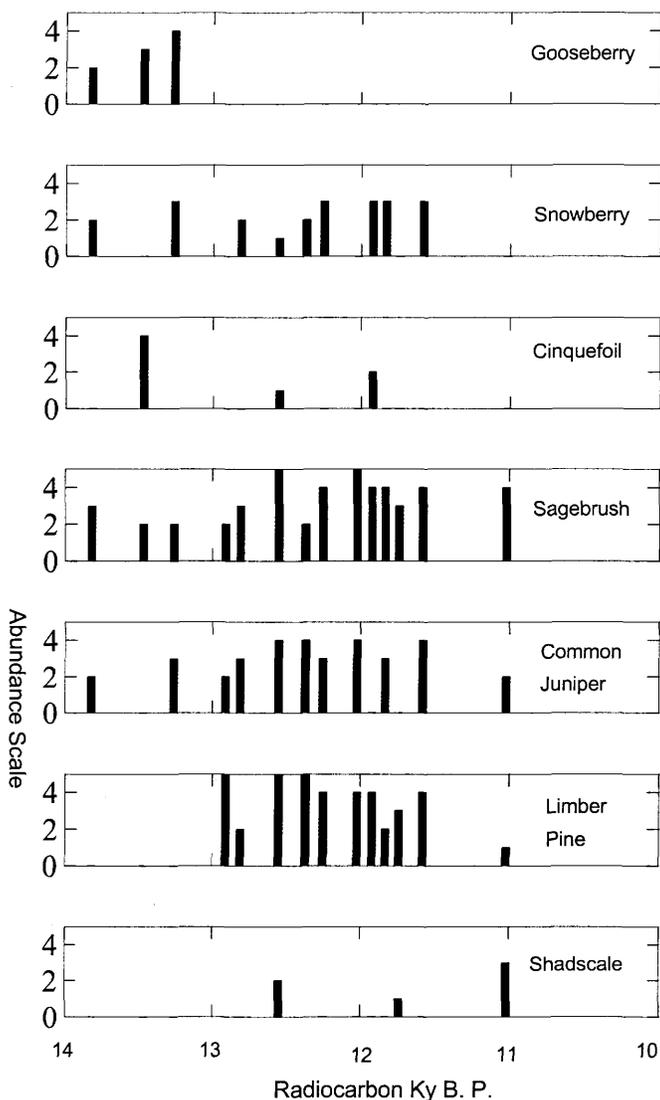


FIGURE 21.—Abundances of major plant constituents from selected radiocarbon-dated strata in packrat middens dating between 14 and 10 Ky B.P. in the northern Bonneville Basin (Rhode and Madsen, 1995). Radiocarbon dates are corrected for  $^{13}\text{C}/^{12}\text{C}$  but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

Together these records indicate warmer and possibly moister conditions ca. 14–12 Ka than during the full glacial, supporting montane meadows and woodlands in the north and more thermophilic woodland plants in the southern part of the Bonneville Basin. However, the climatic amelioration that occurred between 14 and 12 Ka was not so great as to prevent presently subalpine conifers from colonizing large areas at low elevations along the Bonneville highstand shoreline. Rhode and Madsen (1995) used the evidence that limber pine woodlands

expanded substantially to the margins of the Bonneville Basin to suggest that growing season temperatures were  $\sim 6^\circ\text{C}$  cooler than today. Insect assemblages from some of these middens also indicate substantially increased effective moisture relative to today (Scott Elias, pers. comm. to Rhode, 1998). In addition, the presence of fish bones in middens adjacent to the Great Salt Lake Desert and in Homestead Cave, in the Lakeside Range near Great Salt Lake, suggests relatively high lake levels perhaps as late as 11.5 Ka. Together, these biological data conflict with models of the decline of Lake Bonneville to below-modern levels at ca. 13–12 Ka (Benson et al., 1992; Oviatt et al., 1992).

By 12 Ka, the trend to drier conditions apparently strengthened. Pollen from Swan Lake indicates that spruce/pine woodlands were replaced by sagebrush steppe vegetation sometime between 11 and 10 Ka (Bright, 1966), possibly signaling cool but drier conditions during the Younger Dryas. The paleovegetation record from 11 to 10 Ka in the Bonneville Basin, however, is quite sparse at present. Middens dating to this interval are extremely scarce (Figure 21), and the Great Salt Lake C core (Spencer et al., 1984) is marked by a substantial temporal gap dating between ca. 12 and 9.6 Ka (Thompson et al., 1990) (Figure 20). What little data there are suggest a substantial reduction in pine woodlands and an increase in sagebrush–grass and shadscale associations, probably by 11 Ka and certainly by 10 Ka, reflecting the general trend of warming and drying. There is presently not enough evidence in the Bonneville Basin to show that vegetation changes occurring during the Gilbert lake cycle reflected enhanced moisture conditions, through either postulated Younger Dryas cooling (Benson et al., 1992) or increased summer monsoon precipitation (Currey, 1990; Oviatt et al., 1990).

EARLY HOLOCENE (10 TO 7 KA)

Early Holocene midden records are scarce by comparison with the terminal Wisconsin. The reason for the relative dearth of middens dating to the early Holocene remains unknown (Thompson, 1990), but it is possible that a continued warming and drying trend restricted *Neotoma cinerea* (bushy-tailed woodrat) habitat and population size. Fortunately, several pollen records from lacustrine settings exist for the Bonneville Basin and vicinity.

Comparison of vegetation patterns with the Holocene aquatic history of the Bonneville Basin also is hampered by lack of a well-known Holocene lake record for this Basin (Madsen et al., 2001). With the waning of Lake Bonneville after recession from the Provo level, lake level fluctuations became much smaller in scale. These smaller fluctuations are not as well dated as the lake events of the late Pleistocene (but see Currey and Madsen, 1974; Oviatt and McCoy, 1986), and some of the crucial evidence (for very low lake levels) is now under water and mostly inaccessible. It is known that lakes substantially larger than the present Great Salt Lake existed at several times

during the Holocene (Currey et al., 1984). Evidence for an undated but probably early Holocene lake with a level somewhat below the Gilbert shoreline suggests a mesic interval (relative to today) some time between 10 and 7 Ka. Marsh deposits dated 10–9 Ka were identified recently in the vicinity of Wendover and near the Old River Bed channel (D.B. Madsen, pers. comm. to Rhode, 1998). Both marshes indicate greater surface water and a higher regional water table than what prevails today.

Woodrat midden records in the southern Bonneville Basin suggest that woodlands were dominated by newly immigrant Utah juniper and Rocky Mountain juniper, at least toward the end of the early Holocene; bristlecone pine, limber pine, and common juniper persisted in protected montane settings such as north-facing slopes (Thompson, 1990). The Council Hall Cave pollen record suggests that conifers were relatively scarce, whereas trees such as quaking aspen (*Populus tremuloides* Michx.), mountain mahogany, and chokecherry (*Prunus virginiana* L.) increased in abundance, and sagebrush and grass were common (Thompson, 1984). Cooler temperatures in the early Holocene apparently allowed mesophilic plants to grow at lower elevations than today (Thompson, 1990).

In the northern Bonneville Basin, the Great Salt Lake Core C pollen record (Spencer et al., 1984) shows that the abundance of pollen from xerophytic shrub communities relative to conifer woodlands was about the same 9.5 Ka as it was about 12 Ka, bridging the 2500-year-long unconformity in the core (Figure 20). Soon after 9 Ka, however, xeric desert scrub increased strongly at the expense of conifer woodlands.

Packrat middens (Rhode, 2000b; Madsen et al., 2001) also indicate that limber pine woodlands were replaced by more xerophytic sagebrush and shadscale scrub in lowlands by at least 9.5 Ka and probably a millennium earlier, as shadscale steppe continued to expand into the valley bottoms vacated by Lake Bonneville and Lake Gilbert (Figure 22). At the Leppy Overhang locality, a midden sample dating to 9.3 Ka contains remains of shadscale, horsebrush (*Tetradymia* sp.), and other arid desert shrubs, with no conifers represented. A sample dating to ca. 7.5 Ka at the same site is dominated by shadscale, with sagebrush, greasewood, rabbitbrush, Stansbury cliffrose (*Purshia stansburiana* (Torr.) Henrickson), desert snowberry (*Symphoricarpos longiflorus* Gray), and thornberry (*Lycium* sp.) also present. This locality had harbored limber pine woodlands at approximately 11.8–10.8 Ka (see “Late Bonneville Cycle ...” section above in “Bonneville Basin and Eastern Great Basin”). At the Twin Peaks locality, a midden sample that dates to 9.3 Ka is dominated by sagebrush, with shadscale as a relatively minor component. Limber pine, in association with common juniper, sagebrush, and buffaloberry, had occurred at the same locality some 3000 years before. The same contrast can be found in the modern vegetation at the two localities: sagebrush dominates at the Twin Peak locality, whereas the Leppy Overhang site is dominated by shadscale.

### Holocene Packrat Middens, Northeastern Great Basin

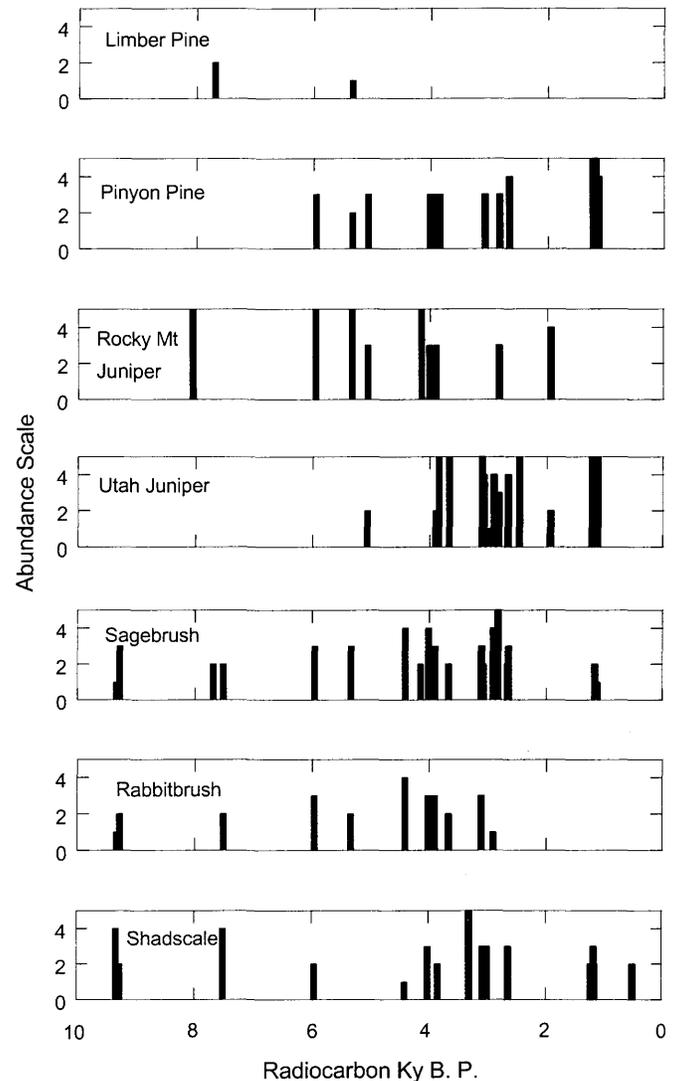


FIGURE 22.—Major plant constituents from selected radiocarbon-dated strata in packrat middens dating younger than 10 Ky B.P. in the northern Bonneville Basin (Rhode and Madsen, 1995; Rhode, 1998, and unpublished data). Radiocarbon dates are corrected for  $^{13}\text{C}/^{12}\text{C}$  but are not calibrated. Abundance values follow an ordinal scale ranging from 0 (none) to 5 (abundant), as described by Rhode and Madsen (1995).

Several records suggest that climatic conditions during the early Holocene were cooler and/or moister than at present, at least before ca. 8.5 Ka. Thompson's (1984) midden data indicating a cooler, mesic early Holocene have been noted previously. Further north, a midden from the Cherry Creek Range dating to ca. 7.7 Ka shows that limber pine survived in sheltered upland settings below its present altitude. Limber pine nut hulls in Danger Cave, directly dating between 8 and 7 Ka, also suggest that populations of this now subalpine conifer grew at relatively lower elevations nearby (Rhode and Madsen, 1998). Lim-

ber pine retreated upslope to its scattered subalpine stations during the middle Holocene, as climates continued to warm and as thermophilous competitors migrated into the region. To the west, woodrat middens from near Gatecliff Shelter in the Toiyama Range, central Nevada, are dominated by mesophilic trees and shrubs such as quaking aspen, serviceberry (*Amelanchier utahensis* Koehne), willow (*Salix* spp.), and Woods' rose (*Rosa woodsii* Lindl.), with sagebrush and rabbitbrush also present; conifers are rare or absent (Thompson and Hattori, 1983).

At Homestead Cave and the Lakeside Range in Utah, small mammal remains also indicate that the early Holocene was relatively cool and moist compared with conditions today (Grayson, 1998). Hackberry apparently was common in the outcrops around the cave and at lower elevations in the Lakeside Range from about 10 to 7 Ka (Hunt et al., 2000; Rhode, 2000b; Madsen et al., 2001). The climate today is too dry to support hackberry around Homestead Cave although it still occurs in the Lakeside Range (Albee et al., 1988) and is commonly found in the more massive and better-watered Oquirrh and Stansbury Mountains not far away. Hackberry prefers rocky substrates where it can absorb water trapped in cracks in outcrops (DeBolt and McCune, 1995). The presence of hackberry in the Lakeside Range during the early Holocene could have resulted from the more mesic conditions (perhaps summer precipitation) of the time, but it also could have resulted from a higher water table and more-saturated rock outcrops remaining from the Bonneville pluvial episode. The early Holocene hackberry in the Lakeside Range coincides with a similar increase in regional abundance of hackberry in southern Nevada, as noted above in the early Holocene section in "Southern Great Basin and Northern Mojave Desert."

Other regional vegetation records indicate substantial warming during the early Holocene, perhaps to temperatures warmer than today. The pollen record from Swan Lake (Bright, 1966) reveals a transition from sagebrush steppe to sagebrush/shadscale steppe ca. 9–8.5 Ka, reflecting increasing xericity through the early Holocene. A similar sequence occurred at Grays Lake (Beiswenger, 1991), where the transition is dated to ca. 8.5 Ka, and Ruby Marsh (Thompson, 1992), where the transition dates from 8.5 to 8 Ka. A decrease in the ratio of conifer pollen to all other pollen from Snowbird Bog (Madsen and Currey, 1979) also indicates an early Holocene warming prior to ca. 8 Ka (Figure 23). These records are consistent with general circulation models, suggesting increased solar insolation and warming of continental interiors during the early Holocene (COHMAP Members, 1988).

It is notable that early Holocene records indicating relatively cooler, moister conditions than today are typically (1) derived from packrat middens, (2) montane in distribution, and (3) more southerly in distribution; whereas those records emphasizing the early Holocene warming trend tend to be (1) pollen based, (2) from lowland or valley bottom settings, and (3) more northerly in distribution. The differing interpretations might have resulted from the different kinds of data sets being inter-

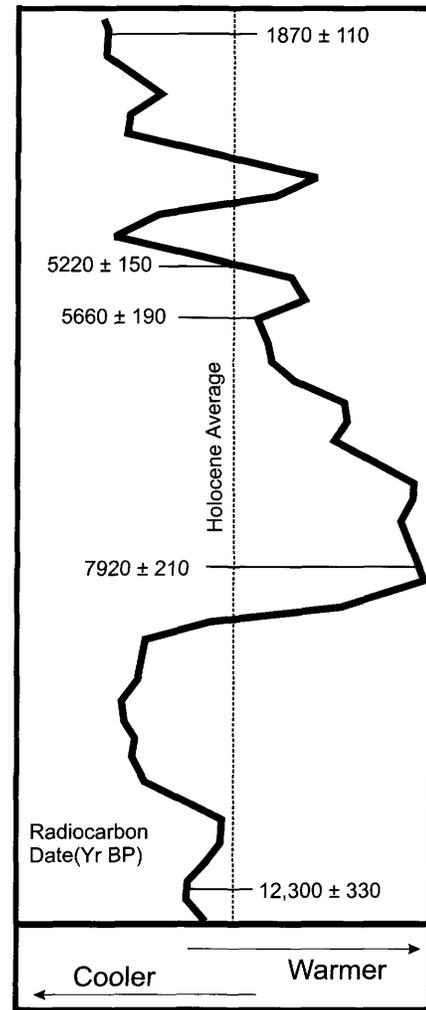


FIGURE 23.—Estimate of Holocene temperature change in the Wasatch Range, illustrated by curve showing changes in the relative abundance ratio of conifer pollen (*Abies* + *Picea* + *Pinus* + *Pseudotsuga*) to all other pollen in Snowbird Bog, Little Cottonwood Canyon (Madsen and Currey, 1979), with the average ratio (dashed line) and selected temporal controls indicated. Cooler temperatures are indicated by relatively greater abundances of conifer pollen. The curve is smoothed by a weighted three-level moving average. (Modified from Madsen, 2000, fig. 5.)

preted, or geographical climate gradients, or the differential response of plants to early Holocene climate in lowland versus montane habitats. Enhanced seasonality resulting from orbital forcing during the early Holocene (Thompson et al., 1993) may have affected montane woodlands in a different way than lowland shrub communities. Vegetational inertia (Cole, 1985; Davis, 1986) may also play a role here. It seems likely that, because of a warmer and drier early Holocene climatic regime, mesophilic plants had already been eliminated from valley floors; and although they had not yet disappeared from uplands they may have been growing there under stress. New techniques for assessing plant physiological stress from macrofossil remains may address this issue.

Beginning in the latest Wisconsin period and continuing through the early Holocene and into the middle Holocene, a variety of plant taxa underwent substantial range shifts, apart from simple changes in local abundance or upslope retreat. These range shifts are best attested by the evidence from pack-rat middens. One example is Rocky Mountain juniper, a temperate mesophilic conifer. First known in the region during the terminal Wisconsin, Rocky Mountain juniper became common in upland settings in the early Holocene and through the middle Holocene as well.

Singleleaf piñon pine also began to expand northward during the early Holocene. Its distribution apparently remained south of Meadow Valley Wash (37°30'N) until at least 8.5 Ka (Madsen, 1973), but by 7 Ka, piñon pine had reached the vicinity of Danger Cave (41°N). Expansion of piñon pine woodlands is typically facilitated by corvid birds, which can carry the heavy pine nuts for distances of up to 22 km (Lanner, 1983). The rapid initial northward expansion is faster, however, than current estimates allow for piñon pine migration via corvid birds (Lanner, 1983; Wells, 1983). The initial spread of piñon pine northward may also have been aided by people who brought pine nuts with them on their journeys (Mehringer, 1986; Madsen and Rhode, 1990; Rhode and Madsen, 1998). The chronology of piñon pine migration is complicated by the Danger Cave remains, which are older than all other piñon pine records north of ~37°N in the central or eastern Great Basin. How it happened to arrive in the vicinity of Danger Cave by 7 Ka is difficult to trace in the absence of any intervening records of earlier age.

Utah juniper was common in the southern Bonneville Basin by the beginning of the Holocene, and it reached the Onaqui and Stansbury Mountains by about 6.6 Ka (Rhode and Madsen, 1995), but it was apparently a rather late arrival elsewhere in the northern Bonneville Basin. Because Utah juniper and piñon pine are rather closely associated today, why do they have distinctly different Holocene migration histories? West et al. (1978) noted that the two taxa have somewhat different climatic requirements and tolerances, and perhaps these climatic factors account for the differences in timing and range.

#### MIDDLE HOLOCENE (7 TO 4 KA)

Vegetation records dating from the middle Holocene are relatively sparse but come from a variety of sources, including woodrat middens, archaeological sites, and pollen cores. These provide limited, but nevertheless useful, information on the timing of migration of certain taxa into the region, on the nature of vegetation community composition, and on climatic conditions during this interval. The general size and level of Great Salt Lake during the period is not known, but it is likely to have been low (Currey, 1980).

As the middle Holocene began in the southern Bonneville Basin, conifers such as limber pine, bristlecone pine, and Rocky Mountain juniper, as well as mesophilic shrubs, had declined substantially in abundance or were restricted to higher

elevations (Thompson, 1984). Piñon pine, Utah juniper, ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) and white fir became increasingly abundant. Thompson (1984, 1990) suggested that increased abundance of some of these taxa may reflect increased amounts of summer precipitation from subtropical sources, as well as warmer growing-season temperatures.

Further west, at Gatecliff Shelter, singleleaf piñon pine appears in the region by about 5.3 Ka (Rhode and Thomas, 1983) in a conifer woodland containing both Rocky Mountain juniper and Utah juniper (Thompson and Hattori, 1983). Using sedimentary evidence from Gatecliff Shelter and nearby Triple T Shelter, and closely following the arguments of Van Devender and Spaulding (1979), Davis (1983) proposed that the interval prior to 6300 years B.P. was relatively cool and winter-wet with relatively abundant snowfall but deficient in summer moisture. Davis thought that after this time until about 5000 years B.P., annual temperatures were somewhat warmer and summer precipitation increased with often intense storms, leading him to support the "moist Altithermal" of Martin (1963). It is not certain how far northward from central Nevada the enhanced stormy summer precipitation regime may have occurred. It is notable that pollen samples from Gatecliff and Triple T Shelters show a marked increase in representation of juniper and pine between 6 and 5 Ka (Thompson and Kautz, 1983). After 5000 years ago, according to Davis (1983), temperatures apparently cooled slightly and summer rainfall decreased in amount.

Several middens dating to the middle Holocene are known from the northern Bonneville Basin and vicinity (Rhode, 2000b; see Figure 22). Upland areas in this region appear to have contained woodlands dominated by Rocky Mountain juniper, with a secondary component of piñon pine. Rocky Mountain juniper grew with piñon pine in the Toano Range, in the northern Pequop Range, and in the Cherry Creek Range; it is the only conifer known from the Silver Island Range. Sagebrush and rabbitbrush were the most common understory shrubs. In a few protected settings, such as the north-facing Icicle Cave in the Pequop Range, limber pine and common juniper were also minor components of the vegetation, growing at relatively low elevations compared with today. Utah juniper was quite scarce in the northern Bonneville Basin. One record from the Toano Range contains Utah juniper remains dating from the middle Holocene, and it is also known from a midden in the Onaqui Range, east of the Bonneville Basin, dating to 6.6 Ka. The dominance of Rocky Mountain juniper, rather than the more thermophilic Utah juniper, may indicate that middle-Holocene climate in the uplands was not so warm and dry as is sometimes thought. Alternatively, it may suggest that growing-season precipitation derived from summer convective storms was more common in the Bonneville Basin than elsewhere in the Great Basin.

Lowland vegetation patterns are better shown in pollen records. At Great Salt Lake, high ratios of shadscale and other chenopod shrubs relative to sagebrush and conifers prevailed

from 7 Ka until about 5.5 Ka, suggesting that the early part of the middle Holocene was warmer and drier than today (Mehring, 1977, 1985). Between 5.5 and 4 Ka, relative pollen ratios approached modern values, suggesting that climatic conditions were generally cooler and/or wetter in the latter part of the middle Holocene than in the first part. At Snowbird Bog in the Wasatch Range, Madsen and Currey (1979) found pollen evidence indicating that the period from 8 to 6 Ka was relatively warm and dry, whereas the following period until 5.2 Ka was warm but wetter (Figure 23). The Ruby Marsh sediment record documents lower-than-modern water levels and an expansion of shadscale at the expense of sagebrush steppe vegetation from ca. 7.4 to 5 Ka. Mission Cross Bog, in the Jarbidge Mountains, shows evidence of an increase in juniper woodland and shadscale steppe and a decline in subalpine woodlands from about 8 to 5 Ka (Thompson, 1984).

#### LATE HOLOCENE (<4 KA)

Great Salt Lake rose in elevation and expanded substantially in area at least twice during the late Holocene (Currey et al., 1984). The lake rose to an elevation of 1284 m, then receded, then advanced again to an elevation of 1287 m, flooding most of the Great Salt Lake Desert and forming a broad shallow lake that extended to the Utah–Nevada border.

The midden record representing the late Holocene is more abundant than that representing the previous several thousand years (Figure 22), possibly because of better preservation of the younger middens, but also perhaps because woodrats may have been more abundant during the late Holocene than earlier. Midden records indicate that the flora of the region was largely modern by this time and that plant taxa were for the most part close to their modern distribution. Many of the midden samples have contents that are quite similar to the vegetation that grows around them today.

Thompson (1984) found only rather modest vegetation changes in the Snake Range and southern Bonneville region, suggesting that late-Holocene climates were relatively stable, at least on the scale recorded in midden plant records (Thompson, 1984). The midden record from the northern Bonneville Basin (Rhode, 2000b) indicates that although modern vegetation associations were largely in place by the late Holocene, the abundance of certain plant taxa within those vegetation associations varied substantially through time (Figure 22). Some taxa only achieved their present importance in plant communities within the last 2000 years. The distribution of some taxa shifted in elevation in response to climatic variation.

A prominent late-Holocene vegetation shift concerns the distribution of Utah juniper and Rocky Mountain juniper. Utah juniper apparently arrived in northeastern Nevada, as noted previously, during the middle to late Holocene. In some areas Utah juniper was a minor component in woodlands dominated by Rocky Mountain juniper (e.g., Cherry Creeks, Silver Island Range); but in other nearby areas, midden contents show it was

the dominant woodland conifer (e.g., Goshute Range). These differences are probably related to differences in elevation or topographic position of the midden sites, as well as to other factors. Utah juniper is the most common juniper today in all of these areas, and Rocky Mountain juniper has become much less common in the last 2000 years. A similar pattern is shown in middens from Gatecliff Shelter, central Nevada, where Rocky Mountain juniper disappears from the midden record between 2.3 and 1.7 Ka (Thompson and Hattori, 1983).

Several midden records from Antelope Island and the Promontory Mountains, near Great Salt Lake, indicate that Utah juniper grew 50–100 m lower during the Neoglacial interval between ca. 3.5 and 2.9 Ka than it occurs today (Rhode, 2000b). Lower-than-modern elevations of Utah juniper are also recorded in middens dating to 2.3 and 1.0 Ka from the Cricket Mountains in the southernmost Bonneville Basin (Madsen, 1984). It is likely that Utah juniper retreated upslope from these relatively low elevations toward elevations where we see it today as the late-Holocene climate warmed and dried after the Neoglacial. Presumably the lower tree line of Utah juniper has migrated up- and downslope several times in response to climatic variation during the past few thousand years.

Another example of late-Holocene range changes may be green mormon tea (*Ephedra viridis* Cov.). Green mormon tea is a common shrub in uplands throughout the region, including the vegetation surrounding midden localities on the western slope of the Goshute Range today, and it is found in modern midden samples in the region; but midden samples dating to 3.8–3.1 Ka lack green mormon tea. Other paleoecological records also indicate that green mormon tea was a late entry into the vegetation of the northern and central Great Basin, within the past 3000 years (e.g., Thompson and Kautz, 1983). It should be noted, however, that mormon tea is generally uncommon in late-Holocene midden samples, suggesting that the lack of mormon tea in middens may be partly related to collection habits of woodrats rather than abundance in the landscape.

Additional late-Holocene vegetation changes of importance are shown in pollen records from the region. A pollen record from Crescent Spring (Mehring, 1977, 1985) shows that sagebrush and conifer pollen became increasingly important after 4 Ka, suggesting overall greater effective moisture than during the middle Holocene, albeit with several warmer and/or drier intervals during the period since then. These warmer/drier excursions occurred approximately 3.2, 2.5, and 1.8 Ka; substantial cool/wet episodes centered on 3.6, 2.7, 2.2, and 1.5 Ka (Mehring, 1985). As noted in previous sections, these periods correspond to drier and wetter periods indicated in the pollen record of the northern Great Basin (Wigand, 1987) and the northern Mojave Desert (Wigand, 1997b).

The pollen record at Ruby Marsh indicates that, after ca. 4.5 Ka, “shadscale declined in importance in the valley bottom and marsh waters deepened, in turn reflecting cooler temperatures and/or greater precipitation” (Thompson, 1992:13). In addition, an increase in sagebrush pollen and higher water levels at

Ruby Marsh during the last 500 years indicate that “the coolest and/or moistest conditions since the early Holocene” presumably correlated with the Little Ice Age (Thompson, 1992:13). The late-Holocene record from Mission Cross Bog in the Jarbidge Mountains shows an increase in pollen from spruce, fir, and pine after 5.0–4.3 Ka, with a peak around 3.6 Ka, suggesting this was the most mesic episode in the last 8000 years (Thompson, 1984). At Swan Lake (Bright, 1966), warm, dry middle-Holocene conditions became cooler by 3.1 Ka, with a lowering of the forest tree line and a decrease in sagebrush steppe. Warmer conditions apparently returned by 1.7 Ka, with increased sagebrush and less limber pine. Cooler late-Holocene climate from ca. 5.0 Ka onward is also reflected in the pollen from Snowbird Bog in the Wasatch Range (Figure 23; Madsen and Currey, 1979).

At Gatecliff Shelter, central Nevada, packrat midden and sedimentary evidence (Davis, 1983; Thompson and Hattori, 1983) indicate that a cool, winter-wet interval began rather suddenly about 3400 years ago, during which time mormon tea became established in the region. The period between 3400 and 2800 years B.P. may have been cooler and moister than any time in the last 6000 years. These records also suggest that summer-dominant rainfall may have appeared between 1500 and 800 years ago.

Pollen and plant macrofossil evidence from archaeological sites (Aikens, 1970; Harper and Alder, 1970, 1972; Kelso, 1970; Dalley, 1976) also document late-Holocene vegetation changes (see Currey and James, 1982). At Swallow Shelter and Hogup Cave, grass pollen began to increase ca. 1.5 Ka, again suggesting an increase in effective growing-season moisture. This increase in summer precipitation may have helped to support the spread and success of the Fremont peoples’ maize-based horticultural systems in the Bonneville Basin from ca. 1.5 to 0.9 Ka. Harper and Alder (1970, 1972) used the record of plant remains from Hogup Cave and Danger Cave to suggest that the last 1000–600 years have been among the driest and warmest of the entire Holocene.

#### DISCUSSION: VEGETATION AND AQUATIC HISTORY IN THE BONNEVILLE BASIN

In general outline, vegetation history, as represented by widespread pollen and macrofossil records, and aquatic history, as represented by the lake chronology and other records, appear to be mostly but not entirely concordant. Shallow saline lakes during the middle Wisconsin are matched with cold but dry limber pine woodlands. As Lake Bonneville began to rise from 28 to 20 Ka, evidence for more mesophilic montane plants became increasingly common. By the time of the Bonneville highstand ca. 16–15 Ka, very cold conditions are reflected in now subalpine conifers in the southern Bonneville Basin and in cold sagebrush steppe tundra in the north. The recession of Lake Bonneville from the Provo shoreline coincides with considerable evidence of expansion of plants requiring warmer and

drier conditions than prevailed during the full glacial. However, as noted above (see discussion of late Bonneville cycle in “Bonneville Basin and Eastern Great Basin”), the terrestrial vegetation record from the northern Bonneville Basin is not consistent with the timing and magnitude of certain models of Lake Bonneville recession (e.g., Oviatt et al., 1992). The postulated Younger Dryas rise of Lake Gilbert is also not strongly reflected in the vegetation records, although available vegetation records are quite rare. Holocene fluctuations in vegetation appear to coincide with lacustrine history of Great Salt Lake, although comparison is limited by the state of knowledge of Holocene lake history and by lags in response of vegetation to climate change.

A number of reasons may account for discordance between lake history and vegetation history:

1. Differential sensitivity or rapidity of response of different systems to the same climatic factors (e.g., inertia of vegetation to climate change).
2. Responses of different systems to different parameters within “climate space” (e.g., temperature versus precipitation; growing-season precipitation versus winter precipitation).
3. The presence of local or regional factors that affect one system but not the other (e.g., downcutting that lowered Lake Bonneville in the absence of climatic change; tectonics or isostatic rebound that altered the configuration of the lake basin; or altered growth tolerances of certain plants in relation to atmospheric chemistry or competitive relationships with other plants).
4. Data gaps in one or both proxy records causing difficulties of correlation.
5. Uncertainties in how one or both proxy records are related to underlying climatic factors.

Causes for some of the discordance between vegetation and aquatic history in the Bonneville Basin (e.g., vegetation change during the post-Provo recession and Gilbert Lake interval) remain to be worked out in detail.

The packrat midden record suggests a substantial north-to-south gradient in both floristic and vegetation representation existed through the most of the record. For one example, bristlecone pine was abundant in the south and nearly absent in the north, replaced by limber pine; for another, during the full glacial the southern area bore conifer forests while a cold sagebrush steppe prevailed in the north. How and why this gradient might have varied through time, and the location of substantial biotic discontinuities, are subjects for future biogeographic research.

#### Summary

The foregoing regional discussions highlight the wealth of empirical evidence now available to reconstruct the history of vegetation in the Great Basin. The combined and complementary evidence found in pollen profiles, packrat middens, ar-

chaeological sites, and other localities present a detailed record of broad regional trends and local variability of vegetation through time.

The existing paleoenvironmental record for the last 35 Ka reveals periods when vegetation changes occurred simultaneously and in the same relative direction throughout the Great Basin. At other times, each of the subregions seems to have responded quite differently. These differences directly reflect the relative influence of monsoonal versus Pacific storm systems during the Holocene and earlier interglacials, and the relative strength of polar air masses during glacials.

Although the vegetation history of the Great Basin is marked by numerous high-frequency changes in climate, there are easily recognizable crosscutting events that can be tracked in each subregion by tracing the response of indicator species. These species are characterized by wide spatial distribution and relatively rapid response to changes in climatic input. In addition, these species are easily identified and can be tracked in one or more of the most commonly used paleoenvironmental data sets mentioned above.

To summarize some of the trends from a basinwide perspective and to get a broader view of Great Basin vegetation history during the last 40,000 years, we compare what was happening in the three regions considered above during a dozen separate snapshot "moments" in the past.

#### 40 KA

The limited empirical record available from this time suggests that vegetation in much of the Great Basin and on the Snake River Plain was dominated by sagebrush or saltbush steppe, with a mosaic of sagebrush, montane brush, and patches of conifers in upland areas. Pollen records from the northeastern Great Basin suggest that conifers were not very abundant in the region (Beiswenger, 1991; Thompson, 1992), although they may have been more common further south (Thompson, 1984). The conifers consisted of limber pine and bristlecone pine at relatively low elevations in the eastern basin, with mesophilic shrubs as understory or shrub layer associates. A cold and somewhat mesic interval is indicated. In the southern Great Basin, woodlands dominated by Utah juniper and mountain mahogany were present in upland areas, where present vegetation appears broadly similar, as well as in lower elevation areas now dominated by desert scrub species (Spaulding, 1985). According to Spaulding, the presence of certain desert plant species in these middens indicate that "winter minimum temperatures were within 2° to 3°C of today's values" (Spaulding, 1985:30). The pollen record from the Bed and Breakfast locality in the Summer Lake basin indicates that sagebrush steppe was widespread. Juniper woodland was present as well but not as abundant as it was to be during the succeeding period. Lower grass pollen values than before 40 Ka and after 34 Ka indicate that conditions were drier during this period than either before or after. Sedge-dominated

marshes together with abundant eutrophic algae (*Botryococcus* sp.) indicate that pluvial Summer Lake was low. The same may have been true of pluvial Lake Lahontan during this period.

#### 32 KA

In the northwestern Great Basin the onset of a series of cool, moist cycles from ~34 to 30 Ka resulted in the extension of patches of mixed-conifer woodland—comprising pines (probably whitebark pine, western white pine (*Pinus monticola* Douglas ex D. Don), and lodgepole pine), fir, and occasional spruce—into relatively low elevations in mountainous terrain. More-continuous woodlands dominated by Utah juniper with an understory of sagebrush grew over much of the area, with a lower elevational range greater than at present. This expansion appears to have climaxed around 32–30 Ka and was followed by a dramatic return to drier conditions. In the southern Great Basin and northern Mojave Desert, subalpine conifers also grew at relatively low elevations in the mountains. Whereas white fir had been a substantial part of this woodland between 34 and 32 Ka, it declined in abundance after 32 Ka, leaving limber pine alone at these lower elevations, which suggests that climate was cool but becoming increasingly arid. Utah juniper was abundant or common from as low as ~750 m in elevation, growing in association with shadscale and rabbitbrush, to elevations as high as 1860 m (Spaulding, 1985). In the northeastern Great Basin, limber pine dominated the patchy mountain woodlands, accompanied by montane shrubs that indicate drier conditions than had occurred at 40 Ka. Sagebrush steppe continued to prevail in valley floors and on the Snake River Plain. In the southern Bonneville Basin, bristlecone pine woodlands dominated the mountains, while sagebrush and shadscale occupied valley bottoms.

#### 28 KA

In the northwestern Great Basin, this time marks the beginning of a major drought stretching from ~28 to 26 Ka. It is immediately preceded and followed by regionally correlatable grass expansions in the woodrat midden pollen record at Pyramid Lake as well as in the sediments of Summer Lake. The drought is characterized by saltbush expansion and is reflected in lowered lake levels throughout the northwestern Great Basin. In the southern Great Basin, Utah juniper continued to grow fairly abundantly at lower elevations, below about 1300 m; piñon pine is virtually unreported the region (Spaulding, 1985). Limber pine and white fir disappeared from the record of the area but may have retreated to widely scattered settings above about 2000 m in elevation. In the eastern Great Basin, sagebrush and shadscale steppe continued to dominate valley settings, but Lake Bonneville was beginning to rise, flooding portions of the valley habitat in that large basin. In montane settings, limber pine was declining in abundance and spruce

increased; montane mesophilic shrubs also increased in abundance. The climate appears to have become wetter and colder than previously.

#### 22 KA

Increasingly moister conditions beginning ~24 Ka were reaching a pre-glacial maximum climax by 22 Ka. A transition toward much colder temperatures, however, was continuing and affecting vegetation in all parts of the Great Basin and the northern Mojave Desert. In the northwest Great Basin, the expansion of patchy woodlands, including subalpine whitebark pine, to elevations below 1380 m reflected moister conditions with a reliable wet season. Lake Lahontan was apparently rising rapidly and was probably at the level of the Astor Pass sill (1222 m), but it had not yet reached the Darwin Pass sill (1265 m) to spill into the Carson Basin (Benson et al., 1995). According to Benson et al. (1995), this rapid rise probably coincided with passage of the jet stream over the Lahontan Basin. In the southern Great Basin and northern Mojave Desert, cooler, wetter conditions are also indicated for this period, as subalpine conifer woodlands dominated by limber pine with some bristlecone pine, and also containing white fir, descended to elevations below 1600 m (Spaulding, 1985; Forester et al., 1996). In the eastern Great Basin, Lake Bonneville had also risen rapidly, and patchy, subalpine conifer woodlands dominated by spruce (in the north) and bristlecone pine (in the south) were present in upland environments. Cold but moister conditions are indicated in the Bonneville Basin and also in the Snake River Plain during that time (Beiswenger, 1991).

#### 18 KA

At the height of the full glacial, vegetation throughout the Great Basin records cold and fairly dry climatic conditions. In the northwest Great Basin, these cold, dry glacial conditions fostered a mixed-shrub steppe comprising primarily sagebrush, saltbushes, and rabbitbrush with rare clumps of juniper in scattered sheltered areas. Whitebark pine, which had appeared between 24 and 22 Ka, disappeared. To the south, cold and fairly dry conditions are also indicated by the widespread presence of limber pine and bristlecone pine, without white fir, in the region's mountains, to elevations as low as 1600 m. Juniper woodlands retreated upward almost 450 m to elevations around 1200 m. Piñon pine was rare to absent in most of these woodlands. In the northeastern Great Basin, a sagebrush steppe-tundra apparently existed in montane settings, with very limited patches of conifers including spruce and occasional limber pine. Southward, bristlecone woodlands prevailed in uplands. Sagebrush steppe dominated in lowland settings, while deepening lakes existed in many of the valley basins. The vegetation is consistent with expectations drawn from global circulation models (COHMAP Members, 1988; Thompson et al., 1993) that suggest atmospheric circulation in the region at the time was dominated by cold, dry air moving southwestward from the continental glacial sheet.

#### 12.5 KA

This period marks the transition from the Pleistocene to the Holocene in the northwestern Great Basin. Whitebark pine reappeared briefly at elevations around 1380 m on the west shore of pluvial Lake Lahontan around 12.5 Ka but disappeared shortly thereafter. Although Utah juniper woodland re-expanded after the glacial maximum, it was sagebrush that experienced its most dramatic expansion of the last 35 Ky during this period. By 11.5 Ka, however, severe drought had not only driven whitebark pine from the area but also had brought an end to the sagebrush expansion and encouraged the regional expansion of saltbushes as well. Pluvial Lake Lahontan dropped dramatically from its late-Pleistocene high at this time. The so-called "Younger Dryas," centered around 10.6 Ka, is evidenced by a renewed abundance of juniper woodland and by an apparent still-stand of pluvial Lake Lahontan. The same pattern of change was occurring in the southern Great Basin and northern Mojave Desert. Limber pine retreated up the mountainsides while juniper retreated from the valley floors. By 10 Ka, limber pine no longer grew below about 2300 m in elevation (Spaulding, 1985), and juniper was approaching its modern elevational distribution. In the northeastern Great Basin, limber pine had expanded widely into lower montane settings. It also occurred at fairly low elevations around the northwest side of the Bonneville Basin in a mosaic with sagebrush, prostrate juniper, and mesophilic shrubs. To the south, woodlands were dominated by bristlecone pine. Thermophilous shrubs such as *Atriplex* spp. were just beginning to appear in the region, and these would expand after ca. 11 Ka as climate grew warmer and drier. It is at this time that plant communities were undergoing major restructuring as they moved into new areas on the landscape. What probably had been a mosaic of highly variable plant community patches occupying discrete microhabitats regulated by slope, aspect, and soils, as well as effective moisture, began the transformation into the more familiar vegetation zones of the Holocene.

#### 9 KA

In the northwestern Great Basin, the early Holocene thermal maximum was characterized by major expansion of desert scrub vegetation around the margins of still-drying pluvial lake basins. In the Carson Sink, a subbasin of pluvial Lake Lahontan, extensive marshes were exploited by Native Americans for food and raw materials to make basketry, matting, and other items. Expansion and density of sagebrush steppe in the uplands reached its Holocene climax at this time. Low-elevation outliers of Utah juniper woodland that had survived early Holocene droughts or had reexpanded during the Younger Dryas finally disappeared. Evidence of monsoonal penetration, which is weak in the northern Great Basin, is strong in the southern Great Basin and northern Mojave Desert during this period. The expansion of grasses without a corresponding ex-

pansion of winter-rainfall-dependent plants suggests that summer rainfall had increased. The appearance of hackberry in locations indicating a proliferation of seeps along cliff-faces suggests the presence then of year-round water where it is not found today. Summer monsoons provided the additional rainfall nurturing these springs. Black mat formation, whether it was related to increased spring discharge or soil formation (or perhaps to the increase in grasses), certainly reflects greater organic production, which may have been stimulated by increased summer precipitation in combination with warm temperatures. In the eastern Great Basin, the early Holocene was marked by warmer and drier conditions than the terminal Wisconsin, but the degree of warming is not certain. Some records indicate substantial warming by ca. 9 Ka to levels as warm or warmer than today, whereas other records indicate that early Holocene climate was cooler and wetter than today, though warmer than the terminal Wisconsin. The limited vegetation record indicates that shadscale and xerophytic shrub associations were well established in valley bottoms and around the margins of the Bonneville Basin, alongside sagebrush steppe. In montane settings, limber pine (in the north) and bristlecone pine (in the south) declined in abundance, and more-temperate conifers, such as Rocky Mountain juniper, began to dominate. Mesophilic mountain shrubs were declining in abundance and were being replaced by more thermophilous plants.

#### 7 KA

Although the thermal maximum had passed, climatic conditions were still harsh, and severe regional drought characterized the northwestern Great Basin. Desert scrub communities dominated the slopes surrounding dry playas. Eolian activity generated extensive, and very active, dune fields downwind of valley bottom playas (Mehring and Wigand, 1986). Absence of vegetation cover prevented stabilization of these dunes for the next 3 Ka. In the southern Great Basin, little information exists from this period. However, the few woodrat middens and pollen records that do exist indicate periodic, severe drought. True Mojave Desert plant species, such as creosote bush and white burrobush, became dominant during this period. Their appearance reflects not only warmer temperatures but also establishment of the current pattern of convective summer storms. On the western fringe of the Great Basin, piñon-juniper woodland was forced to retreat into areas occupied by limber pine and bristlecone pine near the top of the White Mountains. In the eastern Great Basin, warm and relatively dry conditions also prevailed, but a possible increase in growing-season precipitation from summer monsoons may have enhanced the northward migration of piñon pine, ponderosa pine, douglas fir, and other temperate conifers. Rocky Mountain juniper was a major element of woodland forests in the northeastern Great Basin, while limber pine still persisted in protected localities at relatively low elevations. Utah juniper was common in the southern Bonneville Basin.

#### 5.5 KA

This marks the termination of the long middle-Holocene drought in the northern Great Basin as a result of a dramatic increase in winter rainfall. Areas that had been dominated by greasewood just decades earlier were replaced by sagebrush steppe. Ephemeral ponds began to retain water year-round. Periodic droughts still punctuated the next 1.5 Ka, but there was never a return to the conditions that had characterized the middle Holocene. In the southern Great Basin and northern Mojave Desert, renewed growth of peat in the White River Valley, at Ash Meadows, and at Little Lake indicates a rejuvenation of springs in response to the sudden increase in rainfall. Juniper woodland seems also to have begun moving downslope again. Pollen records indicate that the eastern Great Basin at about this time underwent a similar change to relatively cooler and perhaps more winter-wet conditions, as sagebrush and conifers increased slightly at the expense of shadscale and saltbush. A number of middens dating to this moment suggest that montane woodlands in the northeastern Great Basin were dominated by Rocky Mountain juniper and piñon pine, with a small amount of newly immigrant Utah juniper present as well. A similar situation apparently prevailed in the southern Bonneville Basin and into central Nevada, although Utah juniper was more common in these latter areas.

#### 3.5 KA

The climax of the so-called "Neoglacial" or "Neopluvial" in the northwestern Great Basin occurred at this time. Juniper woodland expansion in south-central Oregon, which began dramatically 500 years earlier, reached the first of its three greatest late-Holocene limits. Fostered by major increases in winter precipitation, regional water tables probably reached their late-Holocene maximum ~3.7 Ka. (Two additional expansions of woodland ~2.7 and 2.1 Ka occurred during what remained of the Neoglacial.) In the west-central Great Basin on the east slope of the Sierra Nevada, fir lowered its elevational distribution and previously grassy meadows became sedge-dominated bogs that were soon invaded by birch (*Betula* sp.), and willow. The increase in winter precipitation was not as marked in the southern Great Basin or the northern Mojave Desert. Although each of the three major wet episodes of the Neoglacial are evidenced in the south, they are much less pronounced there than in the north. This period is marked by the increased abundance of piñon pine on the landscape. It clearly becomes a codominant in the semiarid woodland of the southern Great Basin and northern Mojave Desert. In the eastern Great Basin, the Neopluvial episode resulted in increased lake levels; greater abundance of sagebrush, grass, and conifers relative to chenopod shrubs; and Utah juniper occurring at elevations more than 100 m below its current distribution. Climatic conditions substantially cooler and more winter-wet than today are suggested. Rocky Mountain juniper still persisted in some montane settings, but Utah juniper and piñon pine were increasingly the dominant lower-montane conifers represented.

### 1.5 KA

This period marks the climax of late-Holocene warm, wet conditions. Beginning about 1.8 Ka, annual rainfall decreased substantially. At the same time, however, the peak of its annual distribution slipped later into the year, into summer. Grass abundance in sagebrush steppe increased greatly in the northern Great Basin at the same time that juniper woodland contracted. Ponds indicate very shallow eutrophic conditions, though they do not seem to dry seasonally. Although the climatic variability of this period was great, there was an overall increase in precipitation that peaked around 1.5 Ka. Bison followed the expansion of grasses into the sagebrush steppe. Further south in the west-central Great Basin, piñon pine expanded dramatically northward and downward in elevation, finally becoming a major component of the semiarid woodland. In southern Nevada, piñon pine increased in abundance in the woodland as well. Summer-shifted rainfall enabled shallow lakes to survive year-round despite a general decline in annual rainfall. In the eastern Great Basin, an increase in growing-season precipitation at this moment is suggested by increases in grass pollen in some records. Modern plant communities are fairly well established by now, including the presence of mormon tea through most of the region. The increase in summer precipitation may have also facilitated the success and spread of agricultural societies, known as the Fremont cultures, through much of the eastern Great Basin.

### 0.5 KA

Drought beginning around 1 Ka continued with brief interruptions until about 0.35 Ka. Retrenchment of juniper woodland in the northern Great Basin and of piñon-juniper woodland in the west-central Great Basin characterized this period. Increased fire activity marked the retreat of the forests. Ponds that had been wet for almost 5000 years occasionally dried during this period. This drought ended about 0.35 Ka with the Little Ice Age. Renewed expansion of juniper woodland in the northern and western Great Basin marked this period. It was only after the end of the Little Ice Age that piñon pine began its reexpansion in the northern and western Great Basin. Drought also characterized this period in the southern Great Basin and northern Mojave Desert. Saltbush expansion characterized many areas. Lakes became marshes until the wetter conditions of the Little Ice Age led to groundwater recharge and the return of shallow lakes. Expansion of woodland also characterized the Little Ice Age in southern Nevada with piñon pine expansion first occurring at the end of the period. In the eastern Great Basin, the record from 500 years ago is somewhat mixed, possibly reflecting natural variability and the finer resolution that comes with recency. In some areas such as Ruby Marsh, this moment marked the beginning of the coolest and moistest period since the early Holocene, with increases in marsh level and expansion of sagebrush steppe at the expense of saltbush and shadscale. On the other hand, some researchers (e.g. Harper and Alder, 1972) find the last 1000 years to have been among the

warmest and driest of the Holocene. Clearly, the climatic variability inherent in the late Holocene should not be underestimated.

### Retrospective and Future Directions

One of the landmark findings in plant ecology of the last 50 years is the widespread documentation that plants respond in highly individualistic fashion to both long- and short-term changes in climate and other ecological forcing mechanisms. This has led to the understanding that vegetation associations are rather loosely knit assemblages of plant taxa brought together by historical contingency and individual response to environmental factors, instead of strongly coevolved communities held together in a dynamic equilibrium. In the first part of the twentieth century, such a position had been favored by plant ecologists such as Shreve and Hinckley (1937) and Gleason (1939), but it was countered by the prevailing climax community viewpoint of Clements (1916, 1936) and others (e.g., Weaver and Clements, 1938). However, improved understanding of the Late Quaternary paleovegetation record within the last 50 years has provided strong evidence supporting the individualistic, nonequilibrium model (Davis, 1986; Huntley, 1991). In response to climatic amelioration since the last glacial period, plant taxa did not respond as communities or vegetation formations, but singly and uniquely, with different tempos of migration. The rapid rates and directions of the shifts taken by various species may be explained in part by the concepts of thresholds, steady states, and multiple successional pathways described by Tausch et al. (1993). Some taxa responded by large-scale range shifts, others by more spatially restricted shifts in elevation (Thompson, 1988). Such migrations and range expansions did not commence with the Holocene. In the northern Bonneville Basin, for example, substantial expansion of shadscale began about 12 Ka, limber pine began at 13 Ka, and expansion of montane shrubs such as currant occurred before that. Nor did substantial range shifts end in the early or middle Holocene, as the examples of western juniper, Utah juniper, and mormon tea demonstrate. In fact, some major range changes were not completed until the last few hundred years: e.g., singleleaf piñon pine in northwestern Nevada. An additional finding is that plants that now do not occur together very frequently were often associated in the past, when climatic conditions were quite different than anything found today. In western North America, the evidence of this was revealed by numerous packrat midden studies conducted in the 1970s and 1980s (e.g., Van Devender and Spaulding, 1979; Spaulding, 1981, 1985; Thompson, 1984; Cole, 1985; Betancourt, 1990; Van Devender, 1990a, 1990b).

These insights set the modern baseline of understanding for a variety of approaches that seek to explain why changing plant distributions took the form that they did. As the above summary indicates, changing climate has played the major role during the Late Quaternary (Whitlock and Bartlein, 1997) but not the only role. Paleoecologists quickly realized that it was not

simply different tolerances to climate that affected how rapidly plant taxa changed their distributions through time. Available mechanisms for dispersal of disseminules and how well the plant is able to compete with existing vegetation are also important components that figure into the concept of vegetation "inertia," or the occasional apparent lag of biogeographic range response after a climatic change (Cole, 1985; Markgraf, 1986; Thompson, 1990:232–233). In addition, some plants are relatively tolerant to climatic variation and, therefore, did not exhibit substantial range changes through widely variable conditions, whereas other taxa showed extensive range alterations (Barnosky, 1987; Thompson, 1988). Furthermore, the biogeographic patterns of different taxa are also related to the high topographic variability in parts of western North America, especially in the Great Basin, which can create a mosaic of microhabitats that may serve as suitable refugia for dispersed relict populations throughout a region (Whitlock and Bartlein, 1993). Chance may play an important role here too, for not all small, relict populations may survive in all the same microhabitats, simply through stochastic processes. Nonclimatic factors such as atmospheric CO<sub>2</sub> concentration and fire frequency (though these may correlate with climatic parameters) also play major roles in the fitness of plant taxa and their ability to survive and spread.

The population genetics of certain taxa in these settings may be critical to understanding biogeographic patterns (Hamrick et al., 1994). Nowak et al. (1994b) asserted that in the northwestern Great Basin, Utah juniper was present through much of the late Wisconsin and that it probably remained in the region because its interbreeding populations were sufficiently variable genetically to enable the species to adapt via genetic heterogeneity. Following example of Barnosky (1987), these researchers called species with this conservative mode of geographic range movement "orthoselective," and they contrasted Utah juniper with piñon pine, which they considered to be a migratory species, one that expanded its range when climatic conditions are right. It should be noted, however, that the interpretation of Nowak et al. (1994b) regarding the sensitivity of juniper to climate change was based upon a single 35,000-year-long woodrat midden record of juniper from northwestern Nevada. It is clear even from that record that juniper may have been absent from the locality during periods of the most extreme climate conditions, including the glacial maximum and the middle-Holocene drought (Wigand and Nowak, 1992; see discussion of middle Holocene above in "Northern and Western Great Basin"). The pollen record from this midden also suggests substantial variation in the abundance of juniper during the last 35,000 years. For these reasons we disagree with the interpretation of Nowak et al. (1994b) that Utah juniper was as complacent or unchanging as they suggest. We find the distinction drawn by Barnosky (1987), however, to be potentially useful in accounting for differential responses of taxa to climate change (see also Thompson, 1988).

Recall, however, that Utah juniper had a very different history in the northeastern Great Basin, where it was absent since before 50,000 years B.P. until approximately 6600 years B.P. In this region, Utah juniper must be considered migratory rather than orthoselective. Why should this be? Does it relate to the severe continentality of climate in the eastern Great Basin during the late Wisconsin? Is it a function of a possible lack of genetic variability in the eastern Great Basin compared with the western Great Basin (perhaps a lack of introgression with western juniper)? Determining why different plant taxa respond differently to climatic changes is an important challenge for ecology in the twenty-first century, particularly as the global climate and atmospheric composition are undergoing rapid human-induced change, with dramatic ecophysiological response. Fortunately, new genetic techniques are rapidly being developed to allow studies of these issues on fossil materials, providing a longer-term perspective of similar changes in the past.

The view that Great Basin plant communities are, in large measure, products of historical circumstance (a corollary to the recognition that plant taxa have individualistic histories) is partly supported by the fossil record but is also tempered by it. Certain combinations of plants often appear to recur and persist in dynamic equilibria through long periods of time, as appropriate environmental conditions allow. The composition of sagebrush steppe, for example, appears largely unchanged since the terminal Wisconsin and possibly since the middle Wisconsin. Indeed, some researchers see marked long-term stability in many steppe and woodland communities in the eastern Great Basin (Thompson, 1988, 1992; Thompson et al., 1994; Moutoux and Davis, 1995; Davis, 2002). Again, this is not to say that the sagebrush steppe formation did not respond to past climate change; it clearly has, primarily through major shifts in its geographical distribution. In any event, the interplay of individual histories and tolerances that led to long-term associations or recurrence of associated taxa remains to be explored more fully.

Certain plants may have altered their climatic tolerances during the last 30,000 years, affecting their utility as proxy records for climatic change. Limber pine may have substantially increased its water use efficiency after the late Wisconsin in response to rising concentrations of atmospheric CO<sub>2</sub> (Van de Water et al., 1994). If so, it suggests that late-Pleistocene populations were more susceptible to water stress from warm, dry (or cold, dry) growing seasons than are modern populations. If not taken into account, this factor could result in substantial underestimation of the true rainfall and temperature values for the southern Great Basin and the northern Mojave Desert during the late Pleistocene, as projected by Forester et al. (1996). Various species of saltbush also may have altered their tolerances, as the genus apparently went through substantial genetic reassortment during the latest Pleistocene and Holocene when it recolonized valley bottoms vacated by Lakes Bonneville and Lahontan (Stutz, 1978). The effects of genetic variability upon

the climatic tolerances of *Atriplex* species are currently unknown.

In the last few years, some studies of past environments and climates have begun to move beyond documentation of the historical sequence of change in vegetation and climate toward the relationships among climatic input, vegetation response, landscape change, and feedbacks into vegetation change. Indeed, the requirements of current paleoenvironmental studies are leading the field in establishing the climatic limits of many plant species (e.g., Bartlein et al., 1998; Thompson et al., 2000). One recent model that relates climate and plant distributions (Thompson et al., 2000; cf. also Bartlein et al., 1998) uses a geographic grid of current climatic parameters and overlays it onto the current distribution of some of the more common plant species. The model then derives the climatic tolerances of individual plant species through the correspondence of plant species with the modern analogue climate. Once these parameters have been derived they are used to estimate past climates from dated assemblages of plant macrofossils at specific points on the landscape. Contemporaneous, spatially distributed assemblages of macrofossils (e.g., dated woodrat midden strata) can then be used to generate isobars of past rainfall and temperature or other climatic parameters as modeled.

Care should be taken in interpreting the results of such models, however. Bartlein et al. (1998) point out several possible discrepancies between model predictions and actual plant distributions. One potential problem is that plant distributions may be constrained not by climatic forces but by competition with associated or neighboring taxa. For example, Thompson (1990) suggested that the lower limit of limber pine in the mountains of the eastern Great Basin often may be constrained more by competition from piñon pine than by climatic factors. This would not have been the case before the arrival of piñon pine toward the end of the early Holocene. Consequently the forces constraining a plant species' distribution may vary through time—and, indeed, through the range of the plant—in ways that may not be related directly to climate.

Another potential problem is the use of modern plant distributions to establish climatic limits: climatic limits of what? Seedling establishment? Survival of mature individuals? Regenerating plant associations? A modern plant community is not unlike a medieval manuscript that has been reused numerous times; each successive use of the palimpsest manuscript is visible. Likewise, modern species distributions combine currently reproducing populations, relict stands established during previous climatic regimes, and effects of disturbance factors (e.g., insect infestations, fire, pollutants). For example, the old-growth forests of the Sierra Nevada contain large white fir and red fir that were established during cooler, wetter conditions 200–300 years ago. Beneath this canopy lie ponderosa pine and/or Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) established during warmer, drier conditions 100 years ago. Finally, there are saplings of red fir and white fir that were established during the wetter conditions of the late 1970s and early 1980s. A simi-

lar pattern can be seen in the semiarid woodlands of the northern Great Basin where stands of Utah juniper, established as far back as 700–800 years ago, now stand side by side with piñon pines less than 150 years old (Tausch et al., 1981). Testing of the model by predicting the geographic distribution of a particular species based upon current climates would not reveal the problem. Because the data used to generate the model include modern plant distributions affected by both modern and past climates, the model will predict the current distribution of both regenerating and relict plant populations on the current landscape. Therefore the model does not predict the distribution of currently active, regenerating forests.

As noted above, a third problem that may affect use of such models for reconstruction of Pleistocene and early Holocene climates is the uniformitarian assumption that plant taxa have the same response to present-day climate as they did in the past. Anatomical evidence has shown that plants may not have had a stable response to climatic factors—e.g., the change in stomatal density of limber pine from the Pleistocene to Holocene and its relationship to atmospheric CO<sub>2</sub> and water use efficiency (Van de Water et al., 1994). Decreased water use efficiency during the late Wisconsin could have resulted in substantially greater plant sensitivity to climatic conditions of that time. Therefore, estimates of Pleistocene climates obtained by using modern analogue climates that were derived from modern limber pine distribution might be in error (cf. Rhode and Madsen, 1995). In the future, the use of other corroborating proxy data sets and refinement of our understanding of the physiology of the more important indicator plant species will allow us to resolve some of these problems.

Discussion of Late Quaternary vegetation history would not be complete without reference to the effects of human populations upon the distributions of individual plant species and the composition and structure of modern and past plant communities. Two areas of potential effect are especially germane: (1) the role of human land management practices in fire histories, and (2) humans as agents of substantial range expansion of certain taxa. During the last 50 years, Federal land managers have continually discussed the influences of grazings by sheep and cattle and of fire suppression in forming today's rangeland and woodland plant communities (Miller and Wigand, 1994). Indeed, some recognition has even been made of the role of Native Americans' use of fire in shaping the environment as well (Barrett and Arno, 1982). The roles played by Native American populations (if any) in shaping Great Basin vegetation history, however, remain to be much more fully explored.

With respect to fire history, the paleoenvironmental record indicates that climate is still a prime mover (perhaps *the* prime mover) in effecting the frequency and magnitude of fire (e.g., Wigand, 1987; Swetnam, 1990; Swetnam and Betancourt, 1990). A strong deterministic link is clear between climate, fuel build-up, cycles of drought, and the resulting occurrence of fire. That human land use practices are important in this dynamic is also obvious, as amply demonstrated by the historic

record, but the importance of fire in prehistoric Native American "range management" in the Great Basin is, as yet, rather poorly understood (Stewart, 1954, 1955a, 1955b, 1956, 1963, 1982; Downs, 1966; Mellars, 1976; Lewis, 1977, 1982, 1985; Barrett and Arno, 1982; Hemphill, 1983; Fowler, 1996). Prehistoric peoples may have substantially affected fire histories on a local scale. Effects by humans may have been important under certain threshold conditions of population, fuel buildup, and drought, but at present we do not know what thresholds (if any) may have existed or whether the effects were substantial. Interregional correlation among the histories of climate, vegetation, and fire may serve to show that climate is the driving force in regional fire histories in the prehistoric and possibly historic periods and that prehistoric human activities were a relatively minor element in regional fire histories (e.g., Swetnam and Baisan, 1996). A great deal of additional research is needed to determine how the dramatic changes in land use practices (including fire suppression) that occurred during the last 1000 years may have affected plant community distribution and structure in the context of changing climates.

The role of people as disseminators of plant species during the historic period is also clear with regard to cheatgrass (*Bromus tectorum* L.) and other range weeds as well as exotic tree and shrub species. The role of Native Americans in the spread of native plants is less clear. The ethnographic record shows that economically valuable plants were often managed and pruned, collecting areas were cleared or burned or irrigated, and in some cases plants may have been artificially transplanted or sown to increase their range (Steward, 1930, 1938; Downs, 1966; Fowler, 1986, 1996). The magnitude and antiquity of these practices is not known, however (Winter, 1976; Winter and Hogan, 1986). As noted above, people may have had a role in the rapid early Holocene expansion of piñon pine (Mehringer, 1986; Madsen and Rhode, 1990; Rhode and Madsen, 1998). This speculation is based in part upon the rapid rate of piñon pine expansion as indicated by the paleobotanical record compared with the presumed speed of its expansion based on an avian dispersal model, which seems too slow to account for the rate of postglacial reexpansion into the Great Basin. The available archaeological record indicates that early Holocene people consumed and transported piñon pine nuts (Rhode and Madsen, 1998), and mobile human groups could be a much

faster agent of seed dispersal than corvids. But it is not certain whether the avian dispersal model is accurate, nor is the early Holocene piñon pine distribution or its rate of expansion known with enough certainty to completely rule out the avian model. In addition, for any attempt at dissemination of such species to be successful, climatic conditions would have to be favorable. The paleoenvironmental record indicates that piñon pine expansion can be quite rapid, and it is not necessary for human intervention to be involved (Tausch et al., 1981; and see above). The rapid spread of piñon pine during the last 150 years presumably did not have, nor did it need, the benefit of human intervention. It is likewise probable that piñon pine's expansion in the northwestern Great Basin 1.6 Ka was a response to natural processes (i.e., climate) because many other plant species including grasses, juniper, saltbush, and sagebrush responded as well (Wigand, 1997b). The evidence presented in the discussion above suggests that piñon pine has responded as rapidly to stressful climates as it apparently did to favorable climates. Retreat of piñon pine woodland after 0.9 Ka was as rapid as its expansion around 1.6 Ka in the northern Great Basin. The historic expansion of western juniper in the northern Great Basin via animal vectors of seed dispersal has been as dramatic as any prehistoric expansion of plant species. These cases confirm the premise that if conditions are favorable, and appropriate agents of dispersal are available, the plant species will spread. Native Americans may have been appropriate agents of dispersal for some plant species, substantially affecting their ranges, but the role of native peoples in the distribution of piñon pine or other plants in the Great Basin remains uncertain and, indeed, may have been quite limited.

In any case, and as Whitlock and Bartlein (1997) and Prentice et al. (1991) have previously observed in other areas, most of the dramatic changes in plant distributions and community structure observable in the Great Basin during the Late Quaternary were ultimately constrained by climatic causes—although mediated by a host of more local, proximate factors. As our understanding of plant responses to past climates, landscape change, and the role of disturbance phenomena (including fire, plant diseases, insect infestations, and human manipulation) is refined, the lines between paleoecology, modern plant ecology, plant physiology, and genetics will become ever more blurred. These are directions for the next half century of study.

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# Great Basin Mammals and Late Quaternary Climate History

*Donald K. Grayson*

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## ABSTRACT

Our exacting knowledge of the history of small mammals in the Great Basin has had a substantial effect on our understanding of mammalian biogeography in this region but has yet to be adequately incorporated into more general syntheses of Great Basin climate history, particularly those produced by climate modelers. I review herein the rich late-Pleistocene and Holocene small-mammal record recently obtained from Homestead Cave in the northern Bonneville Basin, Utah. Together with a diverse variety of other small-mammal sequences, this record indicates that the early Holocene (ca. 10,000–7500 years B.P. (before present)) climate of the northern Great Basin was cool and moist, not warm and moist as has been argued on the basis of computer modeling. This sequence also demonstrates the substantial effects of the generally hot and dry climate of the middle Holocene (ca. 7500–4500 years B.P.) on small mammals in this area as well as the responses of those mammals to the end of this period. Perhaps most surprisingly, Homestead Cave data document the local extinction and recent recolonization of a species that was at one time felt to be isolated on Great Basin mountains. This discovery joins newly available neocological data in showing that the history of “montane” mammals in the Great Basin is far more complex than once had been thought, and it implies that low-elevation dispersal corridors must be provided in conjunction with the creation of mountain-based wildlife reserves in the Great Basin.

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## Introduction

The volume whose legacy we are now celebrating (Blackwelder et al., 1948) was remarkable in many ways. Barely visible to Quaternary scientists who are not archaeologists is the

fact that Ernst Antevs' contribution to this volume was of fundamental importance in structuring both the chronological assignments of archaeological sites and the interpretation of the record that was dated accordingly. Antevs' work, together with that by archaeologist Luther Cressman, played a major role in ushering in the tradition of conjoint paleoenvironmental and archaeological research in the Great Basin, a tradition that continues to thrive today. Indeed, Antevs (1948) is still cited by Great Basin prehistorians (e.g., Aikens, 1993), and for good reason: on a very general level, he appears to have gotten it right in terms of both his general climatic sequence and the effect of climatic change on human population densities in the Great Basin.

Antevs' Neothermal classification was based essentially on temperature; he argued that it was temperature and not moisture that supported the long-distance correlations that allowed him to date his sequence on the basis of Scandinavian varve chronologies. Because of this, it is interesting to observe that although Antevs routinely characterized the early Holocene, or Anathermal, of the arid west as moister than anything that came later, his view of early Holocene temperatures in this region changed through the years.

In the 1940s and early 1950s, Antevs routinely described the Anathermal as having temperatures that at first were like those of today but that grew warmer, eventually culminating in the famed Altithermal (e.g., Antevs, 1948, 1952). Influenced by the work of Magnus Fries, however, Antevs soon began to characterize the Anathermal as not only the wettest but also the coolest subdivision of his Neothermal sequence (e.g., Antevs, 1953, 1955a, 1955b; see Figure 1).

No longer can there be any question that Antevs was correct in his characterization of the early Holocene in the Great Basin. Because it was clearly moist, one of his descriptions must be right. It remains to be determined, however, whether Antevs I, with a warm and moist early Holocene, or Antevs II, with a cool and moist early Holocene, was closer to the truth. A wide range of empirical data converges to suggest that much of the Great Basin was cool during the early Holocene. Certain climatic models, however, suggest that this period of time was quite warm.

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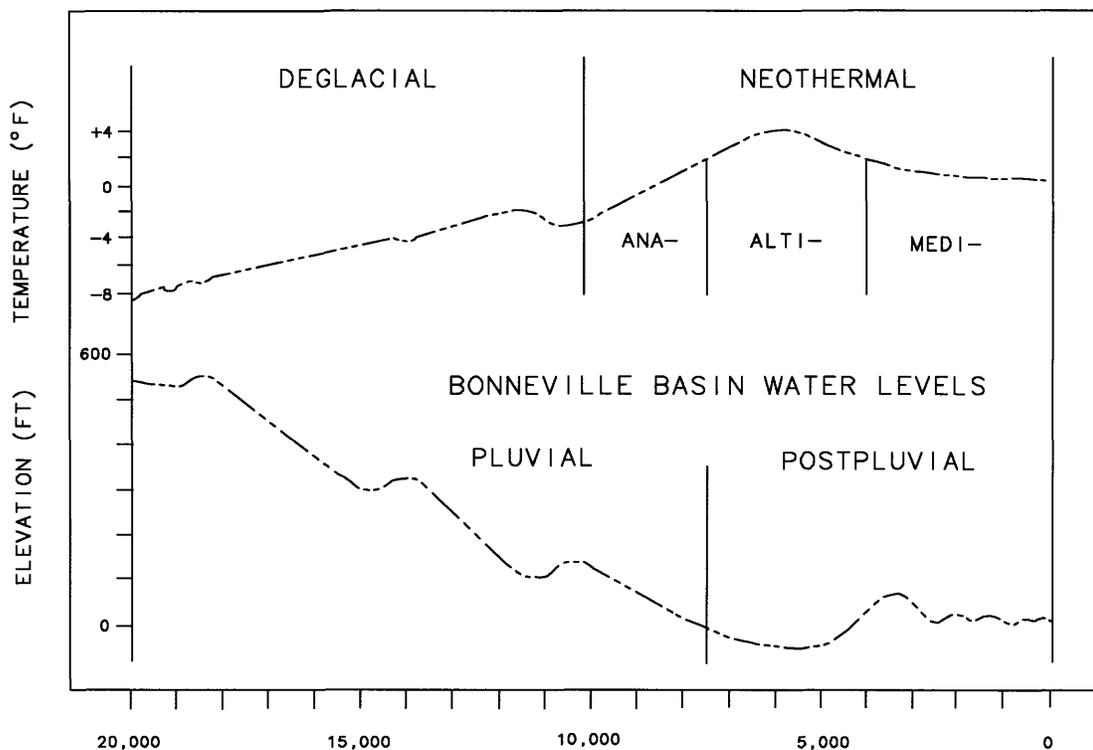


FIGURE 1.—Antevs' later reconstruction of Late Quaternary temperatures in the arid west and water levels in the Bonneville Basin (after Antevs, 1955a) (B.P. = before present, i.e., before 1950; temperature scale indicates deviation from modern conditions).

These conflicting views lead to different interpretations of biotic and moisture history in the Great Basin. I examine herein small-mammal sequences from the latest Pleistocene and Holocene in the Great Basin that are relevant to this issue. Mammal data have been cited by some climatic modelers when those data match the predictions of the models but have been consistently ignored when the data are at odds with model-derived predictions. The greatest mismatch occurs during the early Holocene, the period of primary focus for this paper.

Vertebrates other than small mammals are also relevant to these issues. Fishes are discussed elsewhere in this volume; our paleontological knowledge of reptile and amphibian history from the latest Pleistocene and Holocene has been reviewed by Mead and Bell (1994); and the timing and nature of the extinctions of birds and large mammals within the Great Basin toward the end of the Pleistocene also has been explored (Grayson, 1993, 1994). Given these reviews, I restrict my attention herein to small-mammal history, focusing on the most detailed history available for latest Pleistocene and early Holocene mammals of the Great Basin. This history is provided by Homestead Cave in the northern Bonneville Basin of north-central Utah. I discuss the paleoclimatic implications of the Homestead Cave mammal sequence and examine the implica-

tions of this fauna for our understanding of modern small-mammal distributions within the Great Basin.

### Homestead Cave

Homestead Cave is a few kilometers to the southwest of Great Salt Lake on a northwestern spur of the Lakeside Mountains (Figures 2, 3). This spur, Homestead Knoll, is a low (maximum elevation, 1615 m), rocky promontory that is devoid of active springs and permanent streams. The barren playa of Pleistocene Lake Bonneville is immediately west and northwest of this rocky spur, but the knoll itself supports vegetation dominated by shrubs and grasses in addition to a few scattered junipers (*Juniperus osteosperma*). Shadscale (*Atriplex confertifolia*) and horsebrushes (*Tetradymia* spp.) are the most abundant shrubs, but bud sagebrush (*Artemisia spinescens*), rabbitbrush (*Chrysothamnus* sp.), and greasewood (*Sarcobatus vermiculatus*) are also present, as is big sagebrush (*Artemisia tridentata*) along seasonally moist drainages. Greasewood becomes increasingly common as the valley bottom is approached, whereas the invasive Eurasian cheatgrass (*Bromus* sp.) is abundant on the flats beneath the knoll.

Homestead Cave sits on the northwestern edge of Homestead Knoll at an elevation of 1406 m. Initial test excavations con-

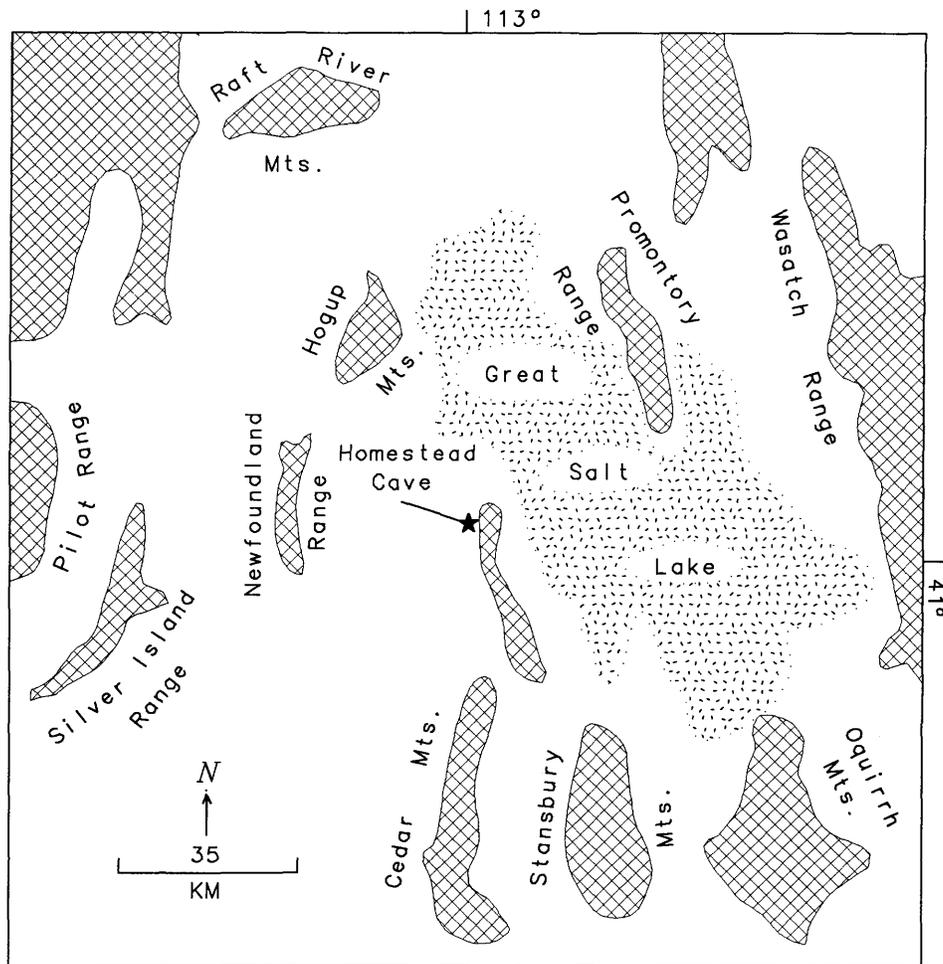


FIGURE 2.—Location of Homestead Cave, northwestern Lakeside Mountains, in the Bonneville Basin, north-central Utah, USA.

ducted by D.B. Madsen of the Utah Geological Survey revealed that the sediments of Homestead Cave are remarkably rich in vertebrate remains. This accumulation was primarily caused by owls using the cave; the deposits contained numerous owl pellets, and many isolated mammal bones and teeth, regardless of their age, still had remains of those pellets adhering to them.

In 1993 and 1994, a 1 × 1 m column sample was stratigraphically excavated from this site, faunal material in that column was collected by sieving the deposits through a nested series of screens with mesh openings that measured 1/4 inch (6.4 mm), 1/8 inch (3.2 mm), and 1/16 inch (1.6 mm). Remains of fishes from the resultant sample were analyzed by J.M. Broughton (University of Utah), those of birds by S.D. Livingston (Desert Research Institute), and the mammals by me. Detailed analyses of all of this material, including the mammals, are presented by Madsen (2000).

The details of the depositional history of the sediments in the cave are not relevant to the arguments developed herein, but I

note that we now have available 21 radiocarbon ( $^{14}\text{C}$ ) dates for the 18 Homestead Cave strata from the column itself (Table 1). These dates document that the earliest stratum within the cave was deposited between about 11,300 and 10,200  $^{14}\text{C}$  yr B.P. (years before present—i.e., before 1950), thus encompassing the period of time that includes the Gilbert phase of Lake Bonneville history. The available radiocarbon chronology indicates that superincumbent stratum II at Homestead Cave accumulated between 8900 and 8500  $^{14}\text{C}$  yr B.P. and, thus, also suggests that there may have been a depositional gap of about 1000  $^{14}\text{C}$  years between the accumulation of Stratum I and Stratum II. No other similar gaps are suggested by the radiocarbon chronology, but because some parts of the sequence remain weakly dated, such gaps may exist although they are undetected. The latest radiocarbon date for the sequence is for Stratum XVII, and it falls at about 1000  $^{14}\text{C}$  yr B.P. The Homestead Cave faunal sequence thus covers the latest Pleistocene and nearly all of the Holocene.

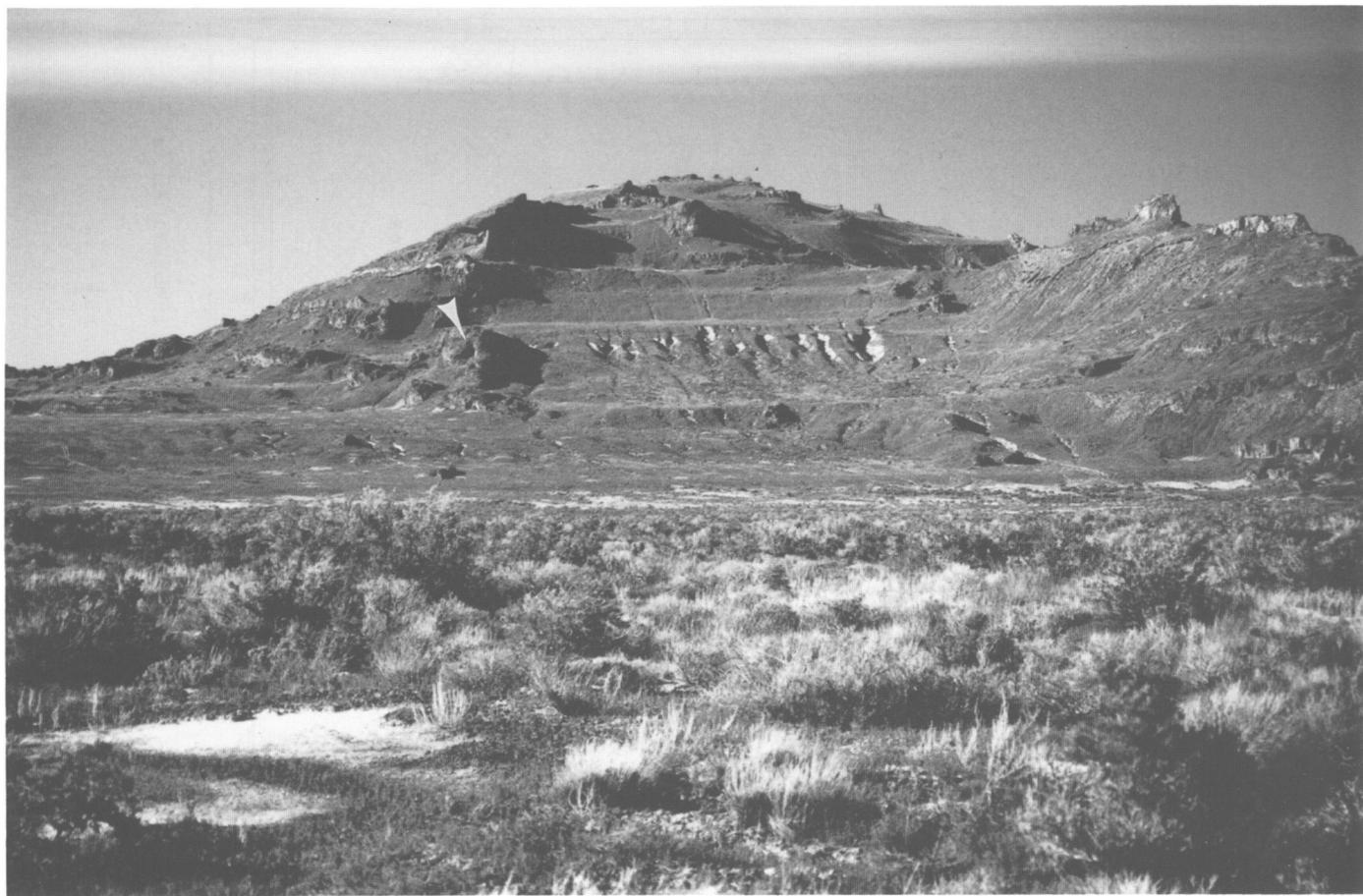


FIGURE 3.—Location of Homestead Cave on Homestead Knoll (white arrow). Prominent terraces were produced by the waters of Pleistocene Lake Bonneville.

The faunal sample that we excavated from Homestead Cave is of almost overwhelming size. Some 184,000 mammal bones and teeth from the 1/4-inch and 1/8-inch sample fractions have been identified to at least the genus level (Table 2). These specimens represent 40 mammalian taxa from 15 of the 18 strata; the faunal assemblages from Strata XIII, XIV, and XV have not been identified, whereas only the kangaroo rats (*Dipodomys* spp.) from Stratum X have been analyzed. The Homestead Cave sample is so large, so well stratified, and so well dated that it provides an unparalleled view of Late Quaternary small-mammal history in the Great Basin. Although my focus herein will be the paleoclimatic implications of this fauna, I will also discuss briefly a series of relevant biogeographic issues that are related to those paleoclimatic matters.

#### Selected Faunal Histories

The paleoclimatic implications of the Homestead Cave mammalian fauna are best understood from analysis of the histories of a group of environmentally sensitive taxa. Discussion of their broader implications follows the individual histories.

Authorities for the mammal taxa discussed herein are provided by Wilson and Reeder, 1993.

#### KANGAROO RATS

The aptly named chisel-toothed kangaroo rat (*Dipodomys microps*) is characterized by flattened, or chisel-shaped, anterior faces and tips of the lower incisors. They are distinctly different from the rounded and pointed, or awl-shaped, lower incisors of Ord's kangaroo rat (*D. ordii*). Kenagy (1972, 1973; see also Garrison and Best, 1990) demonstrated that *D. microps* uses these incisors to shave off the hypersaline external surfaces of *Atriplex* leaves, then consumes the palatable inner portions of those leaves. In contrast, *D. ordii* is primarily a granivore and is often found associated with habitats in which sagebrush is common (Hayssen, 1991). In an analysis of the spatial relationships within the rodent community of Warm Springs Valley, west-central Nevada, O'Farrell (1980) found little spatial overlap between these two species, with *D. microps* restricted to habitats dominated by shadscale. This is not to say that *D. microps* cannot exist in habitats that lack *Atriplex*

TABLE 1.—Radiocarbon (<sup>14</sup>C) dates (years before present, B.P.) from Homestead Cave strata and their calibrated ages, in calendar years, as calculated with CALIB 3.0.3c (Stuiver and Reimer, 1993).

Stratum	<sup>14</sup> C date (years B.P.)	Laboratory number	Calendar age (years)
XVII	1,020 ± 40	Beta 101877	933
XVI	1,200 ± 50	Beta 66940	1,078
XIV	2,850 ± 50	Beta 103692	2,948
XIII	3,480 ± 40	Beta 101878	3,707
XII	3,400 ± 60	Beta 63179	3,632
X	5,330 ± 65	AA 14822	6,105–6,171
VII	6,160 ± 85	AA 14824	7,017
	6,185 ± 105	AA 14825	7,028–7,148
VI	7,120 ± 70	AA 14826	7,912
V	8,230 ± 70	AA 16810	9,210
IV	8,195 ± 85	AA 14823	9,047–9,193
II	8,520 ± 80	AA 14821	9,484
	8,790 ± 90	AA 14820	9,694–9,852
	8,830 ± 240	Beta 63438	9,873
I (upper 5 cm)	10,160 ± 85	AA 14819	11,865
	10,350 ± 80	AA 14818	12,228
I (general)	10,910 ± 60	Beta 72205	12,832
I (lower 5 cm)	11,065 ± 105	AA 14817	12,978
	11,180 ± 85	AA 16808	13,087
	11,265 ± 85	AA 16809	13,172
	11,270 ± 135	AA 14816	13,177

TABLE 2.—Number of identified specimens (NISP) of mammals by stratum at Homestead Cave.

Stratum	Mammals (NISP)
XVIII	1,047
XVII	15,548
XVI	6,296
XII	22,860
XI	10,096
X	6,601 <sup>a</sup>
IX	22,088
VIII	8,289
VII	13,905
VI	24,330
V	5,109
IV	26,615
III	2,884
II	7,855
I	10,275
TOTAL	183,798

<sup>a</sup> Only the kangaroo rats from this stratum have been identified.

or that *D. ordii* cannot exist in habitats in which *Atriplex* is common. When both taxa are present, however, *D. microps* will tend strongly to be found in *Atriplex* habitats, and *D. ordii* will be found in habitats marked by other plant associations, including those dominated by *Artemisia*.

Kangaroo rats are by far the most abundant mammal in the Homestead Cave fauna: 59.1% of the identified specimens (ex-

cluding Stratum X, for which only kangaroo rats were identified) pertain to this genus; of these, some 8300 specimens have been identified to the species level. Figure 4 provides the ratio of *D. microps* to both *D. microps* and *D. ordii* through time at Homestead Cave (including Stratum X) and shows that the late-Pleistocene and early Holocene faunas of this area were marked by abundances of *D. ordii* that have not been seen since. Figure 5 presents the same data in terms of the ratio of *D. microps* to *D. ordii* for each stratum and shows that the middle Holocene, particularly between about 7000 and 5000 <sup>14</sup>C yr B.P., had elevated proportions of *D. microps* compared with

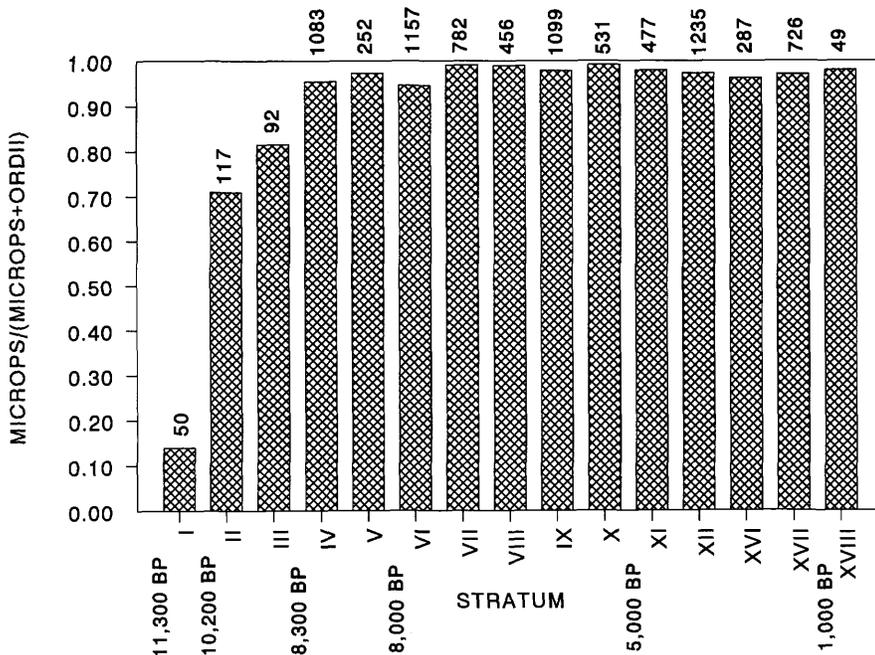


FIGURE 4.—Proportion of the kangaroo rat fauna contributed by *D. microps* at Homestead Cave, by stratum. The total number of *Dipodomys* specimens identified as either *D. microps* or *D. ordii* is above the bar for each stratum. Corresponding ages indicated below the strata are in radiocarbon years.

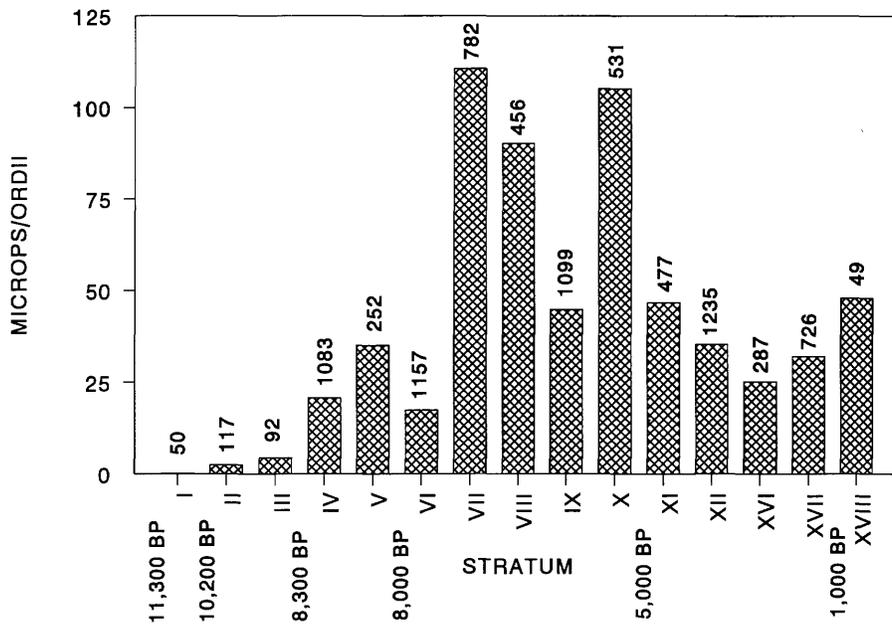


FIGURE 5.—Ratio of *D. microps* to *D. ordii* at Homestead Cave, by stratum. Above the bar for each stratum is the total number of *Dipodomys* specimens identified as either *D. microps* or *D. ordii*. Corresponding radiocarbon ages are indicated below the strata.

what came before and after. This history strongly suggests the progressive replacement of sagebrush by shadscale vegetation during the early Holocene in the Homestead Knoll area, as well as a middle-Holocene peak in xericity here.

It is also possible to take a broader view of the history of *Dipodomys* in the Homestead Knoll area. Although *D. ordii* and *D. microps* may have different environmental implications, they are both kangaroo rats, which in general are extremely well adapted to arid habitats (French, 1993). As a result, chang-

ing relative abundances of kangaroo rats through time in the Homestead Cave fauna should provide a clear indication of local desertification. As Figure 6 shows, kangaroo rats provided a relatively small proportion of the late-Pleistocene fauna at Homestead Cave. During the early Holocene, kangaroo rats became increasingly abundant. Beginning soon after 8300 <sup>14</sup>C yr B.P. (Stratum IV), more than half of the identified mammalian fauna comprised these animals. By about 6200 <sup>14</sup>C yr B.P. (Stratum VII), they began to contribute more than two-thirds of

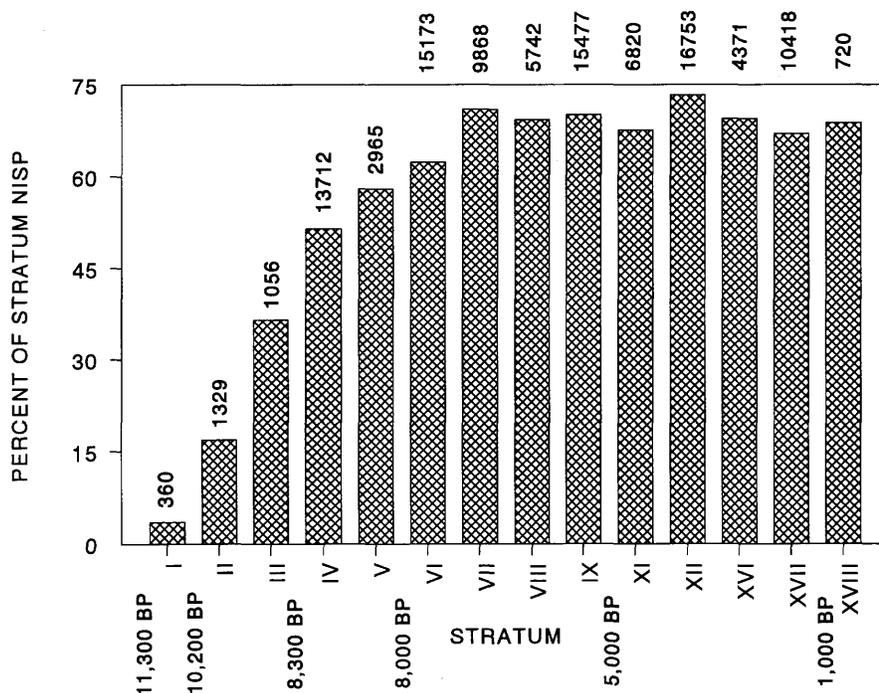


FIGURE 6.—Relative abundance of *Dipodomys* as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of identified *Dipodomys* specimens is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

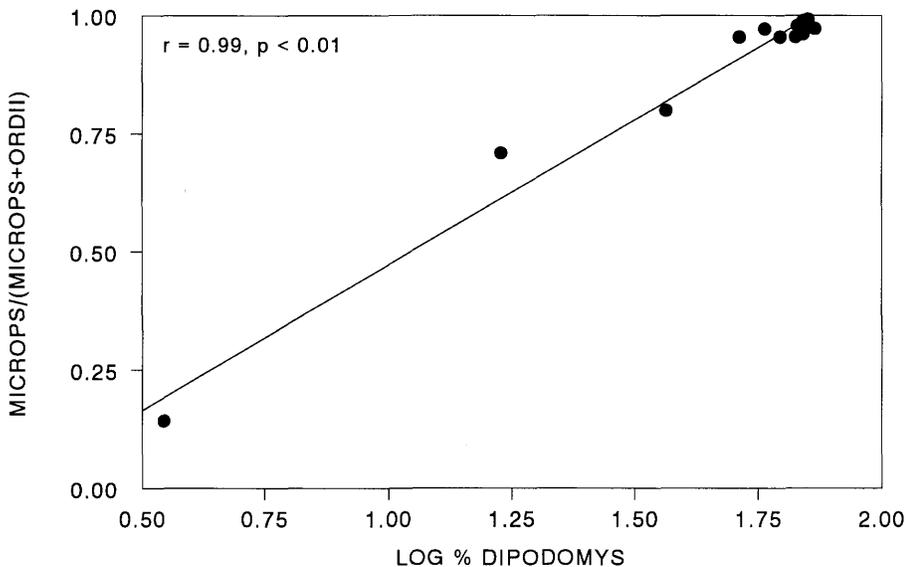


FIGURE 7.—Relationship between the relative abundance of *Dipodomys* (expressed as a logarithm of the percentage of *Dipodomys* specimens in the mammal fauna of each stratum) and the proportion of the kangaroo rat fauna contributed by *D. microps* at Homestead Cave.

the specimens in each stratum and (at least in the analyzed units) were never less than this fraction in subsequent strata.

Given that the increasing abundance of *D. microps* appears to track decreasing abundances of big sagebrush, and that increasing abundances of kangaroo rats in general indicate increasing aridity, I found that the percentage of each stratum's mammal fauna contributed by kangaroo rats is tightly correlated with the proportion of that stratum's kangaroo rat fauna that is contributed by *D. microps* (Figure 7).

#### PYGMY RABBITS

It might be argued that environmental changes other than a replacement of sagebrush by shadscale vegetation might have driven the changing abundances of *D. ordii* documented by the Homestead Cave fauna. After all, *D. ordii* does not require *Atriplex* in its diet. However, the history of pygmy rabbits (*Brachylagus idahoensis*) at Homestead Cave would seem to make sense in no other way.

Pygmy rabbits are heavily dependent on dense stands of big sagebrush, both for food (pygmy rabbit winter diets may be composed of almost nothing else) and as locations for their burrows (Green and Flinders, 1980; Weiss and Verts, 1984; Dobler and Dixon, 1990; Katzner and Parker, 1997). Today they are found, albeit in declining numbers, in the sagebrush valleys of the northern two-thirds of the Great Basin and in the immediately adjacent Columbia Plateau. There is also an isolated, and endangered, set of populations in eastern Washington.

The latest Quaternary history of pygmy rabbits is reasonably well known. In the late Pleistocene, they were found as far south as central New Mexico (Harris, 1985) as well as outside their modern distribution in eastern Washington (Lyman, 1991). Within the Great Basin and adjacent Columbia Plateau, they are known to have undergone two separate declines in

abundance, one at about 10,000 <sup>14</sup>C yr B.P., and a second either at the onset of or during the middle Holocene (Grayson, 1993).

For instance, at Danger Cave (approximately 100 km southwest of Homestead Cave in the Silver Island Range, western Utah, at an elevation of 1314 m), 35 of 37 pygmy rabbit specimens were deposited between about 10,500 and 10,000 <sup>14</sup>C yr B.P., even though the subsequent sequence spans much of the Holocene (Grayson, 1988; Madsen and Rhode, 1990). The first indication that pygmy rabbits had undergone significant prehistoric declines in abundance came from work at the Wasden Site (Snake River plain, southern Idaho), where Butler (1972) showed that they declined dramatically in abundance at about 7000 <sup>14</sup>C yr B.P. The record from the Connley Caves (Fort Rock Basin, south-central Oregon, at 1355 m) is in strong accord with this observation. This site contains deposits that span the intervals from 11,200 to 7200 and from 4400 to 3000 <sup>14</sup>C yr B.P., but whereas pygmy rabbits were common before 7000 <sup>14</sup>C yr B.P., they were rare after that time (Grayson, 1977). Other sites—for instance, Gatecliff Shelter (Toquima Range, central Nevada; see Grayson, 1983)—show similar histories. Both the latest-Pleistocene and middle-Holocene declines in pygmy rabbit abundance appear to be associated with declines in abundance of *Artemisia tridentata* (see the review in Grayson, 1993).

The record for pygmy rabbits at Homestead Cave is clear (Figure 8). These animals were common in the Homestead Knoll area during the late Pleistocene and were clearly present during the early Holocene, but they declined rapidly and had become locally extinct, or nearly so, by 8300 <sup>14</sup>C yr B.P. There is no sure evidence to suggest that pygmy rabbits have been in the Homestead Knoll area during the last 7000 years or so.

Given the tight association between pygmy rabbits and dense stands of big sagebrush, it again is extremely likely that *A. tridentata* began a substantial decline in this area after about

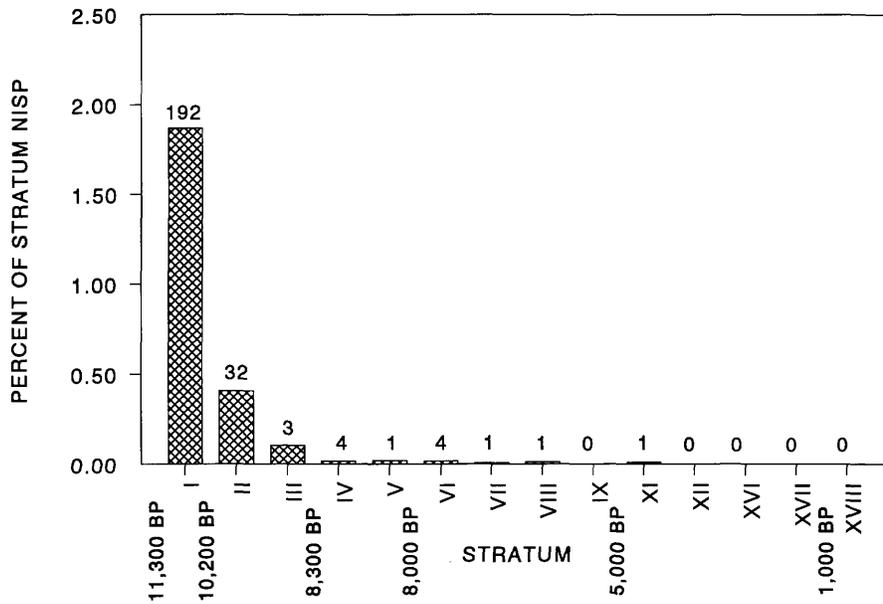


FIGURE 8.—Relative abundance of pygmy rabbits as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of identified *Brachylagus idahoensis* specimens is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

10,000 <sup>14</sup>C yr B.P.; and that soon after 8300 <sup>14</sup>C yr B.P., there were insufficient stands of big sagebrush to support populations of these animals. The record is fully consistent with other paleontological pygmy rabbit data, and it also fully consistent with the local history for *Dipodomys ordii* provided by Homestead Cave.

VOLES

Most species of *Microtus* occupy grassy habitats and live in cool environments. Indeed, these animals show poor ability to thermoregulate at high temperatures, and no species of *Microtus* is restricted in distribution to arid areas. Of the species that

currently occur in the Great Basin even *Microtus longicaudus*, which is least tied to moist habitats, is more common in cooler, moister habitats here than in warmer, drier ones (Getz, 1985; Rose and Birney, 1985; Wunder, 1985).

As Figure 9 shows, *Microtus* was common in the late-Pleistocene and early Holocene deposits of Homestead Cave. Its numbers dwindled dramatically after 8300 <sup>14</sup>C yr B.P., and it has clearly been uncommon in this area for the last 7000 <sup>14</sup>C years.

Much the same is true for *Lemmiscus curtatus* (Figure 10). Sage voles are, as the name suggests, often associated with habitats dominated by stands of tall sagebrush (usually *A. tri-*

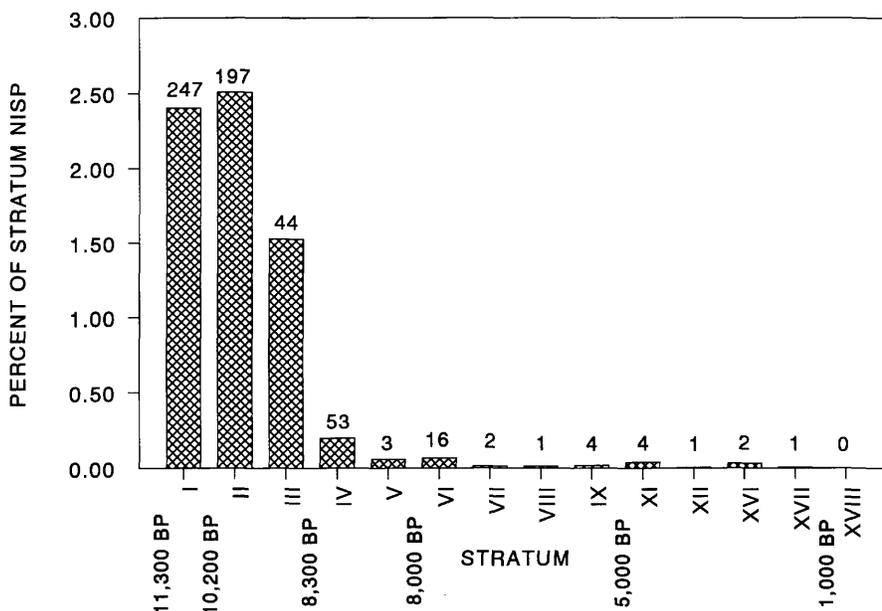


FIGURE 9.—Relative abundance of *Microtus* sp. as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *Microtus* sp. is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

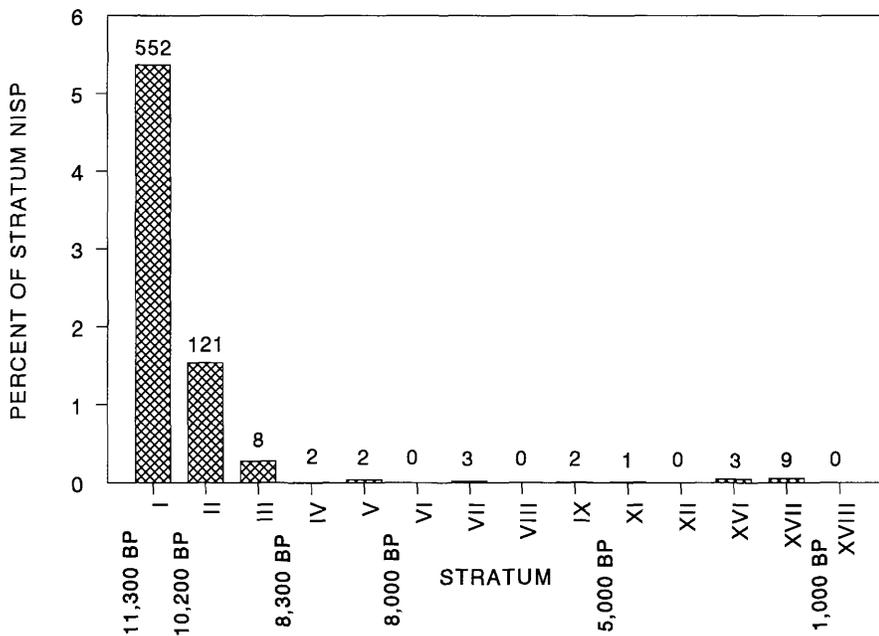


FIGURE 10.—Relative abundance of *Lemmys curtatus* as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *Lemmys curtatus* is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

*dentata*) and grasses, although they can also be found in communities in which the dominant shrub is rabbitbrush as well as in habitats dominated by grasses alone. Within these habitat parameters, there is also some suggestion that sage vole numbers are highest in settings marked by relatively warm winters coupled with cool and moist summers (Hall, 1946; Maser, 1974; Carroll and Genoways, 1980). These animals seem to be able to meet their moisture requirements through the ingestion of green vegetation, and surface moisture is clearly less critical for them than it is for most species of *Microtus*.

In short, *L. curtatus* is most abundant today in habitats dominated by *A. tridentata* and grasses in contexts marked by relatively cool summers. These modern habitat preferences likely account for the strong similarity between the histories of this animal and that of *Brachylagus idahoensis* at Homestead Cave (compare Figures 8, 10). Both were most abundant during the latest Pleistocene in the Homestead Knoll area, both continued to be present during the early Holocene, and both saw their numbers fall dramatically as the early Holocene came to an end in this area at about 8300 <sup>14</sup>C yr B.P.

#### POCKET GOPHERS

Several other taxonomic pairs show similar, though by no means identical, behavior. There are, for example, two species of pocket gopher in Utah today: the northern pocket gopher, *Thomomys talpoides*, and Botta's pocket gopher, *T. bottae*. The northern pocket gopher is mostly confined to the mountains and high valleys of the state (although it has been reported from the Promontory Peninsula: see Durrant, 1952), whereas *T. bottae* resides in Utah's lower valleys. To my knowledge, only *T. bottae* is known from the region immediately west of the Great Salt Lake.

Pocket gophers are also abundant in the Homestead Cave fauna. Approximately 15,000 specimens have been identified from the Homestead sample, of which 969 have been identified to the species level. Although Stratum I at Homestead provided only two gopher specimens that could be identified to species, both of these are *T. talpoides*. All identified gopher specimens from later strata represent *T. bottae*.

#### POCKET MICE

Figure 11 shows the conjoined histories of two of the three species of pocket mouse represented in the Homestead Cave fauna: the little pocket mouse, *Perognathus longimembris*, and the Great Basin pocket mouse, *P. parvus* (the long-tailed pocket mouse, *Chaetodipus formosus*, is the third species). *Perognathus longimembris* is common in the valleys and on the lower mountain slopes of the Great Basin and often co-occurs with *P. parvus*. This latter, however, ranges into altitudes far higher than those tolerated by the little pocket mouse. Hall (1946), for instance, noted that the highest elevation in Nevada from which *P. longimembris* had then been found was 6500 ft (1981 m) but that *P. parvus* routinely occupied higher elevation habitats—for instance, at 10,000 ft (3048 m) on Mt. Grant in central Nevada. *Perognathus parvus* is also found well into British Columbia, Canada, but the little pocket mouse exists no further north than southeastern Oregon (Hall, 1981).

Given what I have reported about the faunal sequence at Homestead Cave, it is perhaps no surprise that *P. parvus* was the abundant pocket mouse in deposits from the late Pleistocene in Homestead Cave and that *P. longimembris* was not present in the fauna during that time. The little pocket mouse first appeared in Stratum II, sometime after 10,000 <sup>14</sup>C yr B.P. In comparison with *P. longimembris*, *P. parvus* remains fairly

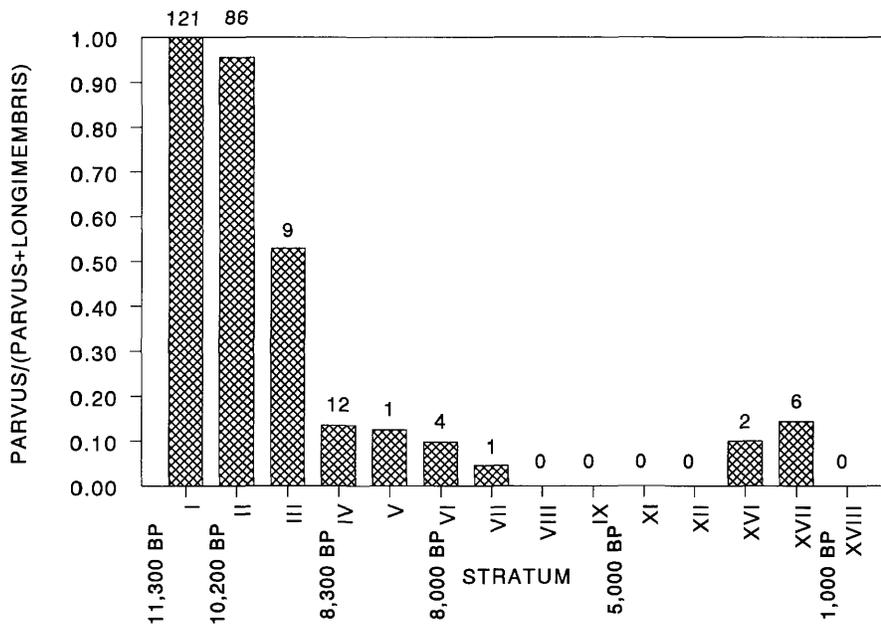


FIGURE 11.—Ratio of *Perognathus parvus* to *P. parvus* and *P. longimembris* at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *P. parvus* is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

common through the early Holocene. It becomes rare, however, during the early centuries of the middle Holocene, appears to have become regionally extinct between about 6000 and 2000  $^{14}\text{C}$  yr B.P., and does not reappear until late prehistoric times.

#### WOODRATS

Two species of woodrat are widespread in the modern Great Basin: *Neotoma lepida*, the desert woodrat, and *N. cinerea*, the bushy-tailed woodrat. *Neotoma lepida* is found in the lower elevations of much of the Great Basin, whereas *N. cinerea* tends to occupy the mountains and the more northerly high valleys of the region. In addition, *N. cinerea* ranges as far north as the Northwest Territories, Canada, whereas *N. lepida* extends no further north than central Oregon (Hall, 1981). Both species are found on Homestead Knoll today (Grayson et al., 1996).

Woodrats are abundant in the Homestead Cave deposits: only Stratum XVIII has fewer than 650 specimens identified to the species level. As Figure 12 shows, *Neotoma cinerea* was the dominant woodrat in the Homestead Knoll area during the late Pleistocene and remained common through much of the early Holocene. After about 8300  $^{14}\text{C}$  yr B.P., it underwent a dramatic decline; *Neotoma lepida* became, and has remained, the numerically dominant woodrat in the Homestead Knoll area. Indeed, bushy-tailed woodrats seem to have become locally extinct around 5000  $^{14}\text{C}$  yr B.P. and may have recolonized the area shortly before 1000  $^{14}\text{C}$  yr B.P. (see "Recolonization and Small-Mammal Biogeography," below).

The history of bushy-tailed woodrats at Homestead Cave is quite similar to that provided by the much smaller sample of vertebrate remains provided by Danger Cave, where 95% (125)

of the bushy-tailed woodrat specimens in the entire faunal assemblage were deposited between about 10,500 and 7000  $^{14}\text{C}$  yr B.P. The remaining six specimens found in Danger Cave deposits were scattered across the subsequent 7000 years of history registered in this site.

#### MARMOTS

Yellow-bellied marmots (*Marmota flaviventris*), which also tend strongly to be found only on Great Basin mountains (although descending to much lower elevations to the north), are likewise present in the deeper strata of Homestead Cave (Figure 13). Because the Homestead Cave fauna owes its accumulation largely to owls, and because adult marmots exceed the prey size routinely taken by these birds, it is not surprising that marmots were never abundant in the Homestead Cave deposits. As a result, precisely when these animals became locally extinct cannot be determined, but they are reasonably common in late-Pleistocene Stratum I and appear to have been present in the area until roughly 8000  $^{14}\text{C}$  yr B.P. That 66 specimens were present in the late-Pleistocene and early Holocene Homestead Cave samples clearly documents the presence of local populations of these mammals during these periods. Just as clearly, the complete absence of marmot specimens in these deposits during the last 5000  $^{14}\text{C}$  years shows that they had been extirpated from the area by the end of the middle Holocene—and perhaps long before the end of this period.

Only one other well-dated stratified fauna in the northern Bonneville Basin sheds light on the history of marmots in this area. Danger Cave contains a small sample of marmot specimens that were deposited between about 10,500 and 10,000  $^{14}\text{C}$  yr B.P.; later deposits do not contain the remains of these animals.

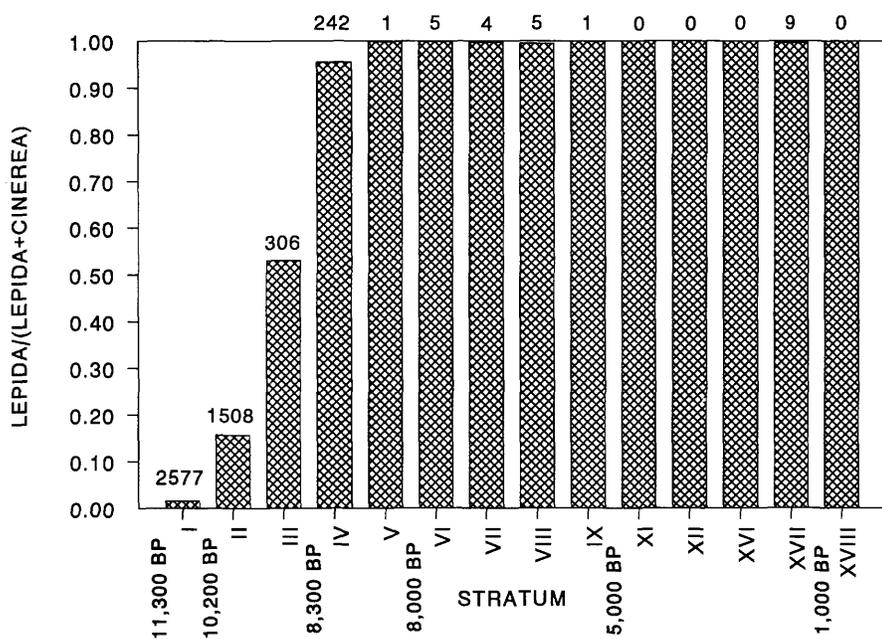


FIGURE 12.—Proportion of the woodrat fauna contributed by *Neotoma lepida* at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *N. cinerea* is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

HARVEST MICE

The western harvest mouse (*Reithrodontomys megalotis*) is found in a wide variety of habitats but is most abundant in settings marked by dense grasses or other herbaceous vegetation (Webster and Jones, 1982). These animals can be found in arid contexts, but in Nevada they tend to be most abundant in places that are both grassy and near water (Hall, 1946), and they may undergo significant population reductions in response to drought (Whitford, 1976).

The history of *Reithrodontomys* at Homestead Cave is summarized in Figure 14 (the numbers plotted in this figure com-

bine specimens identified as *Reithrodontomys* sp. with those identified as *R. megalotis*, the only species demonstrably present in the fauna). These animals were most abundant here during the early Holocene, declined dramatically during the middle Holocene, and rebounded late in prehistoric times.

Paleoclimatic Implications

THE EARLY HOLOCENE

Recent climatic models suggest that the early Holocene in the Great Basin was both wetter and warmer than today, with increased summer insolation causing increased summer mon-

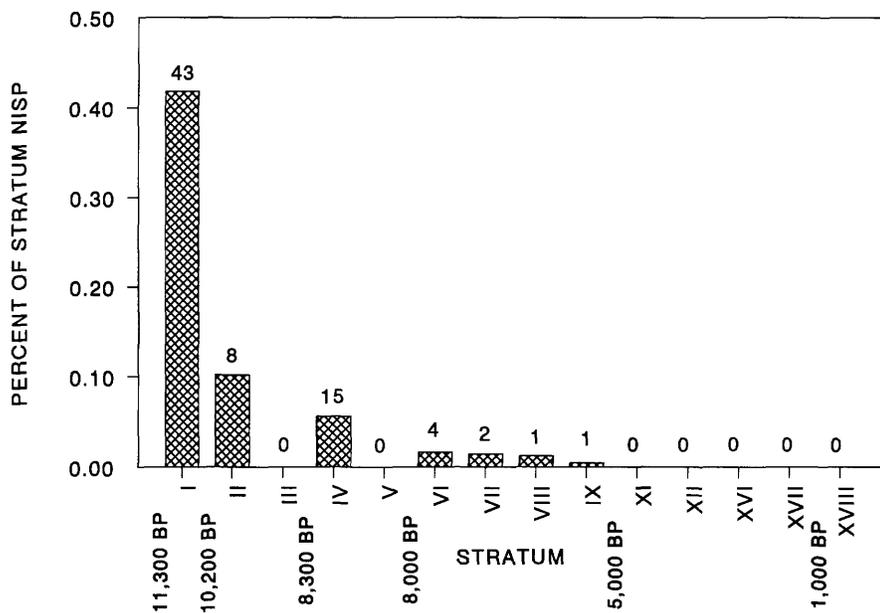


FIGURE 13.—Relative abundance of marmots as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *Marmota flaviventris* is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

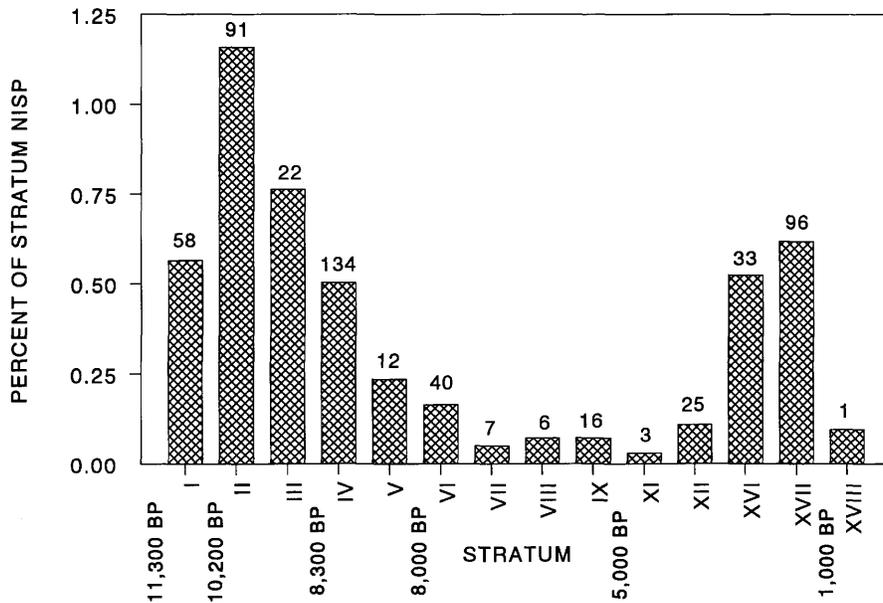


FIGURE 14.—Relative abundance of *Reithrodontomys* as a percentage of the total number of identified specimens (NISP) of mammals at Homestead Cave by stratum, excluding Stratum X. The number of specimens identified as *Reithrodontomys* is above the bar for each stratum. Corresponding radiocarbon ages are indicated below the strata.

soonal precipitation (e.g., Thompson et al., 1993; Mock and Bartlein, 1995). This is similar to what Antevs initially argued, although he would have been quite surprised at reconstructions suggesting that summer temperatures were higher at 9000 than at 6000 yr B.P. (Thompson et al., 1993).

Mammalian data relevant to testing these models have long been available. Curiously, these data most often have been ignored when the models were tested against empirical data, although at times they have been given passing mention (Thompson et al., 1993) or have been selectively cited when they happen to support implications of the models (e.g., Mock and Bartlein, 1995). Thus, it is important to stress that the early Holocene reconstructions provided by the models remain in conflict with a wide variety of mammalian paleontological data from the Great Basin, including data from Homestead Cave. The Homestead Cave mammal data strongly suggest that between about 11,300 and 8300  $^{14}\text{C}$  yr B.P. the Homestead Knoll area was not only substantially wetter than today but also substantially cooler, as Antevs argued during the mid-1950s.

As Bartlein et al. (1995) observed, uncalibrated radiocarbon ages are likely to give very misleading impressions of the relationships between events dated in this fashion and events expressed in calendar years. More to the point, Homestead Cave Stratum II has three radiocarbon dates whose calibrated ages fall between about 9900 and 9500 calendar years ago (Table 1), at about the time that the July Northern Hemisphere insolation maximum is incorporated into the models. Nonetheless, the fauna of this stratum is marked by taxa that do not suggest great warmth.

The early Holocene strata at Homestead Cave are marked by a wide variety of mammals whose modern habitat requirements and distributions strongly suggest that the Homestead Knoll area was relatively cool and moist at that time. The high relative abundances of arvicoline rodents (*Microtus* sp. and *Lem-*

*miscus curtatus*), *Neotoma cinerea*, and *Perognathus parvus* and the presence of *Marmota flaviventris* and *Brachylagus idahoensis* all imply a cool and moist climatic regime here during the early Holocene, albeit less so than during the latest Pleistocene. Even the history of kangaroo rats within Homestead Cave is consistent with this view. These animals compose a relatively small fraction of the Stratum II mammal assemblage; within the Stratum II kangaroo rat fauna, *D. microps* is 2.4 times more common than *D. ordii*, whereas it is 32.0 times more common in late-Holocene Stratum XVII.

The implications of the early Holocene small-mammal fauna from Homestead Cave seem clear. During the time that Stratum II accumulated, the area surrounding this site was marked by fairly dense concentrations of *Artemisia*, presumably *A. tridentata*, with a substantial grass understory. Vegetation and mammals alike existed in a climatic context that was both cool and moist, although not as cool and moist as the period when Stratum I accumulated. This conclusion is in sharp disagreement with the implications of the climatic models for this time and this area (Thompson et al., 1993).

Homestead Cave data are not alone in suggesting that the early Holocene, at least in the more northern parts of the Great Basin, was cool and moist, not warm (see discussions in Grayson, 1993, 1998). For instance, pikas (*Ochotona princeps*) are known from the lower elevations of the Fort Rock Basin of south-central Oregon between 11,200 and 7200  $^{14}\text{C}$  yr B.P.; it is difficult to see how these animals, so dependent on cool summer temperatures (e.g., Smith, 1974), could have existed in such settings during an early Holocene that was warmer, albeit moister, than anything that has come since. Also, 95% of the bushy-tailed woodrat specimens from Danger Cave were deposited during the early Holocene, even though the entire Holocene is represented at the site. Our knowledge of mammal

history for the northern Great Basin is remarkably consistent in this regard (Grayson, 1993). That history implies a cool and moist early Holocene in this region as a whole.

The small-mammal faunas of the early Holocene Great Basin are not necessarily incompatible with warm and moist summers. It is possible that mammals responded to nonanalog environmental conditions in nonanalog ways, although, given the diversity of mammal species involved, this seems unlikely. The same kinds of assessments of paleoenvironmental and, in particular, paleovegetational data, however, that have been used to assess the accuracy of the models (e.g., Mock and Bartlein, 1995) suggest that the mammalian data are strongly at odds with those models in terms of early Holocene temperature regimes in the Great Basin. We would be far better off in our attempts to understand both the models and the arid western climatic history if these data were addressed rather than ignored. Indeed, there is a substantial amount of paleovegetational data also at odds with those models (e.g., Madsen and Currey, 1979; Wigand and Mehringer, 1985; Thompson, 1990, 1992; Grayson, 1993; Rhode and Madsen, 1995).

#### MAMMALIAN RESPONSES TO MIDDLE-HOLOCENE CLIMATES

That the early Holocene mammalian fauna at Homestead Cave implies a climate that was cool and moist will not seem novel to those attentive to the empirical literature dealing with this period. Nor would Ernst Antevs or like-minded researchers of the middle 1950s have been surprised by this conclusion. The most famous part of Antevs' Neothermal model, however, involves not the early Holocene, but the middle Holocene, the period he termed the Altithermal and characterized as distinctly warm and dry (Figure 1).

Many paleoclimatic indicators have shown that whereas Antevs' monolithic view of the middle Holocene was overstated, the middle Holocene in the Great Basin was, in general, quite arid. Consistent with this view, derived mainly from lake level and paleovegetational histories, is that a wide variety of small mammals characteristic of cool and moist habitats declined in abundance, or became locally extinct, in the Great Basin between about 8000 and 7000 years ago (see the review in Grayson, 1993). Until recently, however, no concomitant changes in small-mammal distributions or abundances had been detected in Great Basin mammalian faunas as the middle Holocene ended between about 5000 and 4000 years ago (Grayson, 1993). One implication of this asymmetry is obvious: the end of the early Holocene was, from at least the standpoint of mammals, far more dramatic than was the end of the middle Holocene.

Nonetheless, the well-accepted view of the middle Holocene as generally much hotter and drier than what came before and after suggests that there must be a detectable mammalian response. A few years ago, I argued the following (Grayson, 1993:221):

That we have yet to detect this response in any convincing way probably reflects the fact that the mammal sequences now available for the period from about 5,500 to 3,500 years ago are not sensitive enough to tell us what the changes in mammalian distribution and abundance were at this time.

Homestead Cave shows a broad range of responses to the end of the early Holocene. Arvicoline rodents (*Microtus* and *Lemmiscus*) declined in number dramatically; *Marmota flaviventris* and *Brachylagus idahoensis* became locally extinct; *Neotoma lepida* became the dominant woodrat; *Perognathus longimembris* was the dominant pocket mouse; and *Dipodomys microps* was the dominant kangaroo rat. These responses agree with our knowledge of similar changes elsewhere in the Great Basin at this time (Grayson, 1993).

What is novel, however, is the evidence that this fauna provides concerning changes in mammal abundances during and after the middle Holocene. The abundance of *Reithrodontomys megalotis*, for instance, declined dramatically during the middle Holocene, then rebounded as this period ended. *Dipodomys microps* reached extremely high abundances, compared with those of *D. ordii*, between about 7000 and 5000 <sup>14</sup>C yr B.P. and then declined as the middle Holocene ended (Figure 5). Consistent with the arguments made by others concerning the nature of the middle Holocene, the abundances of *D. microps* are not monolithically high during this period, but instead they rise and fall much as the ratios of grasses to sagebrush rise and fall at Fish and Wildhorse Lakes on Steens Mountain in southeastern Oregon (Mehringer, 1985).

As the middle Holocene ended, not only did *D. ordii* increase in abundance relative to *D. microps* and *Reithrodontomys megalotis* rebound in number, but other mammals returned or increased in abundance as well. *Perognathus parvus* reappeared in the record in Stratum XVI as did *Lemmiscus curtatus* (but note that Strata XIII, XIV, and XV, dating to between about 3500 and 1500 <sup>14</sup>C yr B.P., remain unanalyzed).

Elsewhere, the archaeological record strongly supports the proposition that Great Basin human populations fell dramatically during the hot and dry middle Holocene (Grayson, 1993), an argument that also had been made long ago (e.g., Heizer and Baumhoff, 1965). The Homestead Cave fauna shows just how complex the biotic response to this climatic event was.

Some mammals that were lost from the record as the middle Holocene began never returned (e.g., *Marmota flaviventris* and *Brachylagus idahoensis*). Others underwent substantial reductions in number but remained in the area throughout this period (e.g., *Dipodomys ordii* and *Reithrodontomys megalotis*), then increased in number as, from their perspective, climatic conditions ameliorated. Still others (e.g., *Perognathus parvus* and *Lemmiscus curtatus*) became locally extinct and then recolonized when conditions allowed. The late-Holocene recolonization of the Homestead Knoll area included *Neotoma cinerea*, a mammal that has been assumed by some to be isolated on Great Basin mountains today. It is to this issue that I now turn.

### Recolonization and Small-Mammal Biogeography

In a series of extremely influential articles, Brown (1971, 1978; see also Brown and Lomolino, 1998) examined the modern distributions of several Great Basin mammals that today are primarily found on Great Basin mountains and not in the valleys that separate those mountains. These mammals include such species as yellow-bellied marmots, pikas, golden-mantled ground squirrels (*Spermophilus lateralis*), Nuttall's cottontails (*Sylvilagus nuttallii*), white-tailed jackrabbits (*Lepus townsendii*), and bushy-tailed woodrats. Brown based his arguments on insightful quantitative analyses, which indicated that, among other things, the relationship between the number of montane species on Great Basin mountains and the area of those mountains was marked by a slope characteristic of isolated faunas. Brown concluded that the montane mammals in his analysis reached Great Basin mountain islands during the Pleistocene, that they become fully isolated on those mountains when the Pleistocene came to an end, and that since then there have been extinctions of, but no new colonizations by, these species.

As I have observed elsewhere (e.g., Grayson, 1987, 1993), Brown's model makes several strong predictions about late-Pleistocene and early Holocene small-mammal history in the Great Basin. First, his model predicts that montane mammals currently isolated on Great Basin mountains once must have occupied the lowlands between these mountains, given that those lowlands provided the corridors of access to the mountains. Second, montane mammals found on only some of these ranges must have occurred on other ranges in the past, because the model maintains that the mountains were occupied by a common pool of species, which were reduced to their current numbers by subsequent extinctions. Finally, his model also requires that no Holocene colonizations of these mountains have occurred, because the process driving the differential presence of montane species on massive Great Basin mountains has been extinction, not colonization.

Previous paleontological work has shown that Brown's model was insufficiently dynamic (Grayson, 1993). In particular, it has appeared likely for some time that different mammals became isolated on different ranges at different times; thus specieswise, rather than communitywise, analyses are critical if we are to understand the processes of colonization and extinction that have formed these faunas.

This same paleontological work has, however, provided substantial support for the first two of the predictions made by the model. Homestead Cave provides exactly the same kind of support: the short-tailed weasel (*Mustela erminea*) appears only in Stratum I and *Lepus townsendii* only in Strata I and II; *Marmota flaviventris* is gone by about 8000 <sup>14</sup>C yr B.P. Although *Thomomys talpoides* is not on the list of montane mammals analyzed by Brown, it is also primarily montane in its Great Basin distribution, and it, too, is present only in the late-Pleistocene deposits of Homestead Cave. Not only has previous work provided strong support for the first two of these predictions, but it also has shown that montane mammals have be-

come extinct across all Great Basin mountain ranges during the Holocene (Grayson, 1981).

It has become clear that montane mammals are far more widespread today on Great Basin mountains than was once thought and that the pattern of this distribution is consistent with the argument that both extinctions and Holocene colonizations have been critical to forming that distribution (Grayson and Livingston, 1993; especially Lawlor, 1998). Some of these conclusions have been echoed by Lomolino and Davis (1997) on other grounds.

It is particularly important that Homestead Cave has, for the first time, allowed a detailed assessment of the third of the paleontological predictions I outlined above, demonstrating either the presence or absence of Holocene colonizations of Great Basin mountains by mammals.

One of the more remarkable discoveries during this project was that *Neotoma cinerea*, one of the member species of the montane mammal assemblage, is present in the Homestead Knoll area today. As part of an effort to document the nature of the local small-mammal community in conjunction with analysis of the small-mammal assemblage from Homestead Cave, we trapped (and filmed and released) a bushy-tailed woodrat within Homestead Cave itself, and E. Rickart (University of Utah, Museum of Natural History) discovered several unpublished records for this species in other low-elevation settings in nearby parts of the northern Bonneville Basin (Grayson et al., 1996). These discoveries led us to conclude that bushy-tailed woodrats can colonize low-elevation xeric settings. We also concluded, as did Lawlor (1998) on very different grounds, that modern montane mammal distributions in the Great Basin have been determined by a complex pattern of colonizations and extinctions.

Researchers now have a much clearer view of the history of this mammal in the Homestead Knoll area than was available when Grayson et al. addressed this issue in 1996. *Neotoma cinerea* had become locally extinct here by 5000 <sup>14</sup>C yr B.P., and perhaps well before then, only to reappear in the Homestead Cave fauna at about 1000 <sup>14</sup>C yr B.P. (Figure 12).

It is possible that the nine specimens of this species found in Stratum XVII were the effects of long-distance transport by a raptor (note that the sample available for Stratum XVIII is so small—1047 identified mammalian specimens—that *Neotoma cinerea* would not likely have been detected had it been present at this time). Nonetheless, given that bushy-tailed woodrats exist here today, there can be no question that this species has recolonized the Homestead Cave area during very late-Holocene times. In addition, the reappearance of *Neotoma cinerea* in Stratum XVII was both preceded and accompanied by increases in abundance of a number of other taxa that were suggestive of cooler and/or moister conditions. These taxa include *Dipodomys ordii* (Figure 5), *Lemmiscus curtatus* (Figure 10), *Perognathus parvus* (Figure 11), and *Reithrodontomys megalotis* (Figure 14). Given that *Neotoma cinerea* reappeared at the same time that these other, consistent changes occurred in the

nature of the local faunal community, it seems unlikely that this reappearance is attributable to a low-odds, long-distance dispersal event such as raptor transport.

A wide variety of data are thus joining to suggest precisely how complex the biogeographic history of Great Basin "montane" mammals has been. Although many of these complexities continue to elude us, recent studies make it clear that (1) the degree of isolation of some montane mammals on Great Basin mountains is far less than has been thought, and (2) the distinctive small-mammalian faunas of Great Basin mountains have been shaped by both colonization and extinction.

The practical implications of these results are clear. On the one hand, they show that attempts to predict extinctions under conditions of global warming that require the assumption of isolation (McDonald and Brown, 1992) are problematic (see the discussion in Lawlor, 1998). On the other hand, they suggest that the creation of mountain-based wildlife reserves in the Great Basin must also include low-elevation dispersal corridors. Not only could such corridors prove critical for dispersal under climatic regimes different from those that now characterize the Great Basin, but they are also currently in use by at least some species in at least some places.

### Conclusions

Whereas Great Basin fossil mammal assemblages do not, as yet, shed much light on aquatic history, they reveal the climatic conditions that help control aquatic histories. The most detailed, stratified, and well-dated small-mammal history currently available for the latest Pleistocene and Holocene in the Great Basin has been provided by Homestead Cave in the northern Bonneville Basin. This fauna documents environments that were clearly wetter between about 11,300 and 8300

$^{14}\text{C}$  yr B.P. than any that have been seen in this area since. The Homestead Cave fauna also joins a growing body of data generated by neocologists to show that the history of "montane" mammals in the Great Basin has been far more complex than was once thought.

Whereas the implications that the Homestead Cave fauna has for late-Pleistocene and Holocene moisture history in this region are in full accord with moisture histories derived from climatic models, they are at odds with the temperature histories derived from these models. The Homestead Cave fauna is not alone in suggesting a moist and cool early Holocene in the northern Great Basin, as opposed to the moist and warm early Holocene called for by the models. Although at times recognized as a potential problem by at least some of the modelers (e.g., Thompson et al., 1993), the differences between the climatic conditions called for by the models and those implied by the mammals are stark. The mammal histories have been replicated in so many places by so many taxa that it is unlikely that the problem lies with them but rather with the climatic models instead.

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# Great Basin Peoples and Late Quaternary Aquatic History

*David B. Madsen*

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## ABSTRACT

Great Basin environments are characterized by well-watered upland areas and relatively dry intermountain valleys. Winter snows feed river and lakeside marsh systems during the warmer months but inhibit upland occupation by humans in the winter. Throughout their history, Great Basin foraging peoples dealt with this half-wet, half-dry environment in two basic ways. One adaptive pattern focused on a relatively stationary (but not strictly sedentary) lifestyle around the larger marsh systems at the ends of streams and rivers in Great Basin valleys. The other was characterized by the movement of small groups throughout mountain/valley systems in which the marshes were too small to support a stable year-round existence. The former strategy was more common, and likely preferred, because of the year-round availability of storable resources collected primarily by women. Late Quaternary fluctuations of Great Basin lakes, particularly those that occurred during periods of rapid climate change, had a tremendous effect on Great Basin foragers because of their focus on lakeside marsh resources. Early in the prehistoric sequence, when lakes were relatively high, foraging was focused on lakeside environments. When lakes began to dry up during the middle Holocene, mobile foraging became more common. By the late Holocene when lakes rebounded to some extent, increasing population levels resulted in the widespread use of both adaptive strategies.

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## Introduction

My focus herein is primarily on the relationship between Great Basin peoples and Great Basin lakes rather than on a generalized account of Great Basin prehistory. Detailed summaries of Great Basin archaeology are available in a number of sources (see in particular Madsen and O'Connell, 1982; Beck and Jones, 1997; Kelly, 1997; Beck, 1999). There are also a

number of excellent treatments of environmental conditions in the Great Basin and of the interactions between environmental and adaptive change (e.g., Grayson, 1993; Rhode, 1999; Wiggand and Rhode, 2002). Because these are readily available and summarize most current information on Great Basin prehistory, I emphasize herein the role that resources in and around Great Basin lakes have played in structuring adaptive strategies used by most Great Basin peoples. The southern Great Basin is given rather short shrift because, at present, most basin lakes are located to the north, and most of what we know about lakeside adaptations comes from those areas.

The adaptive strategies employed by Great Basin peoples were largely tempered by the environmental settings in which they lived, and their use of basin lakes and associated marsh systems is best understood in the context of the basinwide geographic distribution of resources as well as the limitation and variation in the amount of precipitation that drives that distribution. Various aspects of Great Basin environments, including geomorphology, flora, fauna, and climates, and the Late Quaternary changes in these environments are described in more detail elsewhere in this volume, but it is important to note several major conditions that structured human behavior. Principal among these is the mountain-and-valley morphology of the Great Basin. As a result of extensional tectonics, the Great Basin consists of a series of long, high, fault block mountain ranges separated by equally long, narrow, relatively flat-bottomed valleys. The mountains typically reach elevations of 3000–4000 m (10,000–13,000 ft.) and, because of orographic effects on storm systems, trap much of the precipitation that falls in the Great Basin. The valleys, on the other hand, are relatively dry, even hyperarid in some locations, because of the rain shadows cast by the sequent mountain ranges. This is true even for the central Great Basin where, because of the east-west dome shape of the basin, valley bottoms are 300–600 m higher than those along the margins.

Fifty years ago, Ernst Antevs, in his landmark 1948 paper on Great Basin climates and peoples, described the region as primarily arid to semiarid, the latter of which remains the term most often used to summarize Great Basin climates. Yet, the basin-and-range topography engenders a climatic regime that may be better described as "hemiarid" (Currey, 1991), a phrase

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that incorporates a basic difference between the wet upland environments of basin mountains and the arid environments of basin valleys. In terms of human adaptation, however, this difference is tempered somewhat by the closed-basin morphology of basin hydrologic systems that traps runoff from mountain precipitation in terminal valley lakes. This capture of mountain precipitation, much of it falling in the form of winter snow that gradually releases water as it melts throughout the rest of the year, creates a situation in which *relatively* lush riverine and lacustrine ecosystems, relying on what is essentially outside water, are found within *relatively* barren desert valley ecosystems supported only by limited local rainfall. In the western Great Basin, these river and lake margin environments include the Donner und Blitzen, Truckee, Carson, Walker, and Owens Rivers and their associated terminal shallow lakes. In the eastern Basin they include the Bear, Weber, Ogden, Jordan, and Sevier Rivers. This pattern is repeated within each interior basin-and-range system, with the largest amount of precipitation falling on upper mountain slopes and running off into small streams and associated terminal lake/marsh systems on valley floors.

The contrast in productivity between the mountain-fed marshes and the surrounding valley floors and foothills, given the limited amount of rainfall in these lower elevation valleys (25–40 cm/yr. at best), is extreme in terms of both plants and the animals they support per unit area. Almost without exception, the amount of available energy passing through the interconnected ecosystems of the Great Basin deserts varies in direct proportion to the amount of available water, and, given the differential distribution of water, there is a sharp difference between the productivity of ecosystems with water and those without it. Put in the simplest of human terms, since hunter-gatherers must rely on the natural distribution of resources, the seasonal and spatial distribution of hunter-gatherers in the Great Basin mirrors the seasonal and spatial distribution of water.

A second critical aspect of Great Basin environments is the seasonality imposed by its middle-latitude setting. At 35°–45°N latitude in an interior continental position, the Great Basin is characterized by warm summers and cold, sometimes harsh, winters. Growing seasons are relatively short, and the amount and variety of available food resources, particularly plant resources, is extremely limited during the winter months. As a result of this marked seasonality, people had to either store resources for winter consumption or situate themselves in localities where resources were available during the winter months. Such localities were relatively few in number because the aridity of Great Basin valleys and the deep winter snows that blanket most of the higher elevations limited the areas where suitable overwintering sites could be found.

These basic parameters of surface morphology and seasonality are accompanied by two additional, but related, environmental factors that were also important in structuring prehistoric human behavior. First, the number and distribution of large herbivores found in Great Basin environments was lim-

ited compared with many other areas of North America, both historically and throughout the Late Quaternary. Because of the basin-and-range morphology of the Great Basin, habitats upon which many grazing animals depend are small and widely scattered, and large prey animals such as antelope, historically, and camels, prehistorically, were limited in number in any one locality (e.g., Steward, 1938). Second, the disparity in the distribution of water makes many of the habitats on which Great Basin peoples relied very sensitive to even short-term climatic changes. Resources away from stream, lake, and spring margin localities are limited and widely scattered, and when lacustrine and riverine habitats are reduced or eliminated by variations in climate, alternative food resources are difficult to acquire.

I outline herein two basic subsistence/settlement strategies that have been observed in both the archaeological and the ethnographic record. These strategies are only part of a continuum of adaptive approaches employed by Great Basin peoples and should not be construed as wholly representative of the Great Basin foraging spectrum. A comparison of the two, however, illustrates most of the primary solutions to the environmental constraints imposed by the basin-and-range morphology of the Great Basin and its hemiarid landscapes. Analyses with optimal foraging models and ethnoarchaeological research indicate that these adaptive strategies can be described best by examining women's gathering activities rather than men's hunting activities, because virtually all Great Basin subsistence/settlement systems focused primarily on plants as opposed to animals. I present ethnographic examples of the two principal adaptive strategies, examine which of these strategies has been most successful throughout the prehistoric sequence, and review them in terms of the paleoenvironmental and archaeological records, particularly in terms of plant resources, beginning with the Pleistocene/Holocene transition and continuing until the Late Prehistoric period.

### Adaptive Strategies and Great Basin Lakes

These hemiarid Great Basin environments, characterized by hot summers and cold winters, high mountains encircling narrow valleys, and abundantly watered habitats located in the midst of arid ecosystems, created an adaptive challenge for Great Basin peoples throughout their 12,000-year history. They dealt with this varied environment in a variety of ways. Primary among these was a focus on the stream-fed, lake margin, marsh environments common to most valley drainage systems. Historically, this marsh adaptation has taken the form of a mobility pattern often referred to as a "limnosedentary" strategy (e.g., Thomas, 1985; Fowler and Fowler, 1990; see also Heizer, 1967; Heizer and Napton, 1970; Madsen, 1982; Janetski, 1986; Janetski and Madsen, 1990), although I prefer to call it simply the "lowland" strategy. This lifestyle was most common where large, stable marshes occurred.

These marshes are situated primarily along the eastern and western margins of the Great Basin in the Lahontan and

Bonneville drainages, where extensive snowpack in the high and massive Sierra Nevada and Wasatch mountains provide large amounts of water; however, similar marshes, such as the Ruby, Warner, and Malheur marsh areas, also occur adjacent to several of the large central and northwestern basin ranges.

Peoples living within these large marsh areas were not sedentary in the strict sense; rather, they moved around within the marsh, collecting an array of seeds, tubers, and small animals throughout the year. Virtually all of these resources were relatively expensive to procure (in terms of time spent for the number of calories gained) but had the advantage of being both abundant and closely spaced.

Raven (1993:8) succinctly summarized this lowland marsh strategy, describing human groups as living in "a fairly steady-state population within the marshes (but *not* at individual villages) throughout most of any hypothetical year:"

[G]overned chiefly by the exigencies of women's foraging, small scale adjustments in residence location were made frequently, but the sheer richness, diversity, and predictability of marsh side productivity invited virtually continuous exploitation. Forays outside the immediate marsh precinct generally were short term (i.e., day trips) and for the most part were resource-specific. Foodstuffs were stored as they were collected, usually within shifting habitation sites; stores were tapped as needed by groups overwintering in the vicinity of the marshes. Only occasionally did groups leave the valley floor, as when the marsh simply could not supply a necessary resource (such as toolstone) or when the uplands offered seasonal resource opportunities more energetically profitable (such as the nearly annual pinyon harvest). During such episodes, various upland resources (such as large game) might be taken, and some surplus returned to marshland base camps; life on the valley floor, however, otherwise relied little on mountain resources.

Alternatively, a mobile "upland" strategy was used when valley marsh ecosystems were too small to provide storable surpluses sufficient for overwintering, forcing people to either move themselves to a series of foraging areas, transport a variety of resources to a central area, or (more likely) both. In this strategy, mountain resources in both midslope and alpine areas were important components of the annual round as people moved through a series of foraging localities. However, unless one or more upland resources, such as pine nuts (*Pinus* spp.), were particularly abundant in any given year, sites in or near valley marshes most often continued to be the focus of overwintering stays. This was particularly true where large game animals congregated around the fringes of the marshes during the winter months. Because the transport of bulk resources was relatively expensive (e.g., Jones and Madsen, 1989; Rhode, 1990b; Metcalfe and Barlow, 1992), the preferred alternative (that is, the most economically viable) was usually the sedentary lowland marsh strategy (Kelly, 1995; Zeanah et al., 1995).

These stable lowland and more mobile upland strategies were not fixed and dichotomous but flexible and varied, with permutations of both found through space and time in the Great Basin. Moreover, people could, and did, switch strategies as circumstances demanded. Changes in circumstances often were related to a change in size and/or productivity of the marsh systems.

The degree of sensitivity to climatic change often correlates with the size of the marsh, with small spring-fed and stream-fed marsh systems subject to more variance in terms of both size and productivity. Large marsh systems at the terminus of major rivers are most affected by extreme climatic change because of the differential morphology of valley bottoms and mountain slopes. In response to small-scale climatic change, these large marsh systems move back and forth across the relatively flat valley floors left by Pleistocene lakes, but they remain essentially intact. Although there is often a short period of recovery, modest increases or decreases in available water would not greatly affect the marsh's overall utility for foraging peoples. A marked change in available water, however, can dramatically affect the size of many large marsh systems. This is particularly true when increases in water volume are sufficient to flood the flat valley floors. When this occurs, the configuration of lake-edge marshes changes from broad circumscribed areas at the deltas of major rivers to narrow, linear habitats, increasingly subject to wave impacts, along the steeper valley margins. Even where limited amounts of marsh vegetation occur along these linear patches, the advantage that large marsh systems give, in terms of reduced transport costs, is lost.

#### SHARING, STORAGE, AND COLLECTED RESOURCES

The upland and lowland approaches are examined here with attention to the adaptive strategies of two ethnographically well-known Great Basin groups. With experimentally derived energetic return data for a number of resources commonly collected in the eastern and west-central Great Basin, and by ranking these resources on a seasonal basis, it is possible to evaluate the most economically viable subsistence strategy in any one time and place and to examine how closely the ethnographically known groups matched these predictions. I focused on collected rather than hunted resources for two reasons. One reason is pragmatic in that little or no experimental data were available for commonly hunted Great Basin resources, and what information was available consisted primarily of estimated rather than measured return rates. The second reason is derived from both theory and ethnographic reality.

Evolutionary ecology suggests that among hunter-gatherers (at the very least), men and women have both different reproductive strategies and different resource procurement strategies (Dahlberg, 1981; Hayden, 1981; Hill et al., 1985; Hurtado et al., 1985; Hawkes et al., 1989; Hawkes, 1990; Kaplan and Hill, 1992; Kelly, 1995). This, for a variety of reasons, results in a typical division of labor in which men hunt and women gather. As both a cause and a result of this division of labor, men tend to be more mobile and women more stationary; men come and go from the camps of women and children. Men move farther, faster; they leave camp in pursuit of higher risk/higher return mobile resources and return with more readily transported and concentrated packets of energy. Women, on the other hand,

deal primarily with stationary lower return but lower risk resources that are relatively bulky and not easily transported. It is, in short, often easier to bring the resources of men to the collection location of the women and children than it is to bring the women and children and their resources to the collection location of the men (Steward, 1938; Lee, 1979; Hawkes et al., 1982). To put it another way, wherever the women, children, and old folks are is "home"; it is the place, except in unusual circumstances, to which men return with whatever they have bagged. This pattern is clearly shown in the ethnographic and ethnohistorical literature of the Great Basin. Virtually all descriptions of subsistence/settlement systems are essentially descriptions of *women's* subsistence/settlement systems; they are descriptions of "home." Men come and go, but they are ephemeral to a basic pattern defined by the activities of women and children. Even in the comparatively rare situations wherein hunting activities dictate the location of home, it is nearly always because women and children are also involved in the hunting process, as in antelope or rabbit drives. As a result, in examining the relative mobility patterns of Great Basin hunter-gatherers, it is most appropriate to focus on the activities of women, because it is their procurement strategies that determined both the location of and the duration of stay at any one home settlement.

Optimal foraging and transport models (e.g., Stevens and Krebs, 1986; Hill et al., 1987; Jones and Madsen, 1989; Bettinger, 1991; Kaplan and Hill, 1992; Metcalfe and Barlow, 1992; Kelly, 1995; Zeanah et al., 1995) suggest that Great Basin foragers obtained as much of any given resource as they could, which was then either consumed soon after, cached for later consumption or insurance, or carried elsewhere and consumed or stored. The production and storage of excess is not only economically viable in terms of both time and energy maximization, but it also helps to reduce the element of chance associated with resource availability that is very common in middle-latitude ecosystems. In the Great Basin, where resources are spatially and temporally dispersed and their availability and abundance is difficult to predict, variation can be dampened, as Winterhalder (1986:386) notes, in two opposing but potentially complementary ways, "Foragers can dramatically reduce their food availability variance by pooling and dividing separate catches .... The same functional result is available to one forager able to store and carry over a surplus."

Sharing and storage may be functionally similar in the way they mitigate spatial and temporal resource variation, but the two approaches are operationally quite different. Moreover, although they can be used in a complementary fashion when dealing with a series of different resources, they are not compatibly used for a single resource. That is, it is appropriate to either share a resource surplus immediately among a group or to store it on an individual or family unit basis, but it is likely inappropriate to do both (Kaplan, 1983; Kelly, 1995). On the other hand, it is possible to handle different types of resources in different ways. Within the Great Basin and many other middle-lat-

itude areas, for example, hunted resources can be, and usually were, shared communally, whereas collected resources most often can be, and usually were, stored on an individual basis.

Most hunting activities involve a high degree of chance, and a hunter's skill and hard work will not always predict hunting success in the short run. Moreover, although hunting often is conducted on a group basis, it does not usually generate large surpluses suitable for storage. As a result, sharing of hunted resources, particularly larger animals, among a group of hunters is most appropriate (Kaplan, 1983; Kaplan and Hill, 1992). In the Great Basin, for example:

Large game was usually taken by men, while women gathered plant foods. A hunter was obligated, however, to share large game with other members of the village (Steward, 1938:231).

Large game ... was shared communally with all village members, whether they were related or not. The hunter was privileged to keep only the skin and some special portion of the animal (Steward, 1938:74).

Each man kept his quarry (rabbits) but unsuccessful hunters were given a few (Steward, 1938:98).

Gathering, on the other hand, can nearly always be conducted on an individual basis, and those who work harder and/or longer are nearly always more productive. Moreover, collected resources are generally quite suitable for storage. As a result, collecting and storage of gathered resources on an individual or immediate family basis is most appropriate (Kaplan and Hill, 1992) and was common in the Great Basin:

When gathering these foods, group endeavor might bring the pleasure of companionship, but it did not increase the per capita harvest. In fact ... it usually decreased the harvest .... A woman harvested exclusively for her family (Steward, 1938:230-231).

Gathered seeds were private property. Women shared them only with their husbands, children, and sometimes parents whom they supported (Steward, 1938:72).

A family gathered only for itself and cached the nuts secretly if possible (Steward, 1938:128).

Robbery of cached nuts, even by brothers and sisters of the owners, led to fights ... (Steward, 1938:73).

In short, storage and energy maximization models suggest that in the Great Basin, hunter-gatherers probably collected as much as they could at any one time and then shared (if hunted) or stored (if collected) any surplus.

#### SEASONAL RESOURCE RANKINGS AND PREDICTED BEHAVIOR

Table 1 presents data on collected resources in the northern Great Basin divided into seasonal availability and ranked by energy return rate. Clearly evident is the limited and seasonally biased nature of extant experimental data. Data on a number of important resources, such as fish, are unavailable (but see Larson and Kelly, 1995), and there is little on the energetic returns for available spring flora such as roots and greens. I stress that these return rates should be used with caution, because they each represent a range of values, and those ranges have yet to

TABLE 1.—Seasonal rankings of resources collected by hunter-gatherers in the Great Basin. Resources are seeds unless noted otherwise; *N* = no. of measurements; a question mark (?) indicates data are not available. Sources: Fowler and Walter, 1985; Simms, 1987; Madsen and Kirkman, 1988; Jones and Madsen, 1991; Madsen et al., 1997; Rhode, 1997.

Resource	Average return rate (Cals/hr.)	<i>N</i>
Dec/Jan/Feb		
<i>Typha latifolia</i> rhizome	3,299	3
<i>Typha latifolia</i>	260	24
<i>Scirpus</i> sp. rhizome	200	3
<i>Allenrolfea occidentalis</i>	111	3
Other persistent seeds, such as <i>Suaeda</i> sp.	?	?
Mar/Apr/May		
<i>Lewisia rediviva</i> root	1237	1
<i>Typha latifolia</i> shoots	575	5
<i>Stanleya pinnata</i> greens	417	8
<i>Achuathenum hymenoides</i>	348	4
Other roots and greens	?	?
Jun/Jul/Aug		
<i>Melanoplus sanguinipes</i> (adult insects)	27,649	5
<i>Typha latifolia</i> pollen	5,739	2
<i>Anabrus simplex</i> (adults)	2,959	3
<i>Descurainia pinnata</i>	1,307	1
<i>Elymus salinas</i>	1,238	1
<i>Lepidium</i> sp.	684	2
<i>Scirpus paludosus</i>	470	1
<i>Elymus cinereus</i>	370	2
<i>Scirpus</i> cf. <i>microcarpus</i>	320	1
<i>Phalaris arundinacea</i>	291	2
<i>Sporobolus asperifolius</i>	249	3
<i>Hordeum jubatum</i>	206	2
<i>Carex</i> sp.	202	1
<i>Distichlis stricta</i>	153	2
Sep/Oct/Nov		
<i>Typha latifolia</i> rhizome	3,299	3
<i>Quercus gambelli</i>	2,232 <sup>a</sup>	2
<i>Scirpus acutus</i>	1,699	1
<i>Atriplex nuttalli</i>	1,200	1
<i>Pinus monophylla</i>	1,083 <sup>b</sup>	3
<i>Atriplex confertifolia</i>	1,033	1
<i>Helianthus annuus</i>	504	1
<i>Typha latifolia</i>	260	24
<i>Scirpus</i> sp. rhizome	200	3
<i>Allenrolfea occidentalis</i>	111	3

<sup>a</sup> Maximum return rate; tannin removal would reduce the average value.

<sup>b</sup> Two widely divergent Cal/kg values are available; this represents an average.

be fully determined (e.g., Simms, 1987; Jones and Madsen, 1991; Bettinger, 1993; Zeanah et al., 1995; Madsen and Schmitt, 1998; Madsen et al., 1997; Rhode, 1997; Grayson and Cannon, 1999). Despite the limitations, however, the seasonal rankings are sufficient to allow some general predictions concerning seasonal gathering behavior of northern Great Basin hunter-gatherers.

Beginning in the spring, the most appropriate focus of attention would be on available shoots and roots from newly emergent perennials, with the location and the size of the home set-

tlement dependent on the distribution and abundance of these roots. Toward the end of spring, early seed crops, such as Indian rice grass (*Achnatherum hymenoides*), become available. Most roots and early seeds are in valley bottoms or in the foothills adjacent to valley bottoms, and relatively compact settlements may be appropriate.

In the summer, available high-ranked resources are highly variable in both nature and distribution, ranging from cattail (*Typha* spp.) pollen in valley bottom marshes to insects in upland areas. Many of these summer resources are storable items. Fishing may also be quite worthwhile during this period, but few data are available (but see Raymond and Sobel, 1990; Larson and Kelly, 1995; Butler, 1996; Lindström, 1996; Nauta, 2000). High-altitude resources are probably also highly productive at this time, but no experimental data have been produced. As a result of this diversity of resources, it is probable that an equal diversity in the distribution of local human populations is most appropriate.

In the fall, highly productive seed crops, such as pine nuts and bulrush (*Scirpus* spp.) seeds, are available and constitute resources that can be stored for winter consumption. Most of the upland fall seed crops are relatively dispersed, making small family groups the most appropriate settlement pattern. When resource concentrations occur, however, larger groups may be equally appropriate.

In winter, the few collectible resources available—such as bulrush and cattail rhizomes, bush pickleweed (*Atleurolefea occidentalis*) and seepweed (*Suaeda* spp.) seeds, and, in early winter, saltbush (*Atriplex* spp.) seeds—are located primarily in valley marsh settings. Many winter collectibles are low-return resources; but, with few competing resources in the winter, they are high-ranking, and thus are an appropriate focus for collection during the winter months. Rhizomes maintain their food potential as the winter progresses, and given the scarcity of competing activities, seeds may actually increase in relative worth at that time. Pickleweed, saltbush, and cattail seeds often persist well into the winter but are most profitably collected from late October through December. They can be processed at leisure, however, during later months and, if allowed to dry on the stem, may yield a higher return rate. The costs in time during the winter months for processing resources, such as pickleweed, do not change, but the value of the time does. Because relatively few options exist for food gathering and processing, the processing of previously collected items can be done when the alternate uses for time are limited, thereby increasing the relative value of the resource.

Given this seasonal distribution of resources, general predictions are possible concerning the nature of subsistence/settlement in typical northern Great Basin valley/mountain settings.

*Spring:* Settlements would be situated around marsh habitats for collecting emergent shoots and waterfowl eggs, with logistical trips made to nearby valley margins and foothills to collect roots and greens. Where no marsh resources occurred, settlements would be dispersed in a variety of foothill locations.

**Summer:** Settlement locations would be variable depending on the nature of available resources. Where abundant high-ranked resources such as cattail pollen and fish occurred, settlements would remain concentrated in or near the valley bottom marsh settings. Away from marsh areas, settlements would probably continue to be dispersed, possibly to alpine areas.

**Fall:** Settlements would probably be dispersed and relatively mobile to take advantage of various highly productive and highly ranked resources in widely separated areas. Because the productivity of some of these resources, particularly piñon, was variable from year to year, the nature of the fall dispersion pattern might also have been variable. In most years, settlement would be near marsh areas where a number of highly productive resources occurred close together.

**Winter:** Settlements would be concentrated near stored resources and/or valley bottoms. The amount of stored resources probably would be a basic determinant of winter settlement. Given the difficulty in transporting plant resources, noted earlier, these resources probably would be cached close to their procurement area. Wherever sufficient stored resources were available to last the winter, either in upland or valley bottom locations, winter settlements would be found relatively close. When stored resources were insufficient to last the winter, settlements would be concentrated in valley locations near winter procurement areas.

### Two Great Basin Subsistence/Settlement Patterns

Given these economically based predictions, it is possible to examine two ethnographically and ethnohistorically known Great Basin groups—the Toedökadö, who included a large valley marsh in their subsistence/settlement system, and the Kaibab Paiute, who did not—to determine the appropriateness of energetic efficiency models for understanding both upland and lowland adaptive strategies. These groups, described by Fowler (1982, 1992) and several earlier workers (e.g., Kelly, 1934, 1964; Stewart, 1941; Euler, 1966; Wheat, 1967; Fowler and Fowler, 1971; Thomas, 1985; Fowler, 1989), are sufficiently well known to illustrate the interplay between the type, availability, and abundance of resources, and the ways in which those resources were utilized to maximize energetic efficiency.

#### KAIBAB PAIUTE

Fowler (1982), building primarily upon work by Isabel Kelly (1964), described a series of interrelated camps (termed “economic clusters”) and subsistence strategies used by the Kaibab group of the Southern Paiute that can be compared with the relative resource rankings compiled in Table 1. One of these economic clusters is depicted in Figure 1, showing the seasonal movements of the several interrelated camps. Fowler (1982: 127) summarized the subsistence/settlement patterns of this cluster as follows:

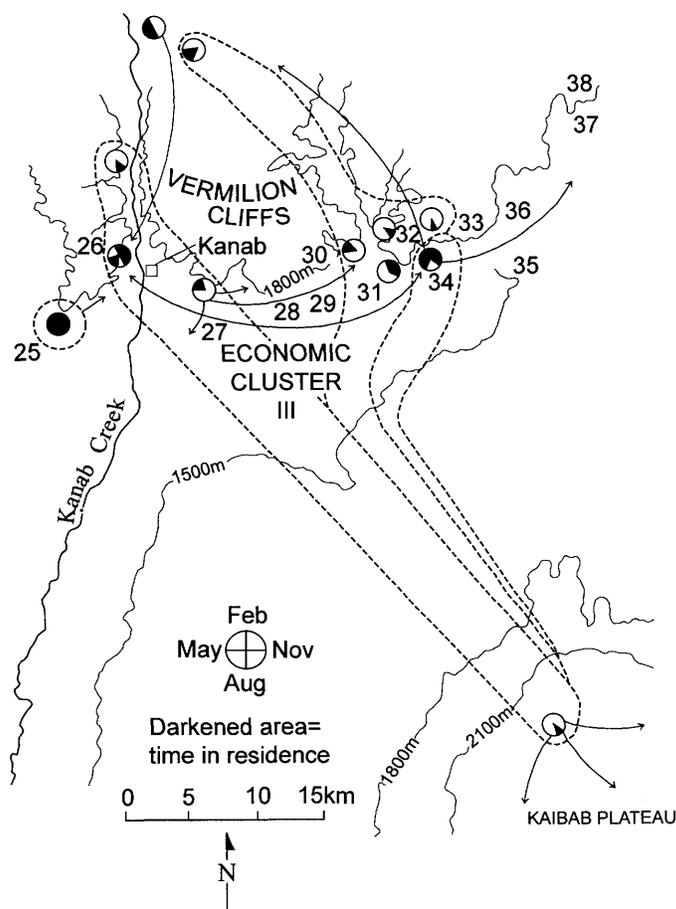


FIGURE 1.—Diagram of Southern Paiute groups in spring: economic cluster III (after Kelly, 1964; and Fowler, 1982). See text for explanation of “camps” and numbered locations.

Camp 25: 2 people, a man and wife; “stayed there all the time”; hunted deer with people from #26.

Camp 26: Large and important settlement of “many” camps (households) the composition of only 3 of which was remembered (16 people—probably 40–50 at site). Winter base, usually also for people from cluster IV (Alton area); moved to #27 in spring for *Peteria* (a root); remained until June when returned to #26 to harvest seeds; occasionally visited Johnson Canyon for *Mentzelia* seeds. In fall moved to cliffs above Three Lakes to harvest *Artemisia* seeds; also hunted deer in Orderville region. Often joined by those of #34 for fall trip to Kaibab Plateau for deer. Returned to #26 before snows.

Camp at springs 30–33: 3 camps, 12 people. Wintered at #31; in spring moved to #30 for *tsii* (a root); in summer visited Alton (IV) for *Balsamorhiza* seeds and remained to harvest. Occasionally stopped at #28, 29 (not inhabited). In fall gathered yucca and pinenuts on mesa above Vermilion Cliffs (at #32). Fall trip to Kaibab for deer.

Camp 34: 4 camps, 13 people. Winter, spring and much of summer at or near #34. In fall returned to #34 before going to Kaibab for deer; sometimes went with #26.

The Southern Paiute lived in an environmentally diverse region and had equally diverse subsistence/settlement systems. Not only did economic clusters, such as the one just described,

have high intercluster variability, but even within an economically interdependent group, individual camps ranged from almost completely sedentary to highly mobile. As a result, it is difficult to generalize a subsistence pattern beyond suggesting that, as one would expect, the energetic efficiency of obtaining local resources varied with resource availability and distribution. That variation, in turn, appears to have been the driving force that defined the diverse subsistence/settlement patterns of the Kaibab Paiute.

Despite this variability, it is clear that the seasonal activities of this group of Southern Paiute closely followed the predicted pattern. Spring activities were oriented towards dispersed root procurement—*Peteria* in the case of one camp, *Tsii* in the case of another. Summer activities were oriented toward the collection of a variety of seeds (such as *Balsamorhiza*, *Chenopodium*, *Epichampes*, *Mentzelia*, and *Urosepses*) in a variety of contexts. Fall activities revolved around the abundance of piñon. In good years, trips for collecting pine nuts were made; in bad years a variety of other resources such as agave or *Artemisia* seeds were taken. Winter locations were apparently dictated by nonfood factors, possibly because, with few exceptions, all year-round collecting activities occurred within a 10–15 km radius. Stored resources were generally cached near the point of collection and transported as needed. Variation was the key, and, as Fowler (1982:127) noted, "... several actualized settlement patterns [had] obtained in this one small area. Some people, perhaps older individuals or a single family, maintained permanent camps; others split winter and summer bases; others moved three or four times during the year."

#### TOEDÖKADÖ

Predictions drawn from the seasonal ranking of collected resources do equally well when examined against a marsh-oriented Great Basin group. Fowler (1982, 1992), Thomas (1985), Larson and Kelly (1995), and Zeanah et al. (1995) have all summarized earlier work on the Toedökadö ("Cattail Eaters") group of Northern Paiute who lived in and around the Stillwater marsh area in the western Great Basin. Like the Kaibab Paiute, mobility in this Northern Paiute region was, in part, dictated by the annual variation in pine nut productivity. However, Thomas (1985:25) suggested that the inherent instability of the upland piñon crop created a flexible and annually variable approach to overwintering:

During most winters they probably maintained a relatively stable residential base, in either marshland or upland settings, depending on the local availability of key fall resources, the quantity of foodstuffs cached during the summer, and the transport costs involved.

Fowler (1992:212), on the other hand, suggested a much tighter focus on the Stillwater and Carson marsh areas:

The picture ... appears to be one of considerable security, a tendency to remain in place in groups of perhaps 20 people or so, and certainly to focus on the richness of the marsh. *Toiwaitu*, 'cattail-place,' was their home, their *tibiwa*, and they seemingly wanted no other. They spent most of the year there, working

out from small to medium-sized villages of cattail houses. If they moved away, it was only for short periods and then they returned.

In early spring, Toedökadö women's subsistence focused on marsh resources, principally on cattail and bulrush shoots and spikes and on sego pondweed (*Potamogeton* sp.) corms. Eggs from a large variety of waterfowl were a principal source of protein. A variety of greens, such as prince's plume (*Stanleya pinnata*), and bulbs, such as *Allium*, were also collected from the lowlands around the periphery of the marsh. In late spring, the largely concentrated Toedökadö broke into smaller family groups to collect a variety of greens and roots. Some moved to different upland areas, principally in the Stillwater Range, to collect *Claytonia*, *Lewisia*, *Lomatium*, and *Perideridia*. Many also trekked to the lower Truckee River for fishing during spring spawning runs. Most of these spring resources were probably consumed immediately, with a limited surplus of storable resources returned to the principal camps along the Carson River delta system. In early summer, a variety of seeds, such as Great Basin wild rye and tansy mustard, were collected and stored from foothill to upland locations. In years when *Achuthenum* and *Mentzelia* seeds were abundant, they too were collected before the summer return to primary base camps. Both the root- and seed-collecting areas were close enough to the primary camps in the marshes to allow these resources to be stored at the point of consumption rather than the point of procurement.

Summer collecting took place principally in the vicinity of the numerous shallow lakes or sloughs along the lower Carson River. Resources included fish—both suckers and chubs—which were available throughout the summer, cattail pollen available in the early summer, and *Scirpus* seeds in late summer. Surpluses from these summer resources were cached near the primary base camps.

In the fall, relatively high-ranking seed resources were found in both lowland and upland areas but were compatible because of slight differences of seasonality. *Scirpus* seeds and other marsh resources, such as cattail rhizomes, remained abundant throughout the early fall, with pine nuts becoming available in midfall. Areas for gathering pine nuts were both adjacent to and relatively far away from the primary base camp. Pine nuts from nearby piñon zones were usually transported to the lower Carson River sites (either immediately or during the course of the winter), whereas the caching and/or transport status of more distant pine nut areas was dependent on the size of the crop. "In exceptional piñon years, base camps were established in the mountains; in ordinary and poor harvest years, residential bases were transplanted from the woodlands to lakeside villages" (Thomas, 1985:22; see also Fowler, 1992:84). The decision was apparently based on whether or not there were sufficient quantities of nuts to last the winter. Even in good years, however, it was apparent that only "some families remained in the hills for the winter, living in 'mountain houses,' while others returned to the winter base camps at the marshes with their accumulated stores" (Fowler, 1982:133). During

winter, the principal resources were items that had been stored during the summer and fall, but along the lower Carson River, "the people also gathered *Suaeda* and *Allenrolfea* seeds," and tui chub were taken by the men (Fowler, 1982:133). Cattail and bulrush roots were also collected throughout the fall and winter (Fowler, 1992; Madsen et al., 1997).

This subsistence/settlement pattern was probably as diverse as that described for the Kaibab Paiute, with some families or small groups staying put for most of the year and others being more mobile. Despite any diversity, however, it appears that seasonal changes in subsistence behavior could be accurately predicted from a diet-breadth, resource-ranking model that focuses on the items collected primarily by women: marsh resources in the early spring, shifting to foothill roots and seeds in the late spring, lacustrine/marsh resources in the summer, mountain seeds for a short period in the fall, and stored resources and lower valley resources in the winter. In terms of actualized settlement patterns, it appears that most of every year was spent at principal base camp settlements along the lower Carson River, with movements to other locations for relatively short periods in the spring and again in the fall (Fowler, 1992; Larson and Kelly, 1995). In exceptionally productive piñon years (probably at best only one out of every four or five years), some families overwintered in the mountains—again, as could be predicted from the diet-breadth model and transportation cost data. Given the difficulty in transporting pine nuts to marsh locations, however, they do not appear to have been a principal dietary resource there (Larson and Kelly, 1995).

The pattern of the men's resource collection strategy in this Northern Paiute group also fits the prediction that "home" was determined primarily by the activities of women, with the men coming and going from this central home base (Fowler, 1992). An excellent example of this is DeQuille's (1963:71) observation of a men's "task group returning to the base camp in the Carson Sink after hunting wood rats in the mountains to the east: 'They had left the Cold Spring (Clan Alpine) mountains at sundown, and had been traveling all night across the desert. They carried small water bottles ..., and were loaded with a species of mountain rat, smoked and dried, packed in oblong hampers made of twisted ropes of grass.'"

Clearly this party of men had left the women, children, and old folks in the principal base camps along the lower Carson River, had traveled some 50–70 km to hunt, and were returning with their catch. Their mobility revolved around that of the women, and in describing the subsistence/settlement pattern of the Toedökadö, it is the women's pattern that was nominally described. This pattern appears to hold throughout what is known of the prehistoric sequence. Examination of gender differences in skeletal remains from the Stillwater marsh area, for example, indicated that males had a much higher incidence of skeletal pathologies associated with running and walking, suggesting that women were much more sedentary than men (Larson et al., 1995).

The Kaibab Paiute and the Toedökadö of the lower Carson River basin are fair examples of the upland and lowland subsistence strategies utilized by most Great Basin peoples. In both cases, the nature and distribution of resources largely structured the degree of mobility. Where subsistence resources were varied, concentrated, available year round, and easily stored close to the point of consumption, as in the large marsh areas at the end of major river systems, people tended to be relatively sedentary and populations tended to be relatively denser than elsewhere. This lowland pattern seems to have been the dominant strategy for the ethnographically known Great Basin groups (Figure 2) as well as for those from much of the last 2000–3000 years (e.g., Madsen, 1979, 1982; Janetski, 1986, 1991; Raven and Elston, 1988; Janetski and Madsen, 1990; Raven, 1990; Rhode, 1990a; Fawcett and Simms, 1993; Aikens and Jenkins, 1994; Larson and Kelly, 1995; Zeanah et al., 1995; Simms et al., 1997), and there is growing consensus that the large marsh systems associated with many terminal lakes were the optimal places for Great Basin hunter-gatherers to live. Similar patterns of intensive marsh use are found throughout the world, particularly at the deltas of major river systems (e.g., Stanley and Warne, 1997).

Exactly how far into the past this dominant lowland adaptive strategy extends is unknown, however, and remains a matter of some debate (e.g., Beck and Jones, 1997; Kelly, 1997). A major cause of this debate is, in large measure, the lack of information on the extent and even location of these terminal marsh systems prior to 3000–5000 years ago (Zeanah et al., 1995; Grayson and Cannon, 1999). It is not even clear why late-Pleistocene to middle-Holocene marshes have rarely been found. Possibly they were buried by later deltaic deposits or eroded during periods of mid-Holocene desiccation. Nonetheless, although only modest amounts of old marsh deposits have been found yet, sufficient data exist to suggest the lowland adaptive pattern is one of long standing in the Great Basin; how regionally widespread it was and what percent of early Great Basin peoples utilized this strategy remain unknown.

### Great Basin Climates and Lakeside Adaptations

#### YOUNGER DRYAS LAKES AND EARLY GREAT BASIN PEOPLES (12,000–10,000 <sup>14</sup>C YEARS B.P.)

Because of the link between adaptive strategies and large valley marsh systems, major changes in the size of Great Basin lakes during the last 12,000 <sup>14</sup>C years have had a dramatic effect on the course of Great Basin prehistory. The Late Quaternary lake sequence is defined in more detail by others in this volume, but briefly, there were five prolonged periods in which the relationship between Great Basin peoples and lakes is most obvious. The first of these was the Younger Dryas, a period between ~11,200 and 10,100 <sup>14</sup>C years ago when Great Basin lakes covered many of the valley floors. This period, commonly known archaeologically as the Paleoindian period, was

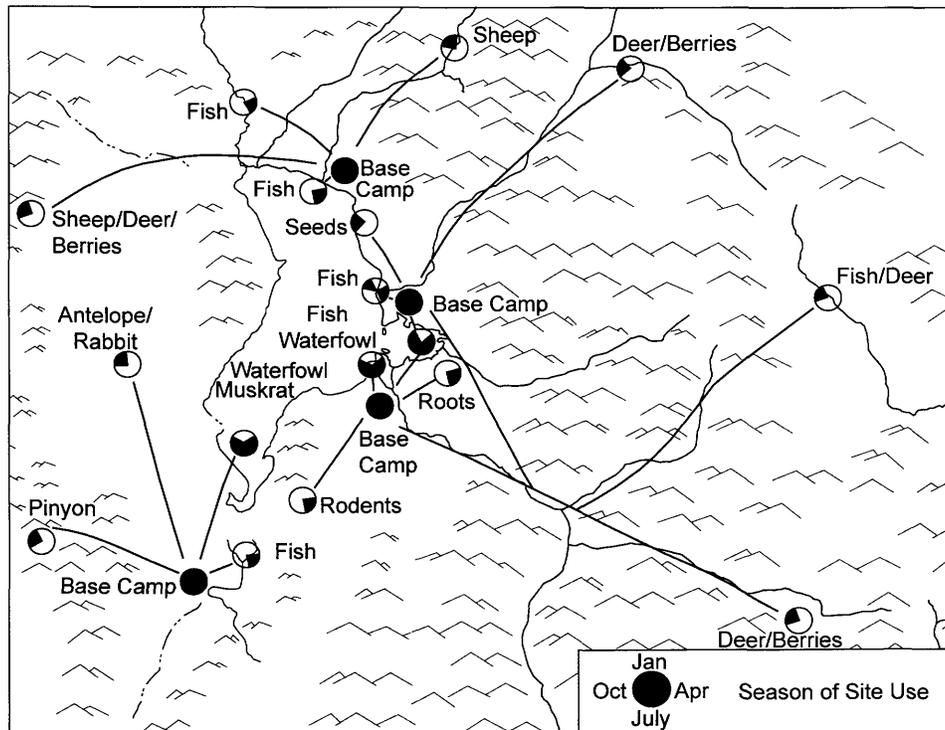


FIGURE 2.—Seasonal mobility of hunter-gatherers on the margin of Utah Lake, a situation very similar to that found in the Stillwater marsh area. Adapted from Janetski (1986).

characterized by large, fluted and stemmed projectile points most often found around the margins of these late Pleistocene lakes (Willig et al., 1988; Beck and Jones, 1997).

What little is known about the adaptive strategy that these people followed is based on inference, because virtually no buried sites containing substantive subsistence data have been recovered. Because numerous sites have been found along the lake margins, these people presumably focused on lake margin habitats, but what exactly they were doing there is unclear. With the exception of the tools found in the Fort Rock basin (Bedwell, 1973) and, perhaps, in Danger Cave (Jennings, 1957), grinding implements found in the Great Basin have been dated from less than 10,000 years ago (Beck and Jones, 1997), but it may be that the absence of older implements is a result of later groups scavenging for ready-made tools (Simms, 1988). Pleistocene megafauna was present in the Great Basin during this time period, but most species were extinct before the known appearance of people in the region, and the few species that remained were not likely to have been found in large numbers (Grayson, 1993, 1994). *Camelops hesternus* (yesterday's camel), *Equus* spp. (horses), and *Mammuthus columbi* (Columbia mammoth) were the only large herbivores that might have been hunted by Great Basin peoples in addition to historically known large game species. (*Nothrotheriops shastensis* (Shasta ground sloth) also may have been available in limited numbers in the southern Great Basin.) There is, however, no example of this extinct fauna having actually been taken, and it seems

likely that the array of subsistence resources collected by early Great Basin peoples was essentially the same as that taken by later groups.

Undoubtedly the biggest environmental difference between the Younger Dryas and later periods is the number and size of marsh systems within the Great Basin (Figure 3). Nearly every valley that contained a lake under full-pluvial conditions also contained standing water during the Younger Dryas (e.g., Currey et al., 1984a; Wells et al., 1989; Benson et al., 1990; Thompson, 1992). In many cases this standing water was relatively shallow, but such conditions may have enhanced the extent of associated marsh habitats. Moreover, there were a number of large spring-supported marsh systems during the Younger Dryas in areas that are now desiccated (e.g., Quade, 1986; Beck and Jones, 1997; Quade et al., 1998). Marsh systems, together with the lake margin areas, were both ubiquitous and larger, whereas population densities were apparently much smaller during the Younger Dryas than during subsequent periods (e.g., Kelly and Todd, 1988; Beck and Jones, 1997). As a result, lowland adaptive strategies were likely in place—but with a slightly different emphasis.

The grinding of seeds is relatively expensive in terms of the number of calories gained for time spent (e.g., Simms, 1987), and until the ratio of people to marsh area increased sufficiently to reduce the abundance of more easily collected resources, it is unlikely that seed grinding would have been extensively employed. The association of Paleindian sites with

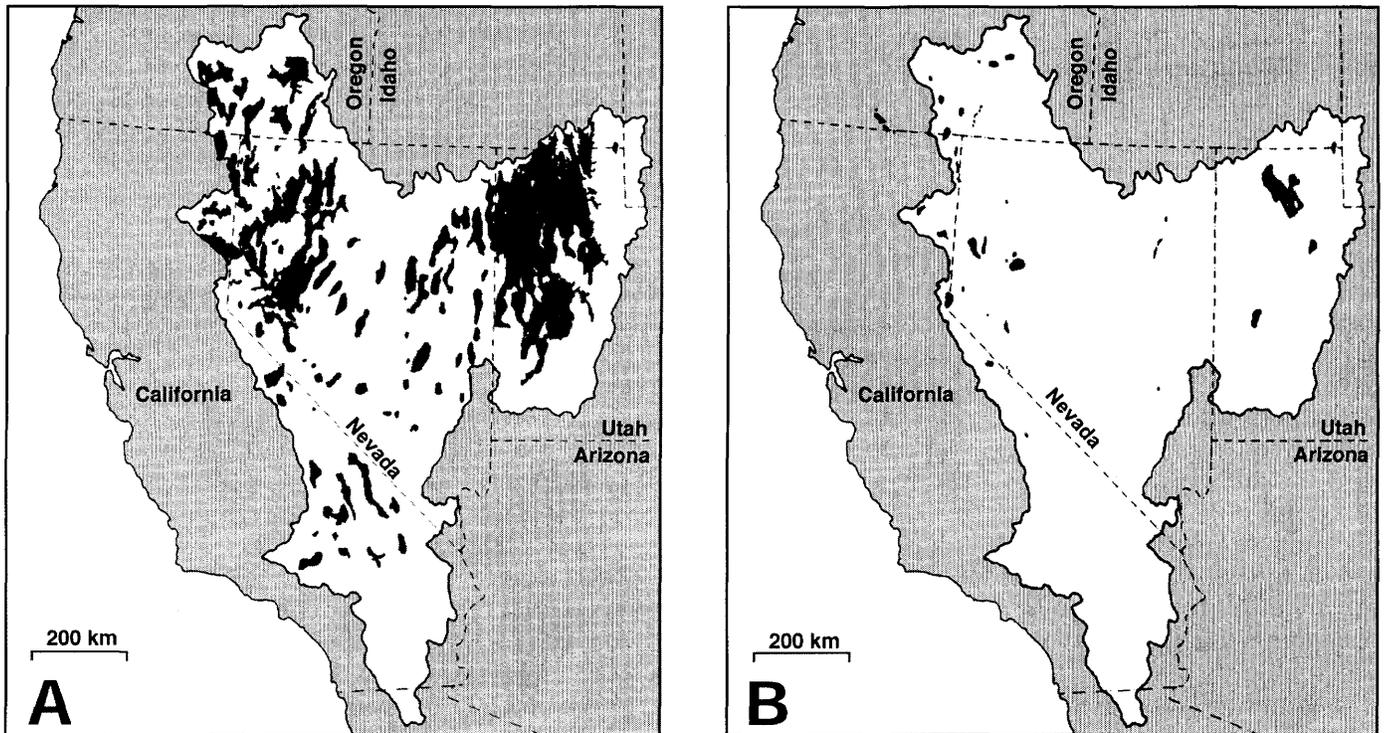


FIGURE 3.—Maps of Great Basin lakes (black areas) at the height of the last Pluvial period (a) and historically (b), which roughly illustrate the differences in size and distribution of marsh habitats between the Younger Dryas and the present.

lake margins and the absence of significant numbers of grinding implements may simply mean that peoples of the Younger Dryas era employed a lowland strategy that focused on higher ranked marsh resources. They operated much like later Archaic peoples but without the extensive grinding of seeds, and the term “Paleoarchaic” may not be inappropriate for these people (see Willig, 1989; Beck and Jones, 1997).

A second major environmental difference between the Paleoindian and later periods may be climatic volatility. If Younger Dryas climates in the Great Basin were as volatile as those defined elsewhere in the world (e.g., Mayewski et al., 1993), populations were probably maintained at relatively low levels because Paleoindian groups would have been repeatedly subjected to periods of stress (Madsen, 1999). For the millennium or so of the Younger Dryas, Great Basin Paleoindians were faced with rapid transitions from one climatic extreme to another. These seem to have been almost light-switch-like, and they certainly occurred within periods of less than a decade. The variance of these extremes was considerably greater during the Younger Dryas than it was during the Holocene (e.g., Stuiver et al., 1995); indeed, the range of climatic variation from one decade to the next was almost as great as the entire range of variation for the Late Wisconsin as a whole (Figure 4).

A third major characteristic that separated environmental conditions in the Younger Dryas from those that occurred sub-

sequently was seasonal equability (e.g., Zielinski and Mershon, 1997). During the Younger Dryas, summers were cooler, perhaps as much as 6° C (e.g., Rhode and Madsen, 1995), and winters may have been warmer (e.g., Elias, 1996) than at present.

These features of Younger Dryas climates had important implications for Great Basin hunter-gatherers. The climatic volatility of the period probably meant that many populations of large herbivores were limited because of their low reproductive rate and extended length of sexual immaturity. Herds would be relatively slow to recover after climatically induced periods of stress and may not have reached optimum numbers before being devastated again by the next climatic change. The availability of ephemeral plants, such as grasses, probably fluctuated in concert with wildly fluctuating climatic conditions. Mature individuals of less ephemeral plant species, such as limber pine (*Pinus flexilis*), probably survived these rapid climatic changes, but their seed production likely varied substantially, and immature individuals may not have survived. This would have led eventually to a reduction in the size of these plant communities. Marsh plants also would have been subjected to this rapid climatic variation, but the effect may have been tempered by their association with large bodies of water, which tend to react more slowly to climatic change. This variation in the environmental proxies of Younger Dryas climates probably tethered Paleoindian groups even more tightly to lake margin habitats.

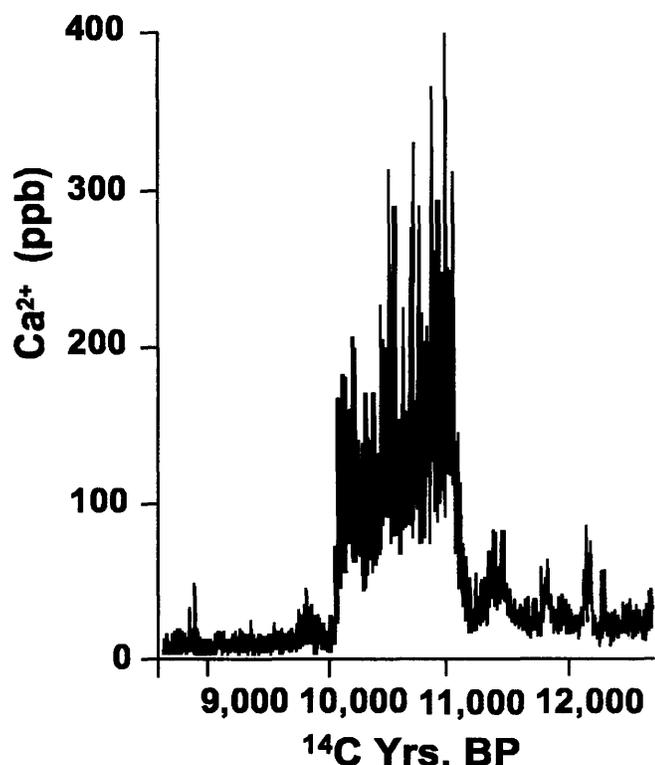


FIGURE 4.—Volatility of Younger Dryas climates as suggested by changes in calcium concentrates present in the GISP2 Greenland ice core (adapted from Mayewski et al., 1993).

#### THE EARLY HOLOCENE TRANSITION (10,000–8000 $^{14}\text{C}$ YEARS B.P.)

After the Younger Dryas, Great Basin lakes regressed to levels approaching, but still higher than, their modern levels. In many areas, particularly the southern Great Basin, many of the large, stable marsh systems disappeared. The lowland adaptive strategy, with seed grinding now definitely a component, was used almost immediately in some areas, and subsistence techniques focusing on the procurement of seeds and small animals (including birds and fish) were employed (Beck and Jones, 1997). Mobile strategies were also in use where marsh systems were of limited size and productivity. Evidence of subsistence at sites like Danger Cave in the eastern Great Basin (Jennings, 1957), Spirit Cave in the western basin (Napton, 1997; Tuohy and Dansie, 1997), and the Fort Rock and Connley Caves in the northwestern basin (Bedwell, 1973; Willig, 1989; Aikens and Jenkins, 1994) suggests that an array of adaptive behaviors, much like those found historically, was in place 10,000–9000  $^{14}\text{C}$  years ago.

The transition from the near full glacial conditions of the Younger Dryas to the near modern conditions of the Holocene apparently took place in a stepwise fashion, with a second abrupt climatic change occurring  $\sim 7500$   $^{14}\text{C}$  years B.P. (e.g., Stein et al., 1994; Brooks et al., 1996; Alley et al., 1997; Stager and Mayewski, 1997). Although this early-to-middle-

Holocene change has been recognized for more than a half century (e.g., Antevs, 1948), the abruptness of the transition has been difficult to detect in the Great Basin because of the lack of chronologically sensitive records. As a result, many archaeological and paleoenvironmental reconstructions have employed Crater Lake tephra as a chronostratigraphic marker to separate early and mid-Holocene environments (e.g., Thomas, 1985). Yet the few available sensitive records suggest that a climate change occurred somewhat earlier than the Mazama ash fall  $\sim 6900$  years ago. A variety of records, including tree rings from the southwestern Great Basin (Feng and Epstein, 1994), pollen sequences from the northwestern basin (Mehringer, 1985; Wigand and Mehringer, 1985) and eastern basin (Madsen and Currey, 1979; Spencer et al., 1984), lake deposits from the central basin (Thompson, 1992), and small mammal records from the northeastern basin (Grayson, 2002 (this volume)), suggests that an abrupt change occurred at or slightly after 8000 radiocarbon years ago. These records, together with a number of others (Grayson, 1993), suggest conditions in the Great Basin during the Preboreal period 10,000–8000 years ago were both cooler and moister than at present. Although no precise estimates of temperature differences have been made, it appears likely that they may have been at least  $2^{\circ}$ – $3^{\circ}$  C cooler on average during the early Holocene. Such a temperature difference is midway between current temperatures and the estimates for those of the Younger Dryas, and it is consistent with both plant (e.g., Wigand and Rhode, 2002) and animal records (e.g., Grayson, 2002).

There is limited evidence that many Great Basin lakes were higher during this period than at any other time during the Holocene. In the eastern Great Basin, for example, Lake Franklin remained high until after  $\sim 9000$  years ago (Thompson, 1992), and the Great Salt Lake was probably at elevations of 1289–1292 m (4230–4240 ft.) at about the same time (e.g., Currey et al., 1984b; Murchison, 1989). If lakes elsewhere were at similar levels (the period is poorly known geomorphologically), then the size and number of Great Basin marsh systems may have been substantially larger than at present, perhaps midway between the historic distribution and that found during the Younger Dryas. This, in turn, may explain why the modified lowland adaptive strategy (i.e., without seed grinding) seems to have extended into the early Holocene in some parts of the Great Basin (e.g., Elston, 1982; Beck and Jones, 1997).

The greatest effect on Great Basin peoples may have resulted less from change in temperatures and absolute amounts of moisture during the early Holocene than from a change in climate variability. Although abrupt climatic changes on the order of a millennium or longer continued to occur during the Holocene (e.g., O'Brien et al., 1995; Overpeck, 1996), the annual to decadal volatility characteristic of the Younger Dryas appears to have been substantially reduced (e.g., Mayewski et al., 1993; Stuiver et al., 1995). This may have provided some environmental stability, which would have allowed newly developed adaptive strategies to become widespread. Perhaps

more importantly, if the advent of increased seasonality in the distribution of moisture during the period (Zielinski and Mershon, 1997) was accompanied by a similar increase in a differential between winter and summer temperatures, then the number and kinds of mobility strategies may have been markedly reduced during at least a portion of the year, as storage and accessibility to areas of winter productivity became increasingly important.

#### MIDDLE-HOLOCENE LAKE REGRESSIONS (8000–5000 <sup>14</sup>C YEARS B.P.)

During the middle Holocene, Great Basin lakes and their associated marsh systems were substantially reduced—and, at some times in some places, eliminated—by a combination of reduced annual precipitation and increased temperatures. This prolonged period was not, however, uniformly hot and dry, and there were a number of short-term intervals during which Great Basin lakes reached or even exceeded their historic average levels (e.g., Mehringer, 1986; Grayson, 1993). Moreover, even during the driest of mid-Holocene climatic intervals, when some of the largest Great Basin lakes may have dried up (e.g., Currey, 1980), it is unlikely that major marsh systems were eliminated completely. For that to happen, major Basin rivers would have had to cease flowing into their terminal basins. The larger marsh systems may have, at times, been reduced to the point where they could not support sedentary populations of any substantial size; and the more ephemeral marsh areas seem to have disappeared completely. Unfortunately, there is little

information available on mid-Holocene marsh sites in the Lahontan and Bonneville Basins, and it is difficult to evaluate the intensity of marsh use during this period. This may be because smaller terminal marsh habitats were located higher in the system and are now covered by later deposits.

Aikens and Madsen (1986) suggested that upland sites in the Bonneville Basin began to appear in large numbers during this time and that the upland strategy developed as the primary foraging approach used by most eastern Great Basin hunter-gatherers during the middle Holocene. Whether or not this pattern holds for the rest of the Great Basin is unclear. Grayson (1993) and Kelly (1997) suggested there was an overall reduction in the number of sites during this period but based this hypothesis on the number of radiocarbon dates for the period from cave sites, many of which were adjacent to marsh localities. Bettinger (1999), however, summarized chronologically sensitive projectile point data from a large number of sites (both open sites and cave/rock shelters) across the Great Basin and suggested that, in terms of numbers of points, which he uses as a proxy for population size, there was a significant increase during the middle Holocene compared with earlier periods (Figure 5). Many of these additional mid-Holocene sites are in upland areas, such as Steens Mountain, in the northeastern Great Basin.

Overall, population changes throughout the Holocene in the Great Basin appear to be related to a straightforward arithmetic growth curve (Figure 6) and not to climatically induced environmental change. Great Basin peoples seem to have merely shifted their adaptive strategy to cope with changes in the kinds

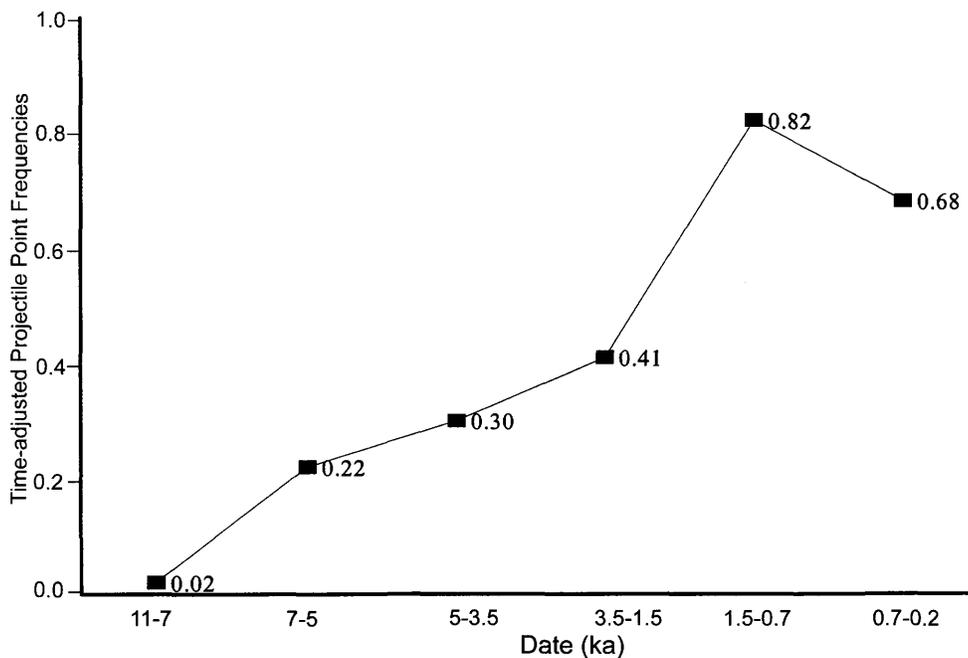


FIGURE 5.—Average time-adjusted frequencies of projectile points from 16 regional surface inventories in the Great Basin, used as a proxy for human population size through time. See Bettinger (1999) for derivation.

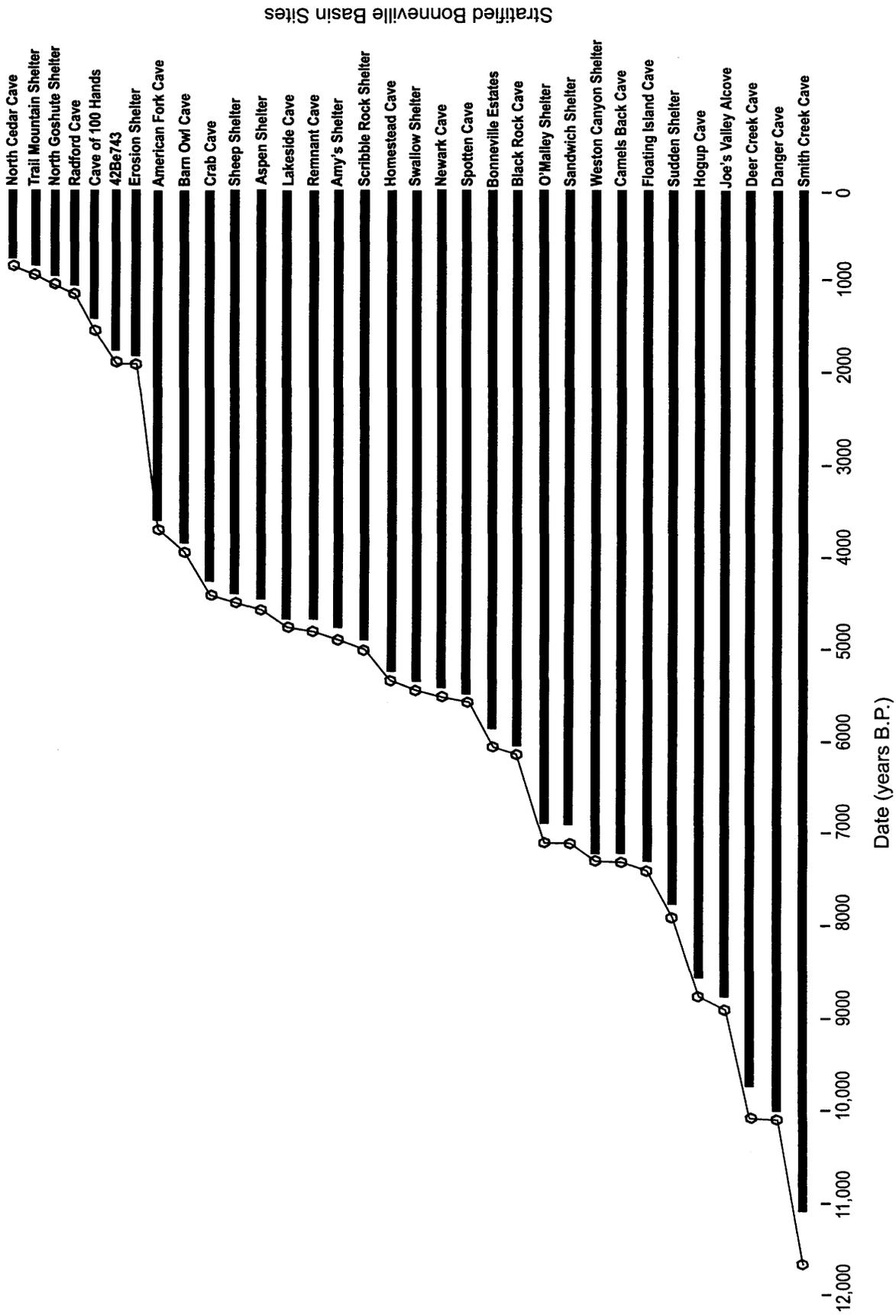


FIGURE 6.—Basal radiocarbon dates from stratified sites in and immediately adjacent to the Bonneville Basin. The distribution of these dates suggests a normal growth curve rather than a regional population decline during the middle Holocene.

and distribution of resources. Even during the middle Holocene, when human populations could be expected to have been most stressed, there seems merely to have been a shift from an emphasis on lowland strategies to an emphasis on upland strategies. Lowland strategies are most economically viable when marshes are large enough to sustain substantial groups of people for long periods. When they are not, people merely shift away from the marshes to a strategy that consists of more frequent moves to a variety of resource areas and a reduction in storage. How true this was in the Great Basin remains to be tested more empirically than through the use of poorly dated projectile points. The difficulty lies in finding a way to date the large numbers of open sites scattered throughout upland areas.

#### NEOPLUVIAL LAKES (5000–2500 <sup>14</sup>C YEARS B.P.)

Most sites in the marshes of the Bonneville and Lahontan Basins and the lake/marsh systems in the northwestern Great Basin date to the Neoglacial and later, when the size and productivity of these marsh systems were greatly enhanced (Raven and Elston, 1988; Janetski and Madsen, 1990; Aikens and Jenkins, 1994; Larson and Kelly, 1995; Zeanah et al., 1995). Smaller marsh systems in interior basin valleys (e.g., the Ruby Marshes) may also have been large enough to serve as the focus of a lowland foraging strategy during this period (e.g., Casjens, 1974; Thompson, 1992). The intensity of these occupations varied through time, in keeping with the episodic nature of environmental change (e.g., Wigand and Rhode, 2002; Oviatt, 2002 (this volume)). Some of these changes were both marked and abrupt. For example, between ~2000 and 3000 years ago Great Salt Lake rapidly transgressed to a highstand of 1287 m (4222 ft.) and flooded the Great Salt Lake Desert to the Utah–Nevada border (McKensie and Eberlie, 1987; Currey, 1990). During these periods of enhanced effective moisture, increased groundwater discharge at many spring-fed marshes, such as Ash Meadows in the southwestern Great Basin (Mehring, 1986), fostered marsh habitats sufficient to support small lowland populations.

Piñon became widespread throughout the Great Basin during this period (Wigand and Rhode, 2002) but the nuts were probably used only sparingly as a subsistence resource until very late in the prehistoric sequence, and then only in locations lacking extensive marsh habitats (Madsen, 1986; Kelly, 1997; Bettinger, 1999). This runs counter to Julian Steward's (1938) ethnographic model of Great Basin subsistence/settlement systems and to extensions of that model to much of the prehistoric sequence (e.g., Jennings, 1957; Thomas, 1985, 1988). The collection and storage of pine nuts does not appear to have been the central feature of Great Basin adaptive strategies during the Neoglacial, even though piñon had largely reached its modern configuration. Rather, limnosedentary strategies were widely employed, with piñon collection and upland strategies used in limited ways.

#### LATE-HOLOCENE ADAPTATIONS (2500–0 <sup>14</sup>C YEARS B.P.)

A principal period of occupation around Great Basin lakes dates to approximately one thousand years ago, when lake levels were again relatively high. In the Bonneville Basin, sites are so numerous on searches dating to this period that it has been informally referred to as the "Fremont" beach because of the predominant cultural materials associated with it. In the Lahontan Basin, this period corresponds to the Underdown Phase, when human occupation of the Carson/Stillwater marshes was at its greatest (Raven and Elston, 1988; Larson and Kelly, 1995; Zeanah et al., 1995). Similarly intensive use has been found around other Great Basin lake/marsh systems (e.g., Aikens and Jenkins, 1994).

Despite these favorable marsh conditions, however, evidence also exists of the extensive mobile use of upland areas throughout the late Holocene. This simultaneous pursuit of both foraging strategies by large numbers of Great Basin peoples appears to have been the result of population growth, with increasing pressure on marsh ecosystems making the upland approach more attractive. In the late Holocene there were simply too many people in the Great Basin, and less economically viable food sources began to be used. It was during this period that the use of piñon as a principal resource began, but this appears to have been related to an overall increase in the use of upland resources rather than to a sudden addition of pine nuts to the diet, and in areas outside the distribution of piñon there is also a contemporaneous increase in the use of upland resources. In the northwestern Great Basin, for example, an adaptive strategy based on upland root procurement developed in much the same way that central and southwestern basin peoples developed an extensive piñon-based upland strategy (Aikens and Jenkins, 1994). Bettinger (1999) suggested that storage became a more critical aspect of virtually all adaptive strategies during this period, including all the permutations of both the lowland and upland approaches, and it appears that mobility was reduced even in areas away from lake margin resources.

#### Great Basin Climatic Change and Human Adaptation

This sequence is very generalized and not greatly different from that identified 50 years ago by Ernst Antevs (1948). In many areas of the Great Basin, however, both environmental and cultural histories can be defined in much greater detail, and these chronologically more tightly controlled sequences do not match the rather broad categories he identified. The hot, dry mid-Holocene "Altithermal" of Antevs, for example, was not nearly as prolonged as he conjectured and was broken up by a number of moister intervals. More importantly, the Altithermal is no longer a blank page in the history of man in North America, and it is now evident that no regional abandonment of low elevation areas occurred. Rather, during such intervals as the Altithermal there was merely a subtle shift in emphasis between two widely used patterns of foraging be-

havior—patterns that had been in use throughout the human history of the Great Basin.

An equally important development during the last 50 years was the recognition of dramatic light-switch-like changes in climatic regimes during the Pleistocene/Holocene transition and in many parts of the Holocene. Antevs and his coworkers defined climatic changes in terms of rather sweeping curves, suggesting these changes were gradual enough to enable Great Basin peoples to adapt to different conditions during the passage of many generations. Now it is clear that a number of major environmental changes occurred within years or decades, certainly within the lifetime of single individuals, and prehistoric adaptive strategies must also have changed in an equally dramatic fashion.

The most common thread between the work of Antevs and that of today is the recognition of a clear correlation between environment change and the behavior of Great Basin hunter-gatherers. There is, however, a substantial difference in how this correlation was conceptualized then and how it is conceptualized now. Fifty years ago, Antevs and many of his coworkers believed in a simplified environmental determinism that had little or no theoretical basis and left no room for multiple behavioral options. Today, theoretically based models of foraging behavior provide a sound economic basis for understanding the evident link between Great Basin environments and prehistoric human behavior. These models suggest the archaeological record in the Great Basin is a product of people having made optimal choices in changing situations, situations that were largely influenced by environmental conditions around Great Basin lakes.

Among Great Basin middle-latitude hunter-gatherers, subsistence and settlement patterns were expressions of adaptive strategies structured around the procuring and storing of collectible foods that either did not have to be transported or for which transport costs could be minimized. This strategy focused on riverine and lacustrine marshes on valley floors, particularly where those marshes were large and stable. This resulted from the relatively large concentration of collectible resources in and near marsh ecosystems, a concentration that,

in the Great Basin, was caused by the differential distribution of water.

Virtually all major basin ecosystems contain one or more collectible and storable food resources whose energetic return rates are relatively high (ephemeral grasses on the foothills in the spring, roots and bulbs in the upper mountain zones during the summer, pine nuts in the piñon–juniper zone during the fall, etc.), but only desert marshes contain a variety of relatively high-ranked resources that are available in nearly every season of the year. Perhaps even more importantly, the concentration of these resources in close proximity would make transportation costs among them virtually nil, and they could be collected and stored together for winter use at almost no cost above that required by the collecting itself. Unless a single resource was productive enough to provide sufficient food for overwintering, as pine nuts may be in some locations every four to five years, individual resources from diverse environmental settings would have to be combined for winter use by transporting them long distances, hence adding substantially to their procurement costs.

In sum, it is possible to predict that Great Basin hunter-gatherers lived in or near major marsh areas for most of the time in most years. That does not mean that they lived a sedentary existence in the marshes or remained relatively immobile for long periods of time. To the contrary, because they maintained the flexibility and mobility that characterizes most hunter-gatherers, they could, and undoubtedly did, react to opportunities in other areas and moved when necessary. What the nature and distribution of the resources associated with many Great Basin lakes gave them was a stable base from which to operate. They could come and go from the marshes to collect grass seeds, roots and bulbs, and pine nuts when such items could be collected more productively than could the local marsh resources. But, unless such plants were abundant enough to support them for the rest of the year, they would return to the marshes again and again throughout the year, particularly in winter. In short, whenever large marsh habitats were available, Great Basin peoples were undoubtedly living in or adjacent to them for a significant part of every year—i.e., eight to nine months in most years.

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