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Middle to late Cenozoic geology, hydrography, and fish evolution in the American Southwest

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ABSTRACT

An evaluation of the poorly understood Cenozoic hydrologic history of the American Southwest using combined geological and biological data yields new insights with implications for tectonic evolution. The Mesozoic Cordilleran orogen next to the continental margin of southwestern North America probably formed the continental divide. Mountain building migrated eastward to cause uplift of the Rocky Mountains during the Late Cretaceous to early Tertiary Laramide orogeny. Closed drainage basins that developed between the two mountain belts trapped lake waters containing fish of Atlantic affinity. Oligocene-Miocene tectonic extension fragmented the western mountain belt and created abundant closed basins that gradually filled with sediments and became conduits for dispersal of fishes of both Pacific and Atlantic affinity. Abrupt arrival of the modern Colorado River to the Mojave-Sonora Desert region at ca. 5 Ma provided a new conduit for fish dispersal. Great dissimilarities in modern fish fauna, including differences in their mitochondrial deoxyribonucleic acid (DNA), indicate that late Miocene runoff from the Colorado Plateau did not flow down the Platte or Rio Grande, or through the Lake Bonneville Basin. Fossil fishes from the upper Miocene part of the Bidahochi Formation on the Colorado Plateau have characteristics that reflect a habitat of large, swift-moving waters, and they are closely related to fossil fishes associated with the Snake and Sacramento Rivers. This evidence suggests that influx of fishes from the ancestral Snake River involved a major drainage, not merely small headwater transfers.

Keywords: Colorado River, drainage evolution, fish evolution, continental divide, Bidahochi Formation.

INTRODUCTION

The middle to late Cenozoic evolution of rivers and drainages in southwestern North America occurred on a stage that was set by the previous 100 m.y. of geologic history and modified

by continued tectonic activity (Cowan and Bruhn, 1992; Miller et al., 1992; Christiansen and Yeats, 1992). This long geologic history can be divided into four major stages, as follows: (1) Late Jurassic and Cretaceous magmatism and faulting created a mountain belt adjacent to the southwestern edge of the North American

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continent that became a major drainage divide. The east side of this mountain belt includes the Cordilleran fold-and-thrust belt, which extends from southernmost Nevada through the Idaho-Wyoming border region and northward to Yukon Territory, and a complex and poorly understood belt of crustal thickening and magmatism that extends southeastward from southernmost Nevada through the Mojave-Sonora Desert region and into northern Mexico. (2) Latest Cretaceous to early Tertiary reverse and thrust faulting and magmatism during the Laramide orogeny formed the Rocky Mountains and created multiple basins, some of which trapped lake waters. (3) Oligocene-Miocene crustal extension generally reduced elevations and converted much of the mountain belt formed in stage 1 into numerous small ranges and intervening basins that now make up the Basin and Range tectonic and physiographic province. Voluminous magmatism at this time also modified landscapes. Drainages within this region were typically closed, and streams ended at playas or lakes. (4) During the last 10–15 m.y., Baja California and southwestern California have been displaced obliquely away from mainland Mexico, which has opened up the Gulf of California and provided an outlet to the sea for nearby drainages in the Basin and Range Province. This event also formed the Transverse Ranges in southern California.

The geologic record of river courses and evolution is remarkably poor. Typically, sediment accumulations derived from paleorivers cannot be associated with well-defined river catchments because of weak specificity of clast types with regard to source area. Furthermore, voluminous river-terminus sediment accumulations generally consist of sand and silt, and conglomerate clasts, if present at all, may represent only the most proximal sediment sources or the most resistant rock types. Incised river courses in intermountain areas typically leave little or no sediment accumulation along their upstream course, and paleoriver valleys and canyons may be obscured by tectonic disruption or erosional destruction, or they may be completely buried by volcanic and sedimentary rocks. Tectonic disruption and burial were so severe during Oligocene-Miocene extension and magmatism in the Basin and Range Province that almost nothing can be confidently stated about pre-late Cenozoic river courses and evolution from the geologic record in this area.

Fish distributions reflect Miocene to present drainage patterns and so potentially provide insight into drainage evolution. Fossil fish have been useful in determining the general form of past hydrography. For example, the Snake River drainage above Hells Canyon was inhabited by Sacramento and Klamath drainage faunas in the late Miocene and Pliocene, prior to capture by a tributary of the Columbia River in the late Pliocene (Smith et al., 2000). Patterns of relationships of modern fish species also reflect capture of neighboring streams by stream piracy (Kuehne and Bailey, 1961; Jenkins and Burkhead, 1993). Unequal erosion rates on watersheds promote stream capture and fish transfer from less erosive to more erosive systems. For example, early postglacial colonization of the Great Lakes drainage by warm-water fishes shows the location of stream captures from the

Susquehanna, Ohio, and Mississippi headwaters (C.L. Smith, 1985), while cold-water fishes indicate routes of entry through glacial outflow streams. The principle guiding this source of hydrographic evidence is that fishes readily colonize suitable habitats, usually through habitable waters, after gaining access. The ranges of freshwater fish species and genera may be restricted by variations in salinity, temperature, stream gradient, and current velocity, as well as competition and predation. The nature of past dispersal routes can be inferred from the morphological and physiological characteristics of the dispersed species or genera. For example, capture of small headwater drainages allows transfer of only small, usually cooler-habitat headwater species, so the kinds of species found across a drainage divide suggest the size and elevation of the aquatic connection. A latent pattern may remain for hundreds of thousands of years or more because of subtle ecological barriers and because evolutionary changes are usually slow and gradual in fishes—evolution of reproductive isolation takes thousands to millions of years in the groups considered here (Smith et al., 2002). The missing element from evidence of past connections, until recently, has been a measure of time.

Use of deoxyribonucleic acid (DNA) nucleotide sequences as a chronometer of branching points in fish evolution has provided a new tool for discerning the surface hydrologic history of drainage basins. Development of DNA sequencing technology and methods for using fossils to calibrate the rate of mutation accumulation allow the evolutionary divergence times between fish groups to be estimated on geological time scales. The segregation of freshwater fish faunas by the appearance of geographic barriers caused by tributary capture, desiccation, waterfalls, volcanism, or tectonics, is now subject to age estimates based on mitochondrial DNA (mtDNA) nucleotide-sequence chronometers.

Two similar expressions of genetic distances are in common use—pair-wise and single lineage rates of molecular substitution (the former is generally 2× the latter) (Swofford et al., 1996). In this method, the numbers of genetic substitutions, reported as percentage of nucleotide differences in homologous DNA sequences or modeled as maximum likelihood differences in phylogenetic tree-branch lengths, are determined and compared between isolated sister populations. For consistency, in this paper, we use the pair-wise percent sequence divergence between two sister lineages. This value, divided by time (divergence time estimated from available fossil occurrences in the lineages of interest), yields an approximate pair-wise rate of change for that gene in those fish (corrected for multiple changes at the same site by the method of Tamura and Nei, 1993). Geological time since the original population was split can then be estimated as the percent sequence divergence divided by the rate of sequence change. Standard deviations of such estimates often range between 10% and 25%.

Some variations in sequence-change rate occur as a function of metabolic rate, which is determined by temperature and body size (Martin and Palumbi, 1993; Gillooly et al., 2005). Small fish and inhabitants of warm southern or lowland waters have higher metabolic rates and may have higher mutation and substitution

rates (Estabrook et al., 2007; Smith and Dowling, this volume). Temperature and body-size estimates can be used to test precision of rate and time estimates. Smith and Dowling (this volume) demonstrate the use of maximum likelihood branch lengths to estimate the distance between taxa or branching nodes on a phylogenetic tree. Habitat temperatures and body size of each individual lineage can be compared with branch lengths to assess their correlation (Estabrook et al., 2007).

Fish DNA studies have turned up surprising hydrologic connections and estimates of their ages. For example, an estimated 1 Ma divergence between northern Mexican pupfish and those in the northeastern Mojave Desert region of southern California, assuming nucleotide substitution rates of around 3% per million years in these small, warm-water fishes, likely requires one or more stream captures that were not previously suspected from geologic studies (see Echelle, this volume). In addition, well-dated geologic events, such as the ca. 5 Ma integration of the modern Colorado River, provide possible opportunities to calibrate rates of DNA change in fish and other aquatic organisms.

This paper is an attempt to break new ground in understanding some issues regarding the biological, hydrological, and geological evolution of southwestern North America using geologic and paleontologic approaches as well as distributional and DNA studies of living fish. It is a direct outgrowth of a 2005 conference, held at California State University's Desert Studies Center at Zzyzx in the central Mojave Desert, on the geologic and biologic evolution of the American Southwest. The conference was organized by Marith Reheis (U.S. Geological Survey [USGS]), Robert Hershler (Smithsonian Institution), and David Miller

(USGS) to facilitate communication within a diverse group of scientists and to promote collaborative research.

OVERVIEW OF TECTONIC EVOLUTION OF THE SOUTHWEST

The present distribution and nature of tectonic provinces in southwestern North America (Fig. 1) reflect a long and complex geologic history. The western Great Plains are an undeformed relict of the low-relief, low-elevation, Paleozoic platform interior of the North American continent, now covered by thick post-Paleozoic sediments (Sloss, 1988; Burgess et al., 1997). The Colorado Plateau is a slightly to moderately deformed fragment of this Paleozoic platform that has been dramatically uplifted and, especially near its edges, buried by Cenozoic volcanic rocks. The other tectonic provinces were severely modified or largely created during the Mesozoic and Cenozoic eras. All of the Phanerozoic geologic processes that produced and modified the various tectonic provinces were either the result of plate-margin interactions or of late Cenozoic, dominantly basaltic magmatism, which was especially voluminous in the Snake River Plain–Yellowstone area and not obviously related to plate-margin tectonics (Burchfiel et al., 1992; area of “Flood basalts and related volcanics” in Fig. 1).

Mountain-building tectonic and magmatic processes that affected western North America for most, if not all, of Mesozoic time were related to subduction of Pacific Ocean lithosphere along the continental margin. Most of the granitic rocks that underlie the Sierra Nevada, western Mojave Desert, and Peninsular Ranges of southern California and northern Baja California were intruded during this time. These granitic rocks are exposed largely because overlying, comagmatic volcanic rocks were removed by erosion or assimilated by younger intrusions. Late Jurassic to Late Cretaceous magmatism was regionally associated with east-directed thrust faulting and folding east of the belt of magmatism, in a belt that extends from the Mojave Desert, across the southern tip of Nevada, through western Utah into westernmost Wyoming and southeastern Idaho, and northward through western Montana and western Alberta (e.g., DeCelles, 2004). Thick clastic sediment sequences were deposited both eastward in the thrust-belt foreland and westward along the continental margin (e.g., the Great Valley sequence), but they are absent in the axial zone of the orogen (e.g., Armstrong, 1972), except at scattered localities where, in at least some cases, clastic sediments were preserved beneath thrust sheets (e.g., Barth et al., 2004). Both crustal shortening and magmatism are inferred to have thickened the crust and thereby produced a large mountain range near the western edge of North America by the end of the Cretaceous (western mountain belt in Fig. 2A). In the Mojave-Sonora Desert region, erosion in the axial zone of this mountain belt uncovered metamorphic and granitic rocks (e.g., Burchfiel and Davis, 1981; Reynolds et al., 1988), many of which must have been exhumed by middle Cenozoic time, because they form the substrate for Oligocene-Miocene volcanic and sedimentary rocks (e.g., Spencer et al., 1995). In the Great Basin, erosion was

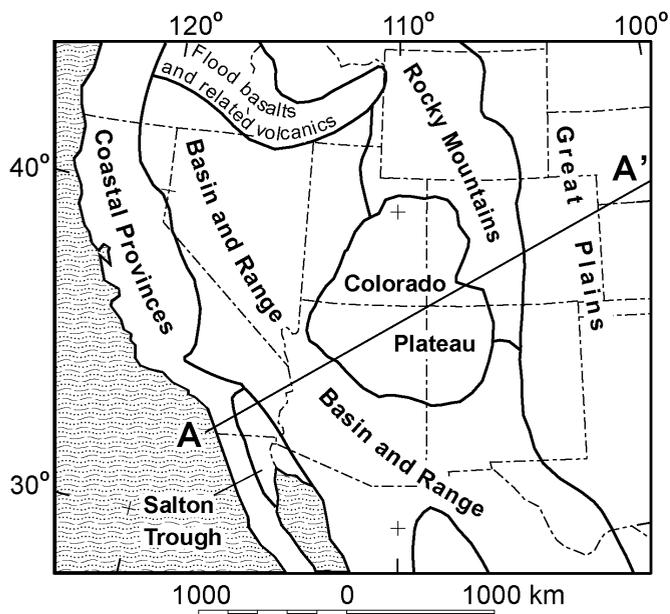


Figure 1. Tectonic provinces of southwestern North America. Cross section A–A' is shown in Figure 2.

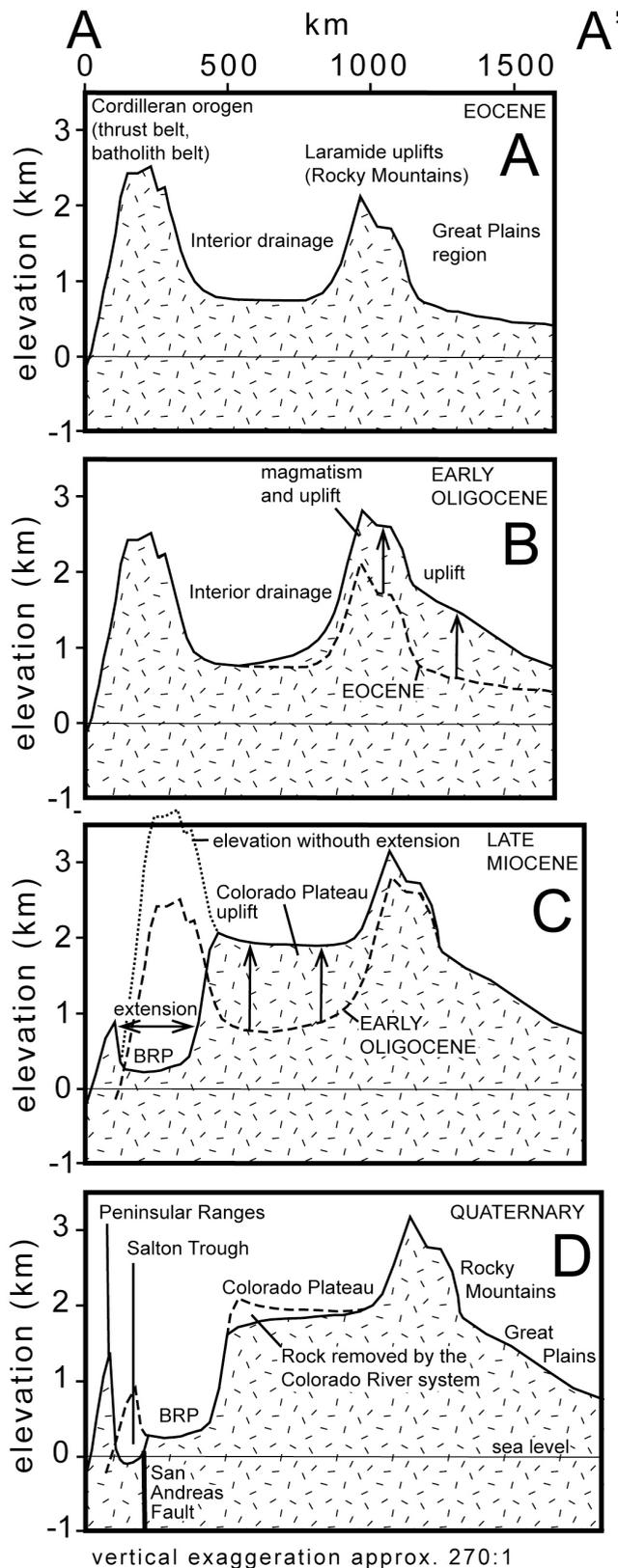


Figure 2. Cross-section diagram of southwestern North America showing changes in regional topography. Location of cross-section line is shown in Figure 1. Pre-Quaternary elevations are inferred based on diverse and in some cases conflicting evidence. BRP—Basin and Range Province.

generally not severe, and upper Paleozoic strata are commonly preserved beneath Paleogene sedimentary rocks (e.g., Armstrong, 1972; Vandervoort and Schmitt, 1990). High paleoelevations are suggested by general lack of thick Cretaceous and Paleogene sedimentary sequences, but paleobotanical evidence is contradictory (Wolfe et al., 1997, 1998; Axelrod, 1998). The high paleoelevations that would be necessary for Cretaceous nondeposition and erosion need not have been substantial if flanking areas were much lower than today, which was certainly the case for the continental interior.

Subduction-related faulting and magmatism migrated inland at ca. 75 Ma to initiate the Laramide orogeny, a Late Cretaceous to late Eocene period of faulting that uplifted the Rocky Mountains and was accompanied by sporadic magmatism (eastern mountain belt in Fig. 2A). Laramide faulting produced a complex pattern of uplifts and flanking basins (Dickinson et al., 1988; Miller et al., 1992). Some basins formed between the Laramide uplifts and the older, western mountain belt. Large Laramide basins include the Green River and Washakie Basins in southwestern Wyoming, the Uinta Basin in northeastern Utah, and the Piceance Creek Basin in northwestern Colorado (Fig. 3). These basins were at times closed and contain substantial lacustrine deposits (area of “internal drainage” in Fig. 2A; Surdam and Stanley, 1979; Johnson, 1985; Dickinson et al., 1988).

Changes in physiography within the tectonic provinces of southwestern North America were largely independent of changes in adjacent provinces due to the localized nature of deformation and magmatism. However, the regional rock and surface uplift that elevated the Colorado Plateau affected multiple provinces. The timing of this uplift has been especially difficult to discern from the geologic record because it was not associated with other clearly linked physiographic or geologic changes. A study based on the influence of air pressure on the size distribution of lava vesicles concluded that uplift had been largely post-Miocene (Sahagian et al., 2002), as have studies of the latest Miocene to early Pliocene Bouse Formation in the lower Colorado River trough, which infer deposition at or below sea level followed by Pliocene-Quaternary uplift to present elevations of up to 550 m (P.B. Smith, 1970; Todd, 1976; Lucchitta, 1979). The interpretation that the Bouse Formation was deposited in marine or estuarine environments is contradicted by geochemical data (Spencer and Patchett, 1997; Poulson and John, 2003). Furthermore, Bouse Formation deposition began with an influx of flood water derived from the north (House et al., 2005, this volume). An estuarine origin for the Bouse Formation requires a conspicuously fortuitous synchronization of floodwater influx from the north with abrupt marine inundation from the south, with spillover locations for these two events more than 200 km apart (Spencer et al., this volume). Some paleobotanical studies from areas peripheral to the Colorado Plateau suggest that uplift occurred before the middle to late Eocene (Gregory and Chase, 1992; Wolfe et al., 1998), whereas others suggest the opposite (Axelrod, 1998). Geodynamic and numerical studies infer thinning of the lithosphere beneath southwestern North America due to partial (Spencer, 1996) or complete (Bird, 1988) removal of the mantle lithosphere during

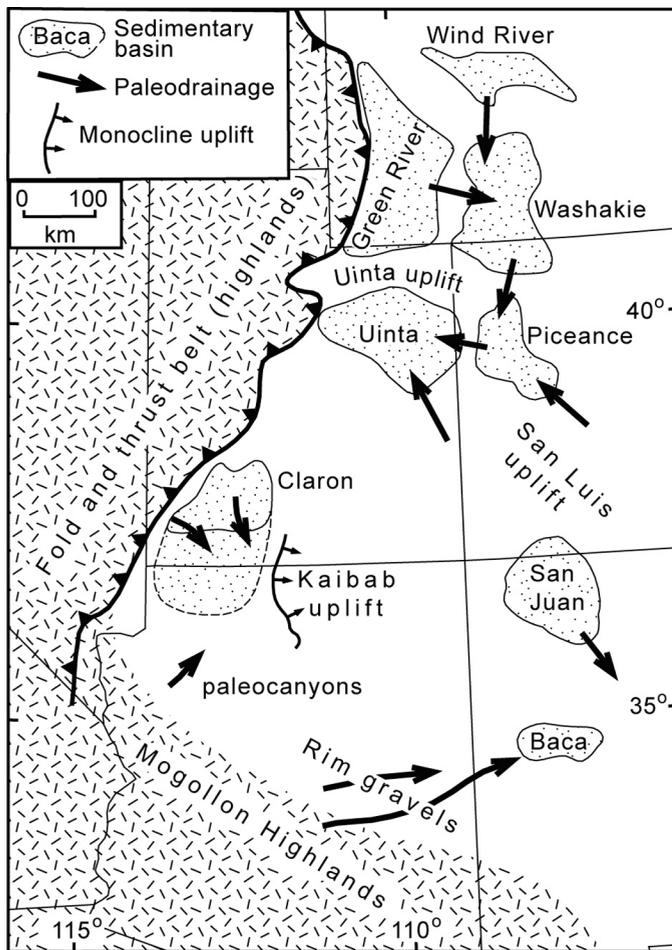


Figure 3. Early Cenozoic (Paleocene and Eocene) basins and sediment dispersal pathways (adapted in part from Dickinson et al., 1988).

Laramide low-angle subduction and replacement with hot, relatively low-density asthenosphere. Uplift due to lithosphere thinning would have occurred sequentially from latest Eocene in the Rocky Mountain region to early to middle Miocene beneath the westernmost Colorado Plateau, southern Great Basin, and Mojave-Sonora Desert region (Figs. 2B and 2C).

The Cretaceous western mountain belt was largely demolished by middle to late Tertiary crustal extension, and in some areas, it was intruded by magmas and covered by volcanic rocks. This crustal extension and volcanism produced the complex physiography of the Basin and Range Province (Fig. 1). Magmatism had migrated eastward during the Laramide orogeny, but then it migrated generally southwestward, so that it returned to what is now the Basin and Range Province during the middle to late Tertiary (Dickinson and Snyder, 1978; Cross and Pilger, 1978). To a first-order approximation, the western mountain belt was extended to double its previous width at the same time its crustal thickness was reduced by half (Hamilton and Meyers, 1966; Wernicke et al., 1982). Crustal thinning reduced relative elevations so that the mountain belt that formerly shed debris onto the Colorado Plateau is now mostly lower than the plateau (Fig. 2C).

Oligocene-Miocene extension in the Basin and Range Province was accompanied by termination of subduction along the southwestern edge of North America and initiation of a transform plate boundary between the Pacific and North American plates (Atwater and Stock, 1998). Plate-boundary transform displacement, initially accommodated by faults along the continental margin, jumped inland in the late Miocene (6–10 Ma) to initiate the southern and central segments of the San Andreas fault and the opening of the Gulf of California. This tectonic event transferred a long sliver of continent, consisting of Baja California and coastal California southwest of the San Andreas fault, from the North American plate to the Pacific plate. Plate divergence (in addition to dominant transform motion) caused the opening of the Gulf of California and Salton Trough and results in their continued widening (Fig. 2D; Lonsdale, 1989; Stock and Hodges, 1989; Oskin and Stock, 2003). A component of plate convergence along the San Andreas transform plate boundary east and north of Los Angeles is associated with reverse faulting and rapid uplift of the San Bernardino and San Gabriel Mountains (e.g., Morton and Matti, 1993; Sadler, 1993).

EOCENE CONTINENTAL DIVIDE

Uplift of the Rocky Mountains during latest Cretaceous to late Eocene time created basins between the Cordilleran thrust belt and the Rocky Mountains. Some of these basins trapped lake waters. Eocene fishes in the diverse fauna of the Green River Formation in southwestern Wyoming, as well as in basin sediments in southeastern British Columbia, belong to Atlantic drainage groups (Wilson, 1977; Grande, 1984). This is consistent with the concept that the coastal Mesozoic mountain belt became the continental divide long before uplift of the Rocky Mountains, and that by the time lake waters were trapped, only Atlantic-affinity fish had access to or were present in stream waters that fed these newly formed lakes.

Eocene southward transgression of fluviially transported clastic sediments, derived in part from Laramide volcanic rocks in the Absaroka volcanic field in northwestern Wyoming, closed off eastward outflow from the Green River and Washakie Basins and diverted outflow to the south into the Piceance Creek Basin and from there westward into the Uinta Basin (Fig. 3; Surdam and Stanley, 1980). The Uinta Basin received water from a large drainage catchment by middle Eocene time, and this water should have included a substantial volume of dissolved salts. It is not known if the basin was closed, but if it was, a considerable volume of salts should be present in its sediments. Doubts that the volume of evaporite sediments in the basin is sufficient to account for the likely riverine influx, and lack of viable outflow paths to the south or southeast, led Dickinson et al. (1988; see also Hansen and Dickinson, 1990) to propose that middle to late Eocene Lake Uinta waters drained westward across the thrust and batholith belts to deposit deltaic sediments in the Tye Formation in what is now coastal Oregon (Heller and Ryberg, 1983; Heller et al., 1987). Hansen (in Hansen and Dickinson 1990) noted, however, that most Eocene Green River Formation fish fossils (Grande,

1984) belong to eastern North American families that are unrepresented in Pacific drainages.

The upper Paleocene to late(?) Eocene Claron Formation in southwestern Utah includes a wide area of calcareous lacustrine strata with lake-margin clastic sediments derived from the west and east. Paleocurrent indicators and lateral facies changes indicate generally southward flow from floodplains in the north to a lake in the south, with bounding highlands on the east and west (Goldstrand, 1994). Northwestern Arizona north of the Colorado River has been stripped of all early Tertiary sediments, so the southward extent of the lake in which Claron lacustrine sediments were deposited is poorly constrained but could have been well south of the present Claron outcrop area (Fig. 3, dashed-line outline south of Claron Basin). This southern extension of the Claron Basin likely would have been bounded on the east by the Kaibab uplift, on the west by the Cordilleran fold-and-thrust belt, and on the south by the Mogollon Highlands.

The upturned southwestern edge of the Colorado Plateau, known as the Mogollon Rim, is a drainage divide separating catchments for the upper and lower reaches of the Colorado River. The low desert region southwest of the Mogollon Rim was much higher in the early to middle Tertiary and formed a mountainous area known as the Mogollon Highlands that shed clastic sediments northeastward onto what is now the Plateau (e.g., Peirce et al., 1979). The Mogollon Highlands were the northeast flank of the western mountain belt that was likely a segment of the continental divide until closed basins developed in the Eocene between the Rocky Mountains and the western mountain belt. Canyons cut into the western Mogollon Highlands that extend onto the plateau were probably conduits for sediment and water delivered to the southern part of the Claron Basin (Fig. 3; Young, 1979, 2001a, 2001b). Similarly, east of Phoenix, Arizona, a late Eocene to Oligocene eastward-flowing drainage system deposited sediments that grade from coarse conglomerate in eastern Arizona (Potochnik and Faulds, 1998; Potochnik, 2001) to lacustrine mudstone in the Baca Basin of central New Mexico (Cather and Johnson, 1984).

The middle Eocene to early Miocene(?) Sespe Formation in the Los Angeles Basin of California contains abundant rounded quartzite cobbles that have likely sources in the Mojave-Sonora Desert region. One distinctive type of quartzite cobble, however, contains abundant red jasper grains and resembles the early Proterozoic Mazatzal Quartzite northeast of Phoenix near the Mogollon Rim (Howard, 2000). As with the proposed Uinta-Tyee paleoriver, Howard's (2000) interpretation that the clasts were derived from the Mazatzal Quartzite requires a transporting river to cross the axis of the mountain belt left by Mesozoic orogenesis. This interpretation is problematic because there is good evidence that the Mazatzal Quartzite was located within an east-flowing drainage system. The Mazatzal Quartzite is not an extensive sedimentary blanket beneath the Paleozoic platform sequence but rather is exposed over a restricted area where it is folded and cut by thrusts of early Proterozoic age (Conway and Silver, 1989; Wrucke and Conway, 1987). Widely exposed early and middle Proterozoic rocks to the southeast, closer to Phoenix,

do not include exposures of Mazatzal Quartzite (Anderson, 1989; Richard et al., 2000). The aurally restricted exposures of Mazatzal Quartzite are located within or directly west of a large area that has been blanketed by late Eocene to Oligocene conglomerate deposited by the east-flowing river system that terminated in the Baca Basin of central New Mexico (Cather and Johnson, 1984; Spencer and Reynolds, 1989; Potochnik, 2001). Clasts in the conglomerate include Laramide volcanic rocks that must have come from the southwest of the Mazatzal Quartzite and closer to the axis of the western mountain belt (Peirce et al., 1979). This paleogeography places the Mazatzal Quartzite well northeast of the continental divide. Most of the area between exposures of Mazatzal Quartzite and coastal California and Baja California is now buried by Miocene volcanic rocks and Miocene or younger sediments. The distinctive quartzite clasts in the Sespe Formation could have been derived from sources in this area that were eroded away or are now buried.

In summary, Mesozoic (primarily Cretaceous) crustal shortening and magmatism created a mountain belt near the continental margin of southwestern North America that shed clastic debris into the thrust-belt foreland to the east and into forearc basins on the west. The Late Cretaceous to early Tertiary Laramide orogeny uplifted the Rocky Mountains and created basins between the Rocky Mountains and the western mountain belt. The Green River Basin, which is one of these basins, contains Eocene fossil fish that have Atlantic Ocean affinities and reveal no evidence of hydrologic connection to the Pacific Ocean. None of the other Laramide basins is known to contain fish with Pacific Ocean affinities. Proposed dispersal of Mazatzal Quartzite cobbles westward or southwestward across the western mountain belt to the Sespe Formation of the Los Angeles area is inconsistent with the position of the Mazatzal Quartzite within and at the head of a large, late Eocene to early Miocene, eastward-directed deposystem leading to the Baca Basin of central New Mexico. The distinctive quartzite clasts in the Sespe Formation were possibly derived from closer sources in the Mojave-Sonora Desert region that are now buried or were eroded away. Further evaluation of the two proposed Eocene drainages that carried sediments across the axis of the western mountain belt is now possible with detrital-zircon geochronology.

BASIN AND RANGE PROVINCE

The late Mesozoic mountain range along the western margin of southwestern North America was drastically modified by middle to late Cenozoic normal faulting and crustal thinning. This tectonic event produced the Basin and Range tectonic province, which is that region that was extended by normal faulting and that now has a characteristic basin and range topography. The province extends from southeastern Oregon and southern Idaho to central Mexico, and includes the Mojave-Sonora Desert region (Fig. 1; Stewart, 1998; Stewart et al., 1998). Voluminous volcanism accompanied Basin and Range tectonism, and many ranges consist largely of middle Tertiary volcanic rocks. Normal faulting continues in seismically active western Nevada, in the region

between Death Valley and Owens Valley in California, and along the Wasatch Front in Utah.

The dearth of early Tertiary sedimentary rocks in the Basin and Range Province can be attributed to its high elevations (see Wolfe et al., 1997, for paleobotanical evidence of past high elevations). Rivers generally carry sediments away from mountain highlands and deliver them to flanking lowlands and to marine environments, thus leaving little or no sedimentary record of their presence in upland areas. This was true of most of the area that was extended to form the Basin and Range Province, with a few exceptions in the Great Basin (Vandervoort and Schmitt, 1990). Crustal thinning associated with largely Oligocene-Miocene normal faulting reduced elevations and broke apart older drainages. Sediment traps were formed within numerous extensional basins. Closed-basin conditions are indicated by evaporite deposits, most of which are still buried (e.g., Peirce, 1976; Faulds et al., 1997). Eventually, the Basin and Range Province became partially bounded by the topographically higher Sierra Nevada, Colorado Plateau, and the Peninsular Ranges, thus increasing sediment accumulations within the province and decreasing or eliminating sediment transport away from the province. As filling continued, isolated basins merged with adjacent basins, so that merged basins now surround many small mountain ranges within the Basin and Range Province. Volcanic fields also modified or blocked preexisting drainages, buried preexisting landscapes, and delivered volcanic flows and tuffs to basins. As a result of severe middle Cenozoic landscape modification, pre-Pliocene drainage patterns vary from poorly known to completely unknown.

The Colorado River, which is the largest river to cross the Basin and Range Province, established its present course at ca. 5 Ma, well after Oligocene to middle Miocene extension and volcanism. The drainage that delivered quartzite clasts to the middle Cenozoic Sespe Formation in the Los Angeles area (Howard, 2000) has been interpreted as the “ancestral Colorado River offset by the San Andreas fault” (Howard, 1996, p. 783). This interpretation is problematic for several reasons: (1) Howard (1996, Fig. 1) shows the “Sespe delta” as occupying the Los Angeles Basin and areas westward along the coast to about Santa Barbara. However, disruption by faulting and 55° to 85° vertical-axis rotation of fault blocks created the Los Angeles Basin after Sespe deposition, so the Sespe-age depositional system is unrelated to the modern geometry of the Los Angeles Basin (Dickinson, 1996). Furthermore, paleocurrent directions northwest of Los Angeles, restored for postdepositional rotations, indicate sediment dispersal dominantly southward along the continental margin, not radially westward and southwestward from the apex of a delta (Dickinson, 1995). (2) Howard (1996) inferred that San Gorgonio Pass, which is now a drainage divide that separates the Los Angeles Basin from the Salton Trough, is a paleovalley eroded by the ancestral Colorado River. However, the rocks on opposite sides of the pass were juxtaposed by displacements within the San Andreas fault system, so the pass could not have existed in its present form until the late Quaternary (Powell, 1993). (3) Howard (1996, p. 783–784) inferred that the distribution of the latest Miocene to early Plio-

cene Bouse Formation reflects a preexisting “paleovalley that extends southeastward from Death Valley to Vidal Valley” and that the paleovalley had a “branching pattern” that “represents the drowned mouth of a well-integrated ancestral Colorado River system.” However, outcrop and well data indicate that the Bouse Formation was deposited across multiple, formerly closed basins separated from each other and from the sea by bedrock highs (Metzger et al., 1973; Metzger and Loeltz, 1973; Buising, 1990; House et al., 2005). These intervening bedrock highs were not up-faulted in post-Bouse time, since the Bouse Formation is not cut by any substantial faults. In conclusion, upper Eocene and Oligocene strata in the greater Los Angeles area could have been derived from areas now drained by the Colorado River and its tributaries, but the rivers that carried these sediments do not appear to have any modern geomorphic remnants.

INFLUX OF FISH

The drainage integration that followed and possibly accompanied middle Tertiary landscape and drainage modification in the Great Basin was associated with influx and mingling of fish species from both Atlantic and Pacific domains. Evidence from fossil fish distributions suggests Miocene north-south hydrologic connections between the Great Basin and adjacent areas. Topminnows (Fundulidae), which have connections to western Mexico (Doadrio et al., 1999), were uncommon but widely distributed in Nevada in the middle to late Miocene (Smith et al., 2002). Muskellunge (*Esox*) of the 11 Ma Deer Butte Formation, southeast Oregon (Cavender et al., 1970), are related to *Esox columbianus* of the Pliocene Ringold Formation in south-central Washington (Smith et al., 2000). Minnows (Cyprinidae), charrs, and trout (Salmonidae) from the Miocene of western Nevada had connections to middle Miocene Clarkia beds of the St. Maries drainage, west-central Idaho, and these genera plus suckers occur in the late Miocene Chalk Hills Formation of southwest Idaho and southeast Oregon (Miller and Smith, 1981; Smith and Miller, 1985; Smith et al., 1982, 2002). Much of east-central Nevada (see following) has been linked with drainages to the south at several times during the Miocene and Pliocene, as indicated by speckled dace, spinedace, spikedace, Sonora suckers, and desert suckers, which are shared among the White, Meadow Valley Wash, Virgin, Gila, and Salt drainages (Fig. 4; Hubbs and Miller, 1948; Miller and Hubbs, 1960; Smith, 1966, 1981; Reynolds and Lindsay, 1999).

Late Miocene and Pliocene fossils indicate development of east-west drainage systems. The diatomite-bearing, late Miocene Truckee Formation in northwestern Nevada contains fossil sticklebacks (Gasterosteidae), which are small, lowland fishes requiring west-flowing Pacific coastal connections (Bell, 1994). Late Miocene catfish (Ictaluridae) in the Truckee Formation and sunfish (Centrarchidae) in Windemere Hills of north-central Nevada are lowland, warm-water fishes with relatives in the Mississippi Basin (Baumgartner, 1982; Smith et al., 2002). Eastern fishes probably crossed the continental divide north of the Colorado

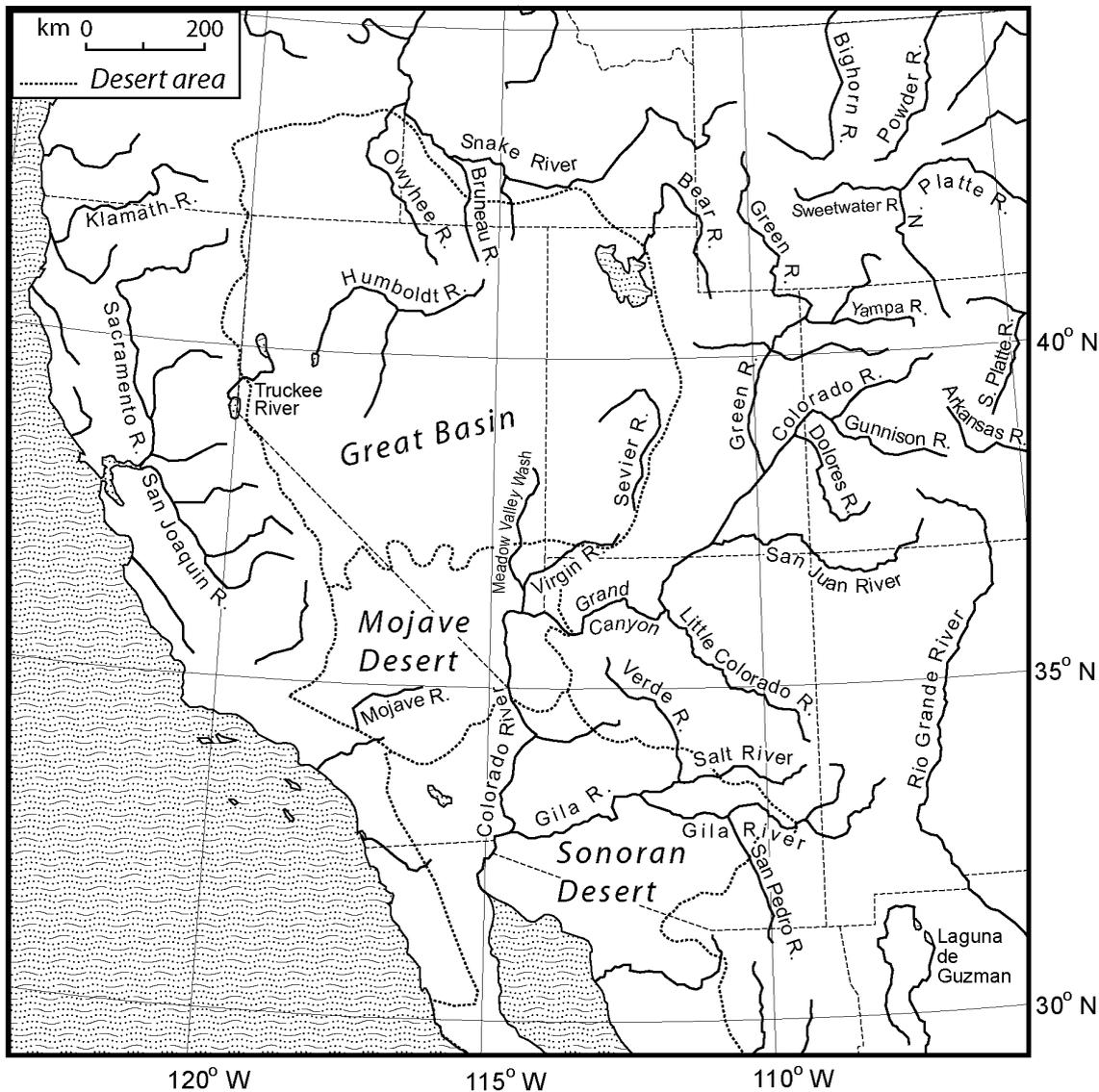


Figure 4. Major rivers of southwestern North America. The late Miocene Chalk Hills Formation is on the south side of the Snake River from the Bruneau River, Idaho, to the Owyhee River, Oregon. The Pliocene Glens Ferry Formation is exposed in the same approximate area but extends somewhat farther upstream and downstream along the Snake River. The Truckee Formation is exposed near the Truckee River in northwestern Nevada.

Plateau, perhaps through rivers that are now part of the Missouri drainage, rather than south, according to congruent distributions of other northern fishes, as well as snails, *Juga*, *Bellamya*, *Bulinna*, and others (Figs. 7–9 and 15 in Taylor, 1985). The Miocene snail, *Valvata idahoensis* (Figs. 12 and 15 in Taylor, 1985), suggests a Miocene drainage connection from the Bonneville Basin to the lower Colorado River Basin in the southernmost Great Basin of Nevada. Bonneville Basin and possibly upper Snake River fish were also connected to the lower Colorado River in the Pliocene, according to mtDNA evidence in speckled dace, spinedace, and leatherside chubs (Dowling et al., 2002; Smith et al., 2002; Smith and Dowling, this volume).

In late Miocene time, diverse minnows, suckers, catfish, and sunfish with relatives in the Snake River Plain were established in a separate basin (Cache Valley Member of the Salt Lake Formation; Long et al., 2006) in northwestern Utah (McClellan, 1977). Middle to late Miocene separation of these fishes is possibly due to uplift of the central Snake River Plain region during eastward migration of the Yellowstone hotspot, and development of south-flowing drainages on the east flank of this uplift (see Beranek et al., 2006). These fishes and associated snails were also part of the Columbia-Snake Rivers and northern Great Basin aquatic faunas at that time (Taylor, 1985). These late Miocene–Pliocene faunas comprise the historically richest aquatic diversity

west of the continental divide in North America and were generally richer than are modern faunas of the area, indicating more abundant and stable aquatic habitats.

In the late Pliocene and early Pleistocene, cooling climates permitted cutthroat trout from western coastal streams to gain access to the eastern Great Basin, upper Colorado River, and Rio Grande drainages (Rogers et al., 1985; Smith et al., 2002), where they persisted through the Pleistocene (Meade et al., 1982) to the Holocene. Pliocene and Pleistocene waters in the Lahontan, Bonneville, and southeast Oregon parts of the Great Basin frequently flowed to the Snake, Sacramento–San Joaquin, and Columbia drainages, especially when pluvial lakes topped drainage divides (Reheis et al., 2002; Smith et al., 2002; Negrini, 2002; Smith and Dowling, this volume).

MIOCENE DRAINAGE OF THE COLORADO PLATEAU

By far, most of the water carried by the Colorado River is derived from the Colorado Plateau and southern Rocky Mountains. The Colorado River did not exit the Colorado Plateau at the Grand Wash Cliffs before ca. 5 Ma, and it is not known where, and if, Colorado Plateau runoff exited the Colorado Plateau before this time.

RELATIONSHIPS AMONG THE GREEN, PLATTE, AND SNAKE RIVERS

Because of proximity and inferred past connections of the upper Green River to the upper Platte River (Fig. 4; e.g., Hansen, 1985), it might seem feasible that some of the Miocene upper Colorado River Basin drained through the Platte. This is precluded for the late Miocene and subsequent periods, however, by the great dissimilarity of fish fauna in the two river systems. Only one species and two genera occur in both the South Platte and Green Rivers. The one common species is the mountain sucker (*Catostomus platyrhynchus*), a headwater inhabitant that is found over a wide area from the Black Hills west to the Willamette Valley of Oregon, as well as in the Pleistocene of Nebraska. The other 38 species in these rivers (27 in the Platte, 11 in the Green) have not crossed the drainage divide except by recent human action. Because of the striking dissimilarity in fish species, it is very unlikely that a significant fraction of the Green or Colorado River drainage basins drained down the Platte in the Miocene.

The relationships of the modern Green River fishes connect to fishes in the Colorado and Snake Rivers (Table 1). The Green River shares all of its species with the Colorado River and seven of its 13 species and seven of eight genera with the Snake River drainage. The seven species are also shared with the Bear River of the Bonneville drainage (see Fig. 8 in Hansen, 1986). The pike-minnow genus, *Ptychocheilus*, however, occurs only in the Green, Colorado, and Sacramento drainages, as well as the Columbia drainage and adjacent areas to the north. Other geographic relationships of Green River genera are also significant—the razorback sucker, *Xyrauchen*, of the Green and Colorado Rivers is related to lake suckers, *Chasmistes*, and the Lost River

sucker, *Deltistes*, of the Miocene and Pliocene Snake River Plain and Klamath River (Smith, 1992). The flannelmouth sucker, *Catostomus latipinnis*, of the Green and Colorado Rivers is related to the largescale sucker, *Catostomus macrocheilus*, of the Snake-Columbia River, and Utah sucker, *Catostomus ardens*, of the Bonneville Basin.

The Snake River above Shoshone Falls, a late Pleistocene, 65-m-high waterfall near Twin Falls, Idaho, has 12 living species including mountain whitefish (*Prosopium williamsoni*), cutthroat trout (*Oncorhynchus clarki*), Utah chub (*Gila atraria*), reddsideshiner (*Richardsonius balteatus*), leatherside chub (*Snyderichthys copei*), speckled dace (*Rhinichthys osculus*), longnose dace (*Rhinichthys cataractae*), Utah sucker (*Catostomus ardens*), mountain sucker (*Catostomus* [*Pantosteus*] *platyrhynchus*), bluehead sucker (*C.* [*Pantosteus*] *discobolus*), mottled sculpin (*Cottus bairdii*), and Paiute sculpin (*Cottus beldingi*). All of these were exchanged, in one or both directions across Redrock Pass (Gilbert, 1890), by the Bonneville flood, dating from 15 ka (Oviatt et al., 1992). Seven fossil species, including four of the above, plus a chiselmouth chub (*Acrocheilus* sp.), northern chub (*Ptychocheilus oregonensis*), and sunfish (*Archoplites*), are known from sediments associated with the Bonneville flood near American Falls on the Snake River (Hearst and Smith, 2002). Six of the Snake River species are represented in the Green River (and one additional form lives in the upper Colorado River but not the Green River) (Table 1). Four Bonneville Basin species and three Pleistocene species are unknown in the Green-Colorado drainage, although three of the four Snake River genera (pikeminnows, *Ptychocheilus*, chubs, *Gila*, and suckers, *Catostomus*) have relatives there (Table 1).

The faunal similarity of the Green River fauna to the upper Snake River fauna is greater than the similarity of the upper Snake River drainage to the lower Snake drainage or the upper Colorado drainage to the lower Colorado drainage (Table 1). Similarity of any part of the Colorado River to the Platte is, by comparison, miniscule, suggesting a strong barrier throughout the Miocene. The generic relationships of Green River to Snake River fauna suggest a substantial middle to late Miocene connection (not necessarily contemporaneously) through the Snake to the Sacramento River drainage. The most likely current hypothesis suggests that the paleo-Green River, headed in eastern Idaho, was draining the central Idaho thrust belt at ca. 15 Ma (Fig. 7 in Beranek et al., 2006). Northeastward migration of the Yellowstone hotspot bulge at ca. 15–4 Ma divided eastern and western Idaho (Pierce and Morgan, 1992; Figs. 8 and 9 in Beranek et al., 2006), isolating the Green River from western Snake River Plain lineages of *Ptychocheilus*, *Gila*, and *Catostomus*. DNA evidence suggests that the Green River and Snake River *Ptychocheilus* were isolated from each other and from the Sacramento population ca. 15 Ma (see following).

RELATIONSHIP OF THE UPPER COLORADO TO THE RIO GRANDE

Possible late Miocene drainage of the upper Colorado River through the valley of the Little Colorado River to the Rio Grande

TABLE 1. FISH SPECIES COMPOSITION OF FAUNAS ABOVE AND BELOW GRAND CANYON

Common name	Genus and species	Other occurrences, restrictions, or relationships
<u>Species inhabiting both upper and lower Colorado River drainages</u>		
Speckled dace	<i>Rhinichthys osculus</i>	Originally from Snake-Columbia in the Pliocene
Colorado pikeminnow	<i>Ptychocheilus lucius</i>	Colorado River endemic, Late Miocene Bidahochi Formation, Arizona
Roundtail chub	<i>Gila robusta</i>	Late Miocene Bidahochi Formation, Arizona
Bonytail chub	<i>Gila elegans</i>	Colorado River endemic
Humpback chub	<i>Gila cypha</i>	Colorado River endemic, Late Miocene Bidahochi Formation, Arizona
Bluehead sucker	<i>Catostomus discobolus</i>	Upper basin to Granite Park, Snake and Bonneville drainages
Flannelmouth sucker	<i>Catostomus latipinnis</i>	Colorado River endemic, Pliocene, Snowflake, Arizona
Razorback sucker	<i>Xyrauchen texanus</i>	Colorado River endemic, Pliocene, southern California
Cutthroat trout	<i>Oncorhynchus clarkii</i>	Upper Colorado drainage, Snake River, Virgin River, Pliocene, Nevada
<u>Species inhabiting upper Colorado, Green, and other Colorado Plateau drainages</u>		
Mountain sucker	<i>Catostomus platyrhynchus</i>	Bonneville, Lahontan, Snake-Columbia, Fraser, Missouri
Mountain whitefish	<i>Prosopium williamsoni</i>	Originally from Snake-Columbia drainage
Mottled sculpin	<i>Cottus bairdii</i>	Originally from Snake-Columbia drainage
Paiute sculpin	<i>Cottus beldingi</i>	Upper Colorado River, originally from Snake-Columbia drainage
Little Colorado spinedace	<i>Lepidomeda vitatta</i>	Little Colorado River endemic, relationships to Basin and Range
<u>Species inhabiting Basin and Range Province and Gila-Salt drainages</u>		
White River chub	<i>Gila jordani</i>	Pluvial White River endemic
Virgin chub	<i>Gila seminuda</i>	Virgin River endemic
Moapa dace	<i>Gila (Moapa) coriacea</i>	Muddy River endemic
Virgin spinedace	<i>Lepidomeda mollispinis</i>	Virgin River—Meadow Valley Wash endemic
Pahrnanagat spinedace	<i>Lepidomeda altivelis</i>	Pluvial White River endemic
White River spinedace	<i>Lepidomeda albivalis</i>	Pluvial White River endemic
Spikedace	<i>Meda fulgida</i>	Gila-Salt drainage endemic
Woundfin	<i>Plagopterus argentissimus</i>	Virgin, Muddy, Gila-Salt drainage endemic
Loach minnow	<i>Tiaroga cobitus</i>	Gila-Salt endemic
Longfin dace	<i>Agosia chrysogaster</i>	Bill Williams, Gila-Salt, south into Mexico
Desert sucker	<i>Catostomus clarki</i>	Lower basin endemic
Sonora sucker	<i>Catostomus insignis</i>	Lower basin endemic, Gila-Salt, and formerly Virgin River
Gila trout	<i>Oncorhynchus gilae</i>	Gila-Salt endemic, from California or Mexico in Pleistocene
Apache trout	<i>Oncorhynchus apache</i>	Salt, Little Colorado River drainages, derived from Gila River in the Pleistocene
Railroad Valley springfish	<i>Crenichthys nevadae</i>	Railroad Valley endemic
White River springfish	<i>Crenichthys baileyi</i>	Pluvial White River Valley endemic
Pahrump killifish	<i>Empetrichthys latos</i>	Pleistocene Moapa drainage, Holocene Pahrump Valley, Nevada
Desert pupfish	<i>Cyprinodon macularius</i>	Lower Colorado, Gila-Salt, Salton Sea drainages, Sonora
Gila topminnow	<i>Poeciliopsis occidentalis</i>	Gila-Salt drainage, originally from Mexico

(McKee et al., 1967) was considered and rejected by Hunt (1969) and is inconsistent with fish evidence. The Colorado River drainage (25 fish species) and Rio Grande drainage (55 fish species) have only two species in common, the cutthroat trout, which arrived in the Pleistocene (Behnke, 1992), and Zuni mountain sucker, which is implicated in Pleistocene stream capture and hybridization (Smith et al., 1983).

Two genera, *Gila* (chubs) and *Catostomus* (suckers), have related species across the divide between the two drainages. A comparison of mitochondrial DNA (mtDNA) among species of these genera allows estimation of the last time since there was a significant hydrographic connection (Table 2). The chubs, *Gila pandora* and *G. nigrescens*, of the Rio Grande and Guzman (Chihuahua) drainages can be compared with the chubs *Gila robusta*,

G. elegans, *G. cypha*, and *G. coriacea* of the Colorado drainage. The cytochrome *b* (*cytb*) genes of the mtDNA of these lineages differ by an average of 10.1% across the drainage divide. An average rate of nucleotide sequence divergence of these six species is 1.1% per m.y., calibrated with fossil ages of large western minnows (Smith et al., 2002). When that rate of change is applied to the mtDNA nucleotide differences between chubs (*Gila*) in the Colorado River and Rio Grande drainages, the minimum age of lineage segregation by the drainage divide is estimated to be 9.2 m.y. (10.1%/1.1% m.y.⁻¹). The *cytb* mtDNA of Sonora and flannelmouth suckers (*Catostomus insignis* and *C. latipinnis*) of the Colorado River drainage differs from the related white sucker (*Catostomus commersoni*) of the Rio Grande drainage by 10.9% and 11.1%, respectively. Using an estimated mtDNA evolution-

TABLE 2. AGE ESTIMATES FOR DRAINAGE ISOLATION EVENTS

	Sequence divergence (%)	Rate (% m.y. ⁻¹)	Estimated age (Ma)
<u>Rio Grande drainage isolation from Colorado River drainage</u>			
<i>Gila pandora</i> and <i>G. nigrescens</i> (Rio Grande and Guzman drainage) vs. <i>Gila robusta</i> , <i>G. elegans</i> , <i>G. cypha</i> , and <i>G. coriacea</i> (Colorado River drainage)*			
Test	10.1 (S.D. = 3.0)	1.1 (S.D. = 0.2)	9.2
<i>Catostomus insignis</i> and <i>C. latipinnis</i> (Colorado drainage) vs. <i>Catostomus commersoni</i> (Rio Grande drainage) [†]			
	10.9 and 11.1	1.17	9.4
<i>Catostomus (Pantosteus) discobolus</i> and <i>C. clarki</i> (Colorado drainage) vs. <i>Catostomus (Pantosteus) plebeius</i> (Rio Grande drainage) [†]			
	10.0 and 9.7	1.17	8.4
<u>Divergences within the Lower Colorado River basin</u>			
Age of origins of divergence among genera: <i>Meda</i> , <i>Lepidomeda</i> , and <i>Plagopterus</i> [§]			
	29–36	3.4	8.5–10.6
<u>Comparison of upper and lower Colorado River Basin lineages</u>			
<i>Catostomus (Pantosteus) clarki</i> (lower Colorado drainage) vs. <i>C. (P.) discobolus</i> (upper Colorado drainage) [†]			
	2.9–4.0	1.17	2.5–3.4
Rate if these two species were isolated by Grand Canyon at 5.5 Ma:			
	2.9–4.0	0.53–0.73	N.A. [#]
<i>Catostomus insignis</i> (lower Colorado drainage) vs. <i>Catostomus latipinnis</i> (originally upper Colorado drainage) [†]			
	6.1	1.17	5.2
Rate if these two species were isolated by the Grand Canyon at 5.5 Ma:			
	6.1	1.11	N.A. [#]
<i>Gila coriacea</i> (Lower Colorado drainage) vs. <i>Gila robusta</i> (originally upper Colorado drainage)*			
	7.7	2.7 (1.7+1.1)	2.9
Rate if these two species were isolated by the Grand Canyon at 5.5 Ma:			
	7.7	1.4	N.A. [#]
<u>Los Angeles Basin isolation from lower Colorado River drainages</u>			
<i>Rhinichthys osculus</i> (Los Angeles Basin) vs. <i>Rhinichthys osculus</i> (Gila River drainage) [§]			
	7.1 (S.D. = 0.4)	3.8	1.9
<i>Gila atraria</i> (Bonneville Basin) vs. <i>Gila orcutti</i> (coastal southern California)**			
	8.3	1.8	4.6
<i>(Pantosteus) santaanae</i> (Los Angeles Basin) vs. <i>C. (Pantosteus) clarki</i> (lower Colorado River drainage)**			
	9.2	1.8–2.1	4.4–5.1

Note: Age estimates for drainage isolation events are based on fish *cytb* mtDNA differences (distances) between separated sister lineages. Rates are calibrated with Miocene and Pliocene fossil ages (Smith et al., 2002) corrected with the method of Marshall (1990).

*Estimated rate based on divergences of several genera of western cyprinids (oldest of eight time horizons = 14 Ma; corrected age = 16.4 Ma; method of Marshall, 1990). Average rate = 1.1% per m.y.

[†]Estimated divergence of *Pantosteus* from its sister subgenus *Catostomus* occurred at 12 Ma (oldest *Catostomus* of eight time horizons = 11 Ma; corrected age = 12 Ma; method of Marshall, 1990). A sample of 28 mtDNA distances between the sister groups averages 22.0% (standard deviation [S.D.] = 2.2%). Rate = 22% per 12 m.y. = 1.8% per m.y.

[§]Estimated divergence time based on southern *Rhinichthys osculus* rates calibrated with fossil *R. osculus* from the Snake River Plain (fossil age = 4 Ma, the oldest of three time horizons; corrected age of divergence = 6.3 Ma; method of Marshall, 1990).

[#]N.A. = not applicable.

**Estimated using previous methods but modified to take into account small body size and faster rate (Estabrook et al., 2007).

ary rate of change of 1.17% per m.y., this difference yields an estimated age of evolutionary divergence of 10.0 Ma (Table 2). The bluehead and desert suckers, *Catostomus (Pantosteus) discobolus* and *C. (P.) clarki*, of the Colorado River drainage differ from the Rio Grande sucker, *Catostomus (Pantosteus) plebeius*, by 10.0% and 9.7%, respectively, for an estimated age of evolutionary divergence of 9.0 Ma (Table 2). Thus, genetic relationships indicate fish exchange between the drainages at ca. 9–10 Ma, but

the dissimilarity of most of the rest of the species in these two drainages suggests that the two drainage basins were distinct well before that time.

BIDAHOCHI FORMATION

The alternative to late Miocene external drainage of Colorado Plateau waters is that plateau drainages may have terminated in

one or more Colorado Plateau lakes, one of which could be represented by the middle Miocene to lowermost Pliocene(?) Bidahochi Formation on the southern Colorado Plateau (e.g., Love, 1989; Gross et al., 2001; Dallegge et al., 2003). Fossil fish evidence factors importantly into this hypothesis. The Colorado pikeminnow (*Ptychocheilus*), the fossil genus *Evomus*, and Colorado River chubs (*Gila robusta* and others) were described from several upper Bidahochi fossil localities near Roberts Mesa, White Cone Peak, and Coliseum Diatreme by Uyeno and Miller (1965). An examination of additional fossils from these localities in the collections of the Museum of Northern Arizona reveals added details. Based on the unique grinding teeth as well as serrated and rounded cleithrum, *Evomus* is a synonym of the blackfish, *Orthodon*, a 30–40-cm-long minnow from the Sacramento River drainage (California) that is known from fossils in the Miocene Chalk Hills Formation and Pliocene Glenns Ferry Formation in the western Snake River Plain (Smith et al., 1982). A concave frontal and elongate pharyngeal arch and teeth are identifiable as *Gila cypha*, the 30–40-cm-long humpback chub that is adapted to the large, swift rivers of the Colorado Plateau and their larger tribu-

aries, including the Yampa, Dolores, and San Juan. Additional isolated bones appear to represent large species in the cyprinid genera *Pogonichthys* (splittail), also of the Sacramento River system, and *Lavinia* (hitch) of the Sacramento drainage and the Miocene and Pliocene Snake River Plain. The large size of some, and the large caudal fins and unique morphology of others, of the Bidahochi fish species (Fig. 5) are not characteristic of slow, shallow-water marshes as proposed for the Bidahochi Formation by Dallegge et al. (2003). On the contrary, numerous White Cone fishes, which sometimes reached lengths of over 75 cm, with more than 20 annual growth rings, indicate large, permanent aquatic habitats associated with a swift-flowing river. These fish fossils were found in sediments deposited in low-energy, distal fluvial, overbank, or deltaic lacustrine environments, and so were unlikely residents of the quiet-water environments in which they were deposited.

Paleoenvironmental interpretation thus suggests that the drainage basin that surrounded Bidahochi lacustrine and distal fluvial environments included substantial streams that possibly drained a significant fraction of the southern Colorado Plateau, at



Figure 5. Three specimens of fishes from the upper Bidahochi Formation, showing enlarged fins and slender caudal peduncles (base of tail fin). These traits are common to four species of *Catostomus* and *Gila* in the Colorado River. Photographs are by Robert L. Sutton, U.S. Geological Survey. The three images are reproduced to the same scale.

least during deposition of the late volcanic to postvolcanic sediments of the upper White Cone member and overlying sediments of the uppermost Bidahochi Formation (uppermost Miocene to, possibly, lowermost Pliocene; Dallegge et al., 2003). Dallegge et al. (2003) inferred that the volume of sediment in the Bidahochi Formation was insufficient to have formed the terminus for a river like the modern Colorado with modern Colorado River sediment transport rates. However, the Bidahochi Formation is roughly a kilometer higher in elevation than the Colorado River in the Grand Canyon. Ancestral Colorado River streams would therefore have had much lower stream gradients on the Colorado Plateau and associated lower sediment transport rates. Furthermore, gradual integration of drainages could have led to increasing influx of water and sediment to the area of the Bidahochi Formation, so that only the uppermost Bidahochi Formation reflects substantial river and sediment influx (e.g., Spencer and Pearthree, 2001).

Fish of the modern Colorado River and fish fossils in the latest Miocene strata of the Bidahochi Formation are related to Holocene and ancient Snake River fauna (see previous discussion). The hydrographic connection between these two areas did not involve a river system flowing from the modern Colorado River drainage basin to the western Snake River plain, however, as indicated by detrital-zircon U-Pb data. Only 15 of 328 detrital zircon grains (4.6%) from six samples of middle to upper Miocene strata in the western Snake River Plain yielded ages older than 150 Ma, which indicates that little or no sand was transported from the Colorado River drainage basin to the western Snake River plain during that time (Beranek et al., 2006). This is consistent, however, with eastward flow from the Snake River Plain to the Colorado Plateau region due to uplift in the southwestern Idaho region related to the migrating Yellowstone hotspot (Beranek et al., 2006). Combined biological and geological evidence thus suggests that the Colorado Plateau was internally drained during the late Miocene, and that the fish fauna from a significant tributary to the ancestral Snake River–Sacramento River system entered the northern Colorado Plateau drainage basin by the latest Miocene. Fish transfer could have occurred because of topographic changes induced by the Yellowstone hotspot bulge when it uplifted western Idaho in the middle to late Miocene.

COLORADO RIVER

The modern Colorado River enters the Basin and Range Province at the Grand Wash Cliffs, which mark the topographic western edge of the Colorado Plateau and an approximate boundary between two distinct fish faunas (Table 1). The down-faulted valley at the foot of the cliffs, Grand Wash trough (e.g., Faulds et al., 2001), contains the upper Miocene, lacustrine Hualapai Limestone, which has been considered a facies of the Muddy Creek Formation (Blair and Armstrong, 1979) or a separate unit (Bohannon, 1984). Facies relationships in the limestone reveal no trace of water or sediment influx from the Colorado River (Lucchitta, 1987), and the strontium isotopic character of the limestone is very unlike that of modern Colorado River water (Spencer and

Patchett, 1997; Patchett and Spencer, 2001). A tephra near the stratigraphic top of the limestone yielded a $^{39}\text{Ar}/^{40}\text{Ar}$ biotite date of 6.0 Ma (Spencer et al., 2001).

Abrupt inundation of the lower Colorado River valley and deposition of the thin basal marl unit of the Bouse Formation occurred after deposition of a 5.5 Ma tephra (House et al., 2005). The marl is overlain by siltstone, which is in turn overlain by Colorado River sand and gravel (Metzger et al., 1973; Metzger and Loeltz, 1973; Buising, 1990). In the southernmost subbasin of its exposure area, the Bouse Formation contains a mix of marine, brackish, and freshwater fossil fauna, suggesting that it was deposited in an estuary (P. Smith, 1970; Todd, 1976). However, the strontium isotopic composition of Bouse carbonates and shells in all areas are similar to that of Colorado River water and unlike that of seawater (Spencer and Patchett, 1997; see also Poulson and John, 2003). Furthermore, basal Bouse Formation strata in northernmost exposures are underlain by flood deposits derived from south-flowing floodwater, which is consistent with the concept that influx of first-arriving Colorado River water triggered Bouse Formation deposition (House et al., 2005, this volume). The maximum elevation of the Bouse Formation, 330 m in a very large southern area and 555 m over a smaller northern area, and its absence in some adjacent areas that should have been inundated because of regional subsidence below sea level are consistent with Bouse Formation deposition in lakes that were formerly closed basins (Spencer et al., this volume). By ca. 5 Ma, Colorado River sands were reaching the Salton Trough (Dorsey et al., 2007), which means that the paleodams below Bouse lakes had been incised and the formerly closed basins (or the estuary) filled with sediments.

Integration of the modern Colorado River and its arrival to the Gulf of California at ca. 5 Ma marks the inception of a very large and newly integrated drainage system. Initiation of this new river represents perhaps the largest hydrographic change in southwestern North America in the Cenozoic, and it marked a large eastward displacement of the continental divide. Pre-integration isolation of the upper basin led to the highest percentage of endemism and the fewest species of any major river drainage in North America (Miller, 1959). The presence of at least two of the most specialized members of the fauna (the Colorado pikeminnow and the humpback chub) in the Bidahochi Formation demonstrates that these members of the fauna, at least, had evolved before integration of the Colorado River. The new river system presented a new environment for fish colonization, dispersal, and evolution, leading to integration of parts of the fish fauna. However, a significant lag time is indicated by the large number of lower Colorado Basin fish species that still have not colonized the basin above Grand Canyon owing to ecological barriers (Table 1).

A notable feature of fish distributions in the modern Colorado River is the distinctness of two fish faunas: The Colorado Plateau group and the Basin and Range group, which are separated in the region of the lower Grand Canyon (Table 1). The Colorado Plateau is the center of distribution of a distinctive, depauperate assemblage of large-bodied fishes adapted to a large rivers—the Colorado pikeminnow, three species of large chubs, and three large suckers.

The pikeminnow and chubs were associated with the upper Bida-hochi Formation. The comparatively rich fauna in the Basin and Range segment includes generally smaller creek species—the desert sucker (*Catostomus clarki*) and Sonora sucker (*C. insignis*), found in the Gila, Salt, Bill Williams, Virgin, and lower Colorado below Grand Canyon (Fig. 4). *Catostomus clarki* is also found in Beaver Dam Wash, Meadow Valley Wash, and pluvial White River streams, where it represents a late Pliocene divergence, like the speckled dace (Smith and Dowling, this volume). The large Gila chubs, Colorado pikeminnow, flannelmouth sucker, and possibly razorback sucker, dispersed downstream following early Pliocene integration of the modern Colorado River. The small speckled dace dispersed downstream from the upper Green River to the southern Bonneville Basin and the Bill Williams drainage in the Pleistocene (Smith and Dowling, this volume).

Six small, creek species of endemic spinedace represent an older Miocene radiation in the lower Colorado River region and its tributaries (Dowling et al., 2002). This unique group consists of the following: the spikedace (*Meda fulgida*) of the Gila and Salt Rivers; White River spinedace (*Lepidomeda albivallis*) of the upper White River; Pahrana-gat spinedace (*L. altivelis*) of Pahrana-gat Valley; Virgin spinedace (*L. mollispinis*) of the Virgin River, Meadow Valley Wash, and Beaver Dam Wash; the endemic Little Colorado River spinedace (*L. vittata*); and woundfin (*Plagopterus argentissimus*) in the Virgin and Gila drainages. The Little Colorado spinedace, *Lepidomeda vittata*, which is the sister to the other forms of *Lepidomeda*, differs genetically by ~10%, implying differentiation in the Pliocene and subsequent immigration of ancestors from the southern Great Basin area up the Colorado River to the Little Colorado River.

The three genera (*Meda*, *Lepidomeda*, and *Plagopterus*) represented by these six fish have distributions that are more difficult to explain. The pair-wise genetic distances among the different genera range from 29% to 36%. The rate of change estimated for speckled dace from this area (3.4% per m.y.) suggests an age of diversification of the spinedace and their relatives between 8.5 and 10.6 Ma (previous estimates by Dowling et al. [2002] are older because the small body size and warm temperatures were not considered [Smith and Dowling, this volume]). This ancient diversification occurred before the Colorado River connected habitats in the Lake Mead area with the lower Gila River. The closed basins that separated the Lake Mead–Muddy Creek Formation area from the lower Gila River were substantial and probably a very effective barrier against migration of the ancestors of these fish until the time of the Bouse Formation and modern Colorado River. The southernmost of these basins, in the Blythe area, contain Bouse sediments in the subsurface down to at least 200 m below sea level. This was a deep basin, probably like Death Valley, but there are no active faults in the region and only one very small fault that offsets the Bouse Formation slightly, so the subsurface geometry of this basin is very similar to the basin geometry at the time of Bouse Formation deposition. Basins to the west that were not incised by the Colorado River are still closed (Bristol, Danby, Cadiz dry lakes, Chuckwalla Valley, and Rice Valley; also Dry

Lake south of Las Vegas, and Red Lake Playa north of Kingman, Arizona). Pre-Colorado (>5 Ma) migration pathways for the ancestors of these three genera and resultant evolutionary divergence are not at all clear and possibly involved upstream or head-water transfers between streams on the west side of the Colorado Plateau that flowed into the Lake Mead area and streams at the head of the ancestral Verde River catchment in Arizona.

Other fishes restricted to the lower Colorado River drainage basin include the Loach minnow (*Tiaroga cobitis*) of the Gila and Salt drainages, the longfin dace (*Agosia chrysogaster*) of the Gila, Salt, and Bill Williams drainages, Moapa dace (*Gila [Moapa] coriacea*) of the Muddy River (lower pluvial White River), White River springfish (*Crenichthys baileyi*) of the pluvial White River drainage, and Railroad Valley springfish (*Crenichthys nevadae*) in Railroad Valley, west of the pluvial White River drainage (Hubbs and Miller, 1948). This diversity (13 endemic species) stands in sharp contrast to the depauperate fauna of the Colorado Plateau. The relationships of this fauna are generally in the Basin and Range Province. Some are distant—springfish have relatives on the Mexican Plateau; all others are closer, e.g., Ash Meadows, Pahrump Valley, the Bonneville Basin and upper Snake River (Dowling et al., 2002; Smith and Dowling, this volume).

The geologically abrupt initiation of the modern Colorado River system provided an aquatic environment for the dispersal of fish from possibly small ancestral ranges into widespread and diverse habitats. This event thus provides a potential calibration of minimum rates of mtDNA evolution for fish species that formed by divergent evolution within the Colorado River system. *Catostomus (Pantosteus) clarki* (desert sucker), of the Basin and Range Province, is the sister species of *C. (P.) discobolus* (blue-head sucker), which is found throughout the upper Colorado River from Pinedale, Wyoming, to Granite Park in Grand Canyon. These two species differ in their mtDNA *cytb* gene by 2.9%–4.0%, suggesting isolation since 2.5–3.4 Ma assuming a rate of 1.17% per m.y. (as mentioned previously). This is a minimum age of evolutionary divergence, however, because these two species have hybridized and exchanged genes since coming into secondary contact (Smith, 1966). If evolutionary divergence of the two species occurred in the modern Colorado River, then their absolute minimum rate of mtDNA evolution is 2.9%–4.0% per 5.5 m.y. = 0.53%–0.73% per m.y. *Catostomus insignis* differs from *Catostomus latipinnis* (flannelmouth sucker), by 6.1%, suggesting isolation since 5.2 Ma, assuming a rate of 1.17% per m.y. If evolutionary divergence of these two species occurred in the modern Colorado River, their absolute minimum rate of mtDNA evolution would be 6.1% per 5.5 m.y. = 1.11% per m.y. *Gila coriacea* (Moapa dace) and its sister species, *G. robusta* (roundtail chub), differ by 7.7%. A pair-wise divergence rate of 2.7% per m.y. between *G. robusta* (large bodied, 1.1% per m.y.) and *G. coriacea* (small bodied, 1.7% per m.y.) suggests isolation since 2.9 Ma. The absolute average minimum rate of mtDNA evolution for these species would be 7.7% per 5.5 m.y. = 1.4% per m.y. The substantial differences in the minimum rates determined for these three pairs of species possibly indicates that evolutionary diver-

gence for at least two of the pairs began significantly after integration of the Colorado River.

Rainbow and cutthroat trouts are significantly diverged, possibly dating back to 8 Ma (Smith et al., 2002). They appear to have colonized the Colorado River drainage basin from two different geographic areas in the Pleistocene because the inland forms differ little from their close relatives. The two kinds of trout in the lower basin, Gila trout, *Oncorhynchus gilae*, of the Gila River headwaters and Apache trout, *O. apache*, in headwaters of the Salt River and Little Colorado River, are related to Rainbow trout, while *Oncorhynchus clarki pleuriticus* of the upper Colorado River Basin (including headwaters of the Virgin River) is a cutthroat trout. They would have reached their present ranges during the glacial stages because they require cold water. The Apache and Gila trouts must have colonized through the lower Gila River, lowermost Colorado River, and drainages that linked the lowermost Colorado to coastal California or coastal Mexico. Colonization of the upper Little Colorado River by migration of Apache trout from the upper Salt River was possibly facilitated by construction of the Quaternary Springerville volcanic field, which now occupies a substantial part of the drainage divide between the two rivers. Perhaps lava flows or cinder cones blocked a headwater tributary of the Salt and diverted it into the Little Colorado, thus transferring the Apache trout. Colorado River cutthroat trout colonized the upper Colorado River Basin from the Snake River and migrated downstream through Grand Canyon to the Virgin River. Although the Virgin River cutthroat trout shares some genes with the Bonneville cutthroat, its colors are those of the cutthroat trout of the upper Green River in the Uinta Mountains.

In summary, the division of Colorado River drainage fishes into upper and lower basin faunas reflects two different time periods. A rather rich, older fauna of spinedaces and related minnows developed in a vaguely defined region centered on the Lake Mead area or possibly in the ancestral Gila-Salt-Verde and/or Bill Williams drainage basins of Arizona. At roughly the same time, a small but distinctive fauna of unusually large minnows gained access to the Bidahochi Formation, possibly from the San Juan and associated rivers of the Colorado Plateau, but ultimately from the Snake-Sacramento River system. These fish are associated with the synvolcanic White Cone member of the Bidahochi Formation (Shoemaker et al., 1962) and overlying upper Bidahochi Formation (Dallegge et al., 2003) and probably date to 6.0–8.5 Ma (Damon and Spencer, 2001; Dallegge et al., 2003). After the Colorado River cut through the Grand Wash cliffs at ca. 5 Ma, several kinds of minnows and suckers dispersed and diverged into separate upper and lower basin habitats separated by the Grand Canyon, where the most successful migrations occurred in the downstream direction.

THE LOWER COLORADO RIVER AND THE LOS ANGELES BASIN

Two of the four distinctive kinds of fishes in the Los Angeles Basin share unmistakable morphological and genetic traits with

fishes of the lower Colorado River Basin. The Santa Ana mountain sucker (*Catostomus* [*Pantosteus*] *santaanae*) and the Los Angeles speckled dace (*Rhinichthys osculus*) have the closest relationships to sister forms in the lower Colorado River Basin and no close relatives in California or Mexico. Neither *Catostomus* nor *Rhinichthys* are represented in the Mojave drainage nor do they have close relatives in the Amargosa–Death Valley region.

The mountain suckers, subgenus *Pantosteus*, diverged from their sister subgenus *Catostomus* at 12 Ma (based on fossils of the subgenus *Catostomus* in eight time horizons, the oldest being 11 Ma; the time of origin was estimated with the method of Marshall, 1990). A sample of 28 mtDNA distances between the sister groups averages 22.0% (standard deviation [S.D.] = 2.2%). If that average distance correctly reflects the time since lineage origin, then 22% per 12 m.y. yields a rate of mtDNA evolution of 1.8% per m.y. The mtDNA of the Santa Ana mountain sucker differs from its relative in the lower Colorado River Basin, the desert sucker, by 9.2%. The age of divergence between *C. (P.) santaanae* and *C. (P.) clarki* is then estimated at 9.2% per (1.8% per m.y.) = 5.1 Ma. A rate of molecular evolution of 2.1% per m.y. is about what would be expected for a fish this size in the warm southern California climate (Smith and Dowling, this volume). The difference between *C. P. clarki* and *C. santaanae*, 9.2%, divided by a molecular evolution rate of 2.1% per m.y., gives an estimated time of isolation of 4.4 m.y. The Los Angeles speckled dace (*Rhinichthys osculus*) differs from its close relatives in the Muddy Creek area and the Gila River Basin by an average of 7.1%. The genetic distance of 7.1% divided by the rate of 3.8% per m.y. gives an isolation time of ~1.9 m.y. (Smith and Dowling, this volume). In conclusion, estimated isolation times for these two pairs of sister fish and two different estimates of mtDNA molecular evolution rates yield a range of evolutionary divergence times between 5.1 and 1.9 Ma. Similarly, the mtDNA of the Utah chub, *Gila atraria*, of the Bonneville Basin and sister species the Arroyo chub, *Gila orcutti*, of southern California coastal streams, differs by 8.3%, implying separation since 4.6 Ma.

Estimated evolutionary divergence times of 5.1–1.9 Ma are ca. 1–4 Ma after the ca. 6 Ma inception of San Andreas fault displacement at modern rates of ~34 km/m.y. (e.g., Dickinson, 1996). Restoration of the ~100–170 km of right-lateral displacement that occurred over the past 3–5 m.y. on the San Andreas fault places the northern end of the Peninsular Ranges, including the eastern Los Angeles Basin area, much closer to the mouth of the Colorado River (Fig. 6). Paleodrainage patterns at that time were likely significantly different than at present, as the northern Peninsular Ranges were juxtaposed across the early San Andreas fault with bedrock now exposed along the north side of the Salton Trough, and uplift of the San Bernardino and San Gabriel Mountains was in its early stages. The ancestors of the Santa Ana Mountain sucker and the Los Angeles speckled dace that lived in headwater regions of the lower Colorado River must have been regularly flushed downstream to near the Colorado River delta, from where they dispersed to headwater regions in the northern Peninsular Ranges by way of streams that are now obscure or

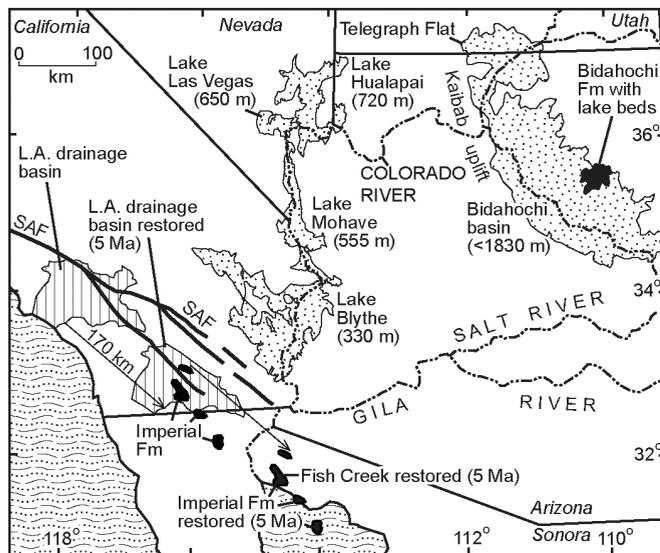


Figure 6. The Mojave-Sonora Desert region and southwestern Colorado Plateau, showing major rivers and some late Cenozoic geologic and hydrologic features. Four lakes shown along lower Colorado River trough represent the outline of lake highstands determined from sediment distributions. The southern two lakes (Mohave and Blythe) contain the ca. 5 Ma Bouse Formation. The Bouse Formation in the Blythe Basin contains marine fossils, but Sr isotopes reveal no influence from seawater. Evidence for the upper two lakes (Las Vegas and Hualapai) consists of limestone and gypsum that are unlike the distinctive marl of the Bouse Formation (Castor and Faulds, 2001; Wallace et al., 2005). In addition, lake beds are present in the middle Miocene to earliest Pliocene Bidahochi Formation in eastern Arizona. If such a lake filled the Little Colorado River valley to an elevation of 1830 m (6000 ft), it should have spilled over at Telegraph Flat in southern Utah (elevation ~1675 m [5500 ft], location ~40 km east of Kanab). If it had spilled over at Telegraph Flat, outflow should have incised a channel and initiated a different Colorado River course than the actual course. Thus, the configuration of such a lake is uncertain, and it must not have reached Telegraph Flat, but the lake appears to have spilled over the Kaibab uplift at a lower elevation to initiate incision of the Grand Canyon and first delivery of Colorado River water to the low desert region (Meek and Douglass, 2001). The four areas of exposed upper Miocene to Pliocene Imperial Formation are also shown, along with the position of those four areas after restoration of 170 km of displacement on the San Andreas fault (SAF). Similarly, the present and restored positions of the Los Angeles (L.A.) Basin are shown. The Imperial Formation includes Pliocene delta-front deposits derived from the Colorado River (e.g., Kerr and Kidwell, 1991). Freshwater fish carried downstream to the delta region could have migrated up northwestern tributaries to headwater regions adjacent to the Los Angeles drainage basin. Headwater captures could have then transferred these fish to the Los Angeles Basin. The Santa Ana mountain sucker and the Los Angeles speckled dace probably reached the Los Angeles basin by this route.

invisible due to multiple geologic processes in an area of very active faulting (see also Minckley et al., 1986). Capture of a small tributary draining to the Colorado River by the Los Angeles Basin, and associated transfer of headwater fish, seems entirely feasible for streams that were cut by active faults and occupied a rapidly changing, tectonically active landscape.

CONCLUSION

A dominant theme in the Cenozoic hydrographic history of southwestern North America is the transfer of an area now encompassed by the large upper Colorado River catchment from the Atlantic to Pacific Basins. This transfer began with Eocene development of closed basins between the Rocky Mountains and the western mountain belt created by Mesozoic magmatism and subduction. Fish fossils from these basins are fundamentally Atlantic and reveal no connection to the Pacific Ocean. Eocene to early Miocene canyons and clastic sediments near the southwestern edge of the Colorado Plateau record generally northeastward stream flow leading to the Baca Basin and, probably, the Claron Basin.

Largely Oligocene-Miocene tectonic extension in the Basin and Range Province and accompanying volcanism obliterated past landscapes and river courses and produced numerous closed basins. As extension and volcanism became less active in the late Cenozoic, closed basins merged, and hydrologic connections developed between adjacent basins. In the northern Great Basin, Miocene and Pliocene fossils record influx of fish from adjacent areas outside the Great Basin. Species diversity and DNA evidence reveal a long period of speciation and evolution, dating back to at least the late Miocene, that occurred in the greater Lake Mead area, or possibly in the ancestral Bill Williams-Verde-Gila drainage basins in Arizona, followed by migration into the greater Lake Mead area following arrival of the Colorado River. These fish entered the Colorado River after the river arrived in the Basin and Range Province at ca. 5 Ma.

The dissimilarity of fish fauna indicates that late Miocene runoff from the Colorado Plateau did not flow down the ancestral Rio Grande or Platte River. Significant faunal exchange occurred with the Snake River, however, as indicated both by modern fish and late Miocene fish in the Bidahochi Formation and the Snake River Plain, as well as recent genera in the Sacramento River drainage. This connection is surprising because large fishes, requiring large rivers, were involved in the Miocene exchanges. A lack of zircon sand grains in pre-Pliocene sediments of the Snake River Plain indicates that late Miocene Colorado Plateau and thrust-belt runoff did not enter the western Snake River until the Pliocene, so Miocene transfer of fish from the ancestral Snake River to the upper Colorado Plateau drainage basin likely occurred due to transfer of a significant stream from the upper ancestral Snake River to the ancestral upper Colorado River drainage. This could have occurred due to uplift associated with late Miocene magmatism along the Snake-Yellowstone hotspot track and development of a significant regional eastward slope on the east flank of this uplift in southern Idaho (Beranek et al., 2006).

The Colorado River arrived abruptly at ca. 5 Ma to the Basin and Range Province, filled formerly closed basins, and spilled over basin divides, eventually reaching the Gulf of California and carving the lower Colorado River valley. This event was probably the largest Cenozoic hydrographic change in southwestern North America. The Gila River underwent similar upstream basin

filling and spilling and reached the Gulf of California at about the same time (e.g., Dickinson, 2003). These new rivers and their tributaries provided dispersal routes for rainbow trout, which migrated from coastal areas to the mountains of central Arizona and southwestern New Mexico, and cutthroat trout, which migrated down the upper Colorado to the Virgin River. Dispersal of dace and suckers from ancestral habitats, possibly in the Muddy Creek (Lake Mead) area, to the Los Angeles Basin also was made possible by early Pliocene birth of the Colorado River (and perhaps the Gila River, if ancestral habitats were in central Arizona). These dispersals were likely facilitated by drainage transfers associated with the highly active San Andreas fault and movement on related faults of the greater Los Angeles area and Salton Trough. Adaptation and speciation within the separate Miocene parts of the Colorado River system produced separate faunas that are mixed only to the extent that upper basin fish migrated downstream through Grand Canyon. Aquatic environmental conditions resulting from the 5 Ma integration of the Colorado River system continue to present opportunities and challenges for fish dispersal and adaptation to accessible but still uncolonized environments.

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