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*Geography of
Western North
American
Freshwater Fishes:
Description and
Relationships to
Intracontinental
Tectonism*

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DEFINITIONS	521	Fishes of the Region	538
DESCRIPTION OF THE REGION	521	Coastal Oregon and Northern California	539
Geologic Framework	523	Coastal Streams of Oregon	539
Overview	523	Klamath River Basin	554
Physiography and Geology of Subareas	525	Northern California Coastal	555
Paleohydrography	530	Great Basin	556
Paleoclimatology	536	Inland Basins of Oregon ("Oregon Lakes")	557
ZOOGEOGRAPHY	538		

Lahontan System	551	Coastal Rivers of Northwestern Mainland Mexico	589
Death Valley "System"	555		
North-Central Great Basin	558		
Bonneville Basin	570	DISCUSSION AND SUMMARY	593
Sacramento-San Joaquin System	573	Fossil Record	594
Colorado River Basin	578	Characteristics of the Modern Fauna	595
Southwestern California and Northwestern Mexico	594	Tectonism and Fish Distribution	597
South Coastal California and Baja California	597	EPILOGUE	611
		ACKNOWLEDGMENTS	613

Cretaceous ichthyofaunas of western North America consisted only of archaic fishes. No recognized members of teleostean groups that now constitute most of the fauna were present (Estes 1970). It was not until Late Paleocene, about 55 million years ago (mya), and during Eocene (53–37 mya), when freshwater faunas dominated by teleosts appeared in the fossil record (Patterson 1981a). Eocene faunas (Wilson 1977; Grande 1980) show little resemblance to those of Miocene (23–5 mya) to present (R. R. Miller 1959a, 1965; Uyeno and Miller 1963; Cavender et al. 1970; G. R. Smith 1981a; Grande et al. 1982). Appearance and expansion of the modern fauna in Oligocene and Miocene coincided with declines of archaic groups and of teleosts such as hiodontids, umbrids, esocids, ictalurids and centrarchids to or near extinction in most of what is now western North America by Pliocene (5–1.8 mya) times (G. R. Smith 1981a). Many genera and species of extant groups also disappeared, yet some contemporary genera and species had representatives in Middle Tertiary (G. R. Smith 1978, 1981a; M. L. Smith 1981).

Modern fishes are thus far older than conditions under which we find them today, and their distributions often reflect a remarkable

array of events. Taxa that persist have dealt with far more spectacular geologic and climatic events than their counterparts in other parts of the Continent. Environmental effects of plate tectonics (Atwater 1970; Ernst 1981), inland mountain building and volcanism (Dickinson and Snyder 1978; Armentrout et al. 1979), plus trends of ever-increasing aridity despite oscillations toward wetter conditions during glaciation in Pleistocene (Axelrod 1979; Hoover et al. 1982), all took their toll. Historic distributions are further changed because of the recent activities of humans. Extinction rates are rapidly increasing and a substantial percentage of species comprising the western ichthyofauna is in imminent danger of disappearing (R. R. Miller 1946c, 1961b, 1972a, 1977, 1981; Minckley and Deacon 1968; Moyle 1973, 1974; Moyle and Nichols 1973, 1974; Pister 1974, 1981; Deacon 1979; Deacon et al. 1979; Johnson and Rinne 1982; Meffe 1983; Meffe et al. 1983; Minckley 1983).

Objectives of this chapter are to place this scientifically valuable and unique fauna in modern perspective. We present a summary of Cenozoic geology, paleohydrography and paleoclimatology; review previous studies of western fishes; outline inter- and intrabasin

zoogeographic patterns; and discuss their relations to complex patterns of landscape and drainage evolution.

DEFINITIONS

It is expedient at the onset to define some relevant terms and principles and to mention some of our taxonomic usages. Our definition of dispersal restricts it to movement between or within drainages via direct surface hydrographic connections, whether organisms participate actively or passively. In some instances of passive dispersal, such as stream capture, our definition encompasses vicariance, just as a taxon increasing its range without crossing barriers then fragmenting may be termed "vicariance in disguise" (Platnick and Nelson 1978). We base our discussion on the assumption that allopatric speciation has prevailed in western fishes, although we recognize evidence and theory indicating that sympatric or parapatric divergence may occur (Kosswig 1963; Grant 1971; Endler 1973, 1977). We further emphasize principles of vicariance biogeography (Croizat 1958, 1964, 1978; Croizat et al. 1974; Rosen 1975a,b, 1978, 1979; Platnick and Nelson 1978; Nelson and Rosen 1981; Nelson and Platnick 1981) and construct area relationships based on geologic evidence from throughout the Cenozoic.

We have generally applied the principle of minimum age of origin. Presence of fossil evidence of reasonable dating is construed as the minimum age of a taxon's presence in an area, but does not preclude its earlier presence (Rosen 1975a; Parenti 1981a,b; Patterson 1981b). Single fossils provide discrete data points in time and further are in no way informative as to persistence of a taxon in an area or as to possibilities for multiple invasions. Area relationships of fossils furthermore must be interpreted with caution since tectonic displacements have altered spatial relationships

between fossil localities and their places of deposition.

Lastly, one must keep in mind the long-term insular nature of western drainages and obvious dependency of fishes on habitat continuity. Presence of fishes demands continuous aquatic conditions since their time of origin. The absence of fishes may either mean they never arrived in an apparently suitable habitat, or that water supplies failed for a few moments in time. It follows that time and extinction under such conditions may be related almost as intimately as time and chance for vicariance or dispersal, and that these processes may be difficult to separate in causal interpretations of distributional patterns (G. R. Smith 1981a).

We have generally followed taxonomy of Robins et al. (1980), where applicable, with exceptions noted when appropriate in text and tables. In addition, Minckley and Hendrickson retain the catostomid genus *Pantosteus* (Minckley 1973); Bond favors use of *Pantosteus* as a subgenus of *Catostomus* (G. R. Smith 1966; Robins et al. 1980). The former is applied here through majority opinion. *Gila intermedia*, considered part of the *G. robusta* complex by Robins et al. (1980), is afforded specific status (Rinne and Minckley 1970; Minckley 1973; Rinne 1976). We also follow Parenti (1981a) in placing the genera *Crenichthys* and *Empetrichthys* as primitive, egg-laying members of the family Goodeidae. (See R. R. Miller and Smith, Chapter 14, for an alternative taxonomic allocation.)

DESCRIPTION OF THE REGION

The vast area with which we are concerned is bounded on the east by the Continental Divide and on the west by the Pacific Ocean (Fig. 15.1). To the north lies the Columbia River system. Our southern boundary is more diffuse, on the basis of biological grounds rather

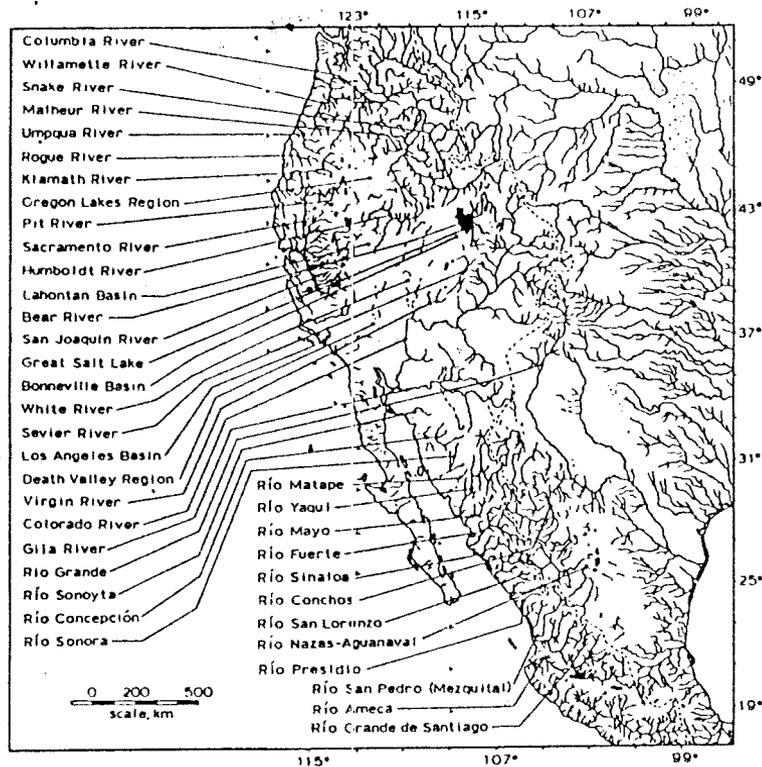


Figure 15.1 Sketch map of major drainages of western North America, showing study area (west of Continental Divide [---], south of Columbia River Basin and north of Río Grande de Santiago Basin) and some major features emphasized in text.

than on geography. A faunal break previously recognized by Meek (1903, 1904) and R. R. Miller (1959a) north of the Río Grande de Santiago Basin of Mexico was selected as a southern limit.

The Basin and Range Physiographic Province (Fenneman 1931) comprises most of this region. Basin and Range topography dominates between the Sierra Nevada and Rocky

Mountains from Oregon and southern Idaho (King 1977) south through Nevada, Utah and Arizona. It then passes along the coast, including part of what is now Baja California (Dokka and Merriam 1982), and into the northern Mexican Plateau on both sides of the Sierra Madre Occidental (Hamilton and Myers 1966; de Cserna 1975; Loring 1976; Demant and Cocheme 1982) (Fig. 15.2). A large per-

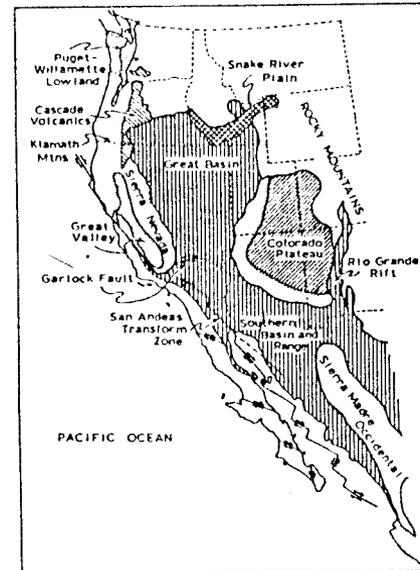


Figure 15.2 Sketch map of some major structural features and physiographic regions of western North America emphasized in text.

centage of this province is endorheic, and was variously so through much of Cenozoic. Rivers that originate in highlands end in adjacent closed basins that hold temporary or permanent lakes. Major mountain ranges include Coast Ranges of Oregon and California, the Klamath-Cascade-Sierra Nevada axes, the Sierra Madre Occidental, the Rocky Mountain axis and highlands of and associated with the Colorado Plateau (Fig. 15.2).

Geologic Framework

Overview

Formation of landscape components in western North America has been variable in time

and process, and recent interpretations of plate tectonics have provided a wealth of new information. A broad perspective of geologic structure and history of the region as currently visualized reveals patterns germane to present fish distributions. Furthermore, regional topography is intimately related to interplate tectonics. Geophysical models of spatial and temporal responses to changing geometry and velocity of displacements among the North American, Pacific, Farallon, Juan de Fuca and Cocos lithospheric plates (Atwater 1970; Coney 1978a; Menard 1978; Dickinson 1979; Barash and Venkatakrishnan 1982; Engebretson et al. in Page 1982) offer insights into physiographic relationships obscured by subsequent tectonism. We apply standards of reference for geologic events based on the time scales of Berggren and Van Couvering (1974), Haq et al. (1977), and Hardenbo and Berggren (1978) for Cenozoic epochs.

As variously reviewed by Nur and Ben Avraham (1977, 1981, 1982), Beck et al. (1980), Coney et al. (1980), Ben Avraham et al. (1981), Irwin (1981), Magill and Cox (1981), McLaughlin et al. (1982), McWilliams and Howell (1982), Page (1982), Stevens (1982), and Marlow and Cooper (1983), essentially all of North America west of the present Basin and Range Province north to include Alaska consists of a heterogeneous array of allochthonous terranes. These have been accreted onto the edge of the North American Craton from Paleozoic to as recently as Late Miocene. Many of these terranes are of oceanic lithosphere, but continental fragments have been identified.

Geographic origins of some fragments are obscure since paleogeographic data fail to provide information on paleolongitudes. However, determinable paleolatitudes of terrane origins are generally south of present positions. Proposed origins of exotic terranes from vanished continental masses (Nur and Ben Avraham 1977, 1981) have yet to be substantiated (Batten and Schwackert 1981; Tedford

1981). However, northward displacements of masses along the west coast of North America are well documented (Beck 1980; Cowan 1982; Page 1982; Stone et al. 1982).

Responses to changing velocity and geometry of interplate collisions have not been as a single, cohesive North American Craton, but as a conglomeration of intracontinental aseismic subplates (Suppe et al. 1975; R. B. Smith 1978; Eaton 1979; Beck and Plumley 1979; Beck et al. 1980; Magill and Cox 1981; McWilliams and Howell 1982; Page 1982) or schollen (Livaccari 1979) bounded by seismic zones (R. B. Smith and Sbar 1974; Hill 1978; R. B. Smith 1978; Hunt 1979). Some subplates are accreted terranes that have independently experienced horizontal, vertical and rotational movements within the Continent. Other intracontinental subplates east of allochthonous terranes consist of large, cohesive blocks of the original Craton, including the Great Basin-High Lava Plains, Colorado Plateau, Northern Rocky Mountains-Columbia Plateau and Sierra Nevada (Armstrong 1978; R. B. Smith 1978; Humphrey and Wong 1983). Paleomagnetic and stratigraphic data indicate that the allochthonous western Cascade Mountains, Oregon Coastal Ranges and Klamath Mountains, from northern California to Washington, are bound together to behave as a single, coherent subplate (Magill and Cox 1981; Globerman et al. 1982). The Mohave Desert Block, between the Transverse Ranges and Garlock Fault of southern California and Nevada, apparently also behaves as an independent aseismic unit (Livaccari 1979; Burchfiel and Davis 1981; Dibblee 1981; Dokka 1983). Baja California, although fragmented into a series of smaller units, has been displaced north-northwest for a substantial distance, as has much of southwestern California.

Compressive interactions between the Pacific and North American plates produced a Late Cretaceous eastward sweep of magmatism from the coast across what is now the

Sierra Nevada (Evernden and Kistler 1970) and Basin and Range (Burchfiel and Davis 1975) to create a broad band of tectonism and orogeny in the classic Laramide Axis (Armstrong et al. 1969; Armstrong 1974). Laramide deformation continued from Cretaceous into Eocene to create the ancestral Rocky Mountains and a broad, uniformly elevated region (Coney 1978a,b; Damon 1979; Young 1982) including Drewes' (1978) Cordilleran Orogenic Belt, extending from southern Mexico via the Sierra Madre Occidental through Basin and Range north to Alaska.

Following epeirogenic uplift, a period of igneous and tectonic quiescence (Dickinson and Snyder 1978; Shafiqullah et al. 1978; 1980) associated with global reorganization of plate interactions about 40 mya (Zoback et al. 1981; Sykes et al. 1982) resulted in Late Eocene-Early Oligocene erosional surfaces over virtually all the western Continent from Canada well into Mexico. Fragmentary but conclusive evidence of this broad surface, in the form of wide-spread regional unconformities preserved beneath flat-flowing Oligocene extrusives, has been reviewed by Epis and Chapin (1975), Scarborough and Peirce (1978) and Gressens (1981).

Reinitiation of tectonism throughout the region was synchronous with a southwestward sweep of renewed magmatism in Oligocene, to arrive again near the west coast by Early Miocene (Christiansen and Lipman 1972; Dickinson 1981; Gastil et al. 1981; Anderson 1982). It was also nearly synchronous with collision of the East Pacific Rise and the North American Plate about 29 mya (Atwater 1970). This event changed the former convergence margin to the right-lateral strike-slip San Andreas Transform system (Atwater 1970; B. M. Page 1981, 1982). Shearing and rotation of lithospheric subplates extended far inland. Allochthonous terranes west of the Basin and Range experienced varying degrees of rotation and displacement (L. Wright 1976; Beck et al.

1980; Magill and Cox 1981). Increments of the Farallon Plate continued to be consumed on both sides of the transform, and triple junctions among remnants of the Farallon (the northern Cocos and southern Juan de Fuca plates) and Pacific plates migrated north and south along the Continental margin (Atwater 1970; Dickinson and Snyder 1978; 1979a,b). Volcanic activity continues north and south near migrating triple junctions, where plate descent progresses today.

Mobility of the western cordillera and relative stability of the Colorado Plateau and Laramide Axis required extension in the intervening region. Extensional stresses developed originally under a north-55°-east-directed axis (Coney 1978a; Eaton 1979; Eaton et al. 1978; Livaccari 1979; Zoback et al. 1981; Laughlin et al. 1983) to produce broad structural fault-bounded basins and ranges orthogonal to stress (north-northwest). During the same time, the Colorado Plateau began dextral rotation to produce an early manifestation of a new tectonic regime beginning around 27 mya in opening and extension of the Rio Grande Rift along its trailing edge (Chapin and Seager 1975; Livaccari 1979; Kelly 1979; Cape et al. 1983). Extensional structures with consistent north-northwest orientation took shape from 27 mya to 10 mya throughout the incipient Basin and Range and in areas now covered by Columbia River Basalts and the Snake River Plain (Christiansen and McKee 1978; Zoback et al. 1981). Vertical displacement began to develop relative to the Colorado Plateau and Sierra Nevada region (Christiansen 1966; Hay 1976; Best and Hamblin 1978; Christiansen and McKee 1978; Shafiqullah et al. 1980; Young 1982). Large structural troughs such as Walker Lane through Death Valley, Las Vegas Valley shear zone, Oregon-Nevada lineament and perhaps a Texas lineament, likely interconnected the presently separated southern and northern Basin and Range provinces and parts of Oregon since covered by volcanics (Stewart 1967, 1971, 1978;

Stewart et al. 1968, 1975; Longwell 1974; Eaton 1979; Bohannon 1979, 1981; Laughlin et al. 1983). Other diverse structural alignments similarly extend along north to north-northwest trends (Silver and Anderson 1974; Coney 1978a,b, 1979; Eaton 1979; Anderson 1981; Rehrig 1981).

Increased tectonism 13-10 mya produced the present topography of the southern Basin and Range along the old north-55°-east structural alignment (Fig. 15.3). About 10 mya the stress axis in the northern Basin and Range (Great Basin) suddenly shifted clockwise to produce structures that intersect at 45° and disrupt those developed earlier (Zoback et al. 1981). Tectonism has continued in the Great Basin with both right-lateral (Stewart et al. 1968; Stewart 1978) and vertical displacements on faults, but the southern Basin and Range has been relatively quiescent since 10 mya. Marked separation of the southern and northern Basin and Range provinces by the Mohave Block resulted from uplift, rotation and northward movement of the California Transverse Ranges within the bend of the San Andreas Transform (Livaccari 1979; Dibblee 1981).

Physiography and Geology of Subareas

The Oregon Coast Ranges were accreted in Eocene (Magill and Cox 1981), and subsequently behaved as part of the Klamath-Cascade Block, although separated from the Cascades by the Puget-Willamette Lowland. The Cascade Mountains consist of arc volcanics originating inboard of the coastal, westward rotating block(s) (Simpson and Cox 1977; Hammond 1979). The Klamath Mountains, which bridge the Coast Ranges to the Cascades south of this lowland, are overlapped by Cascade volcanics (Figs. 15.2 and 15.3). Dextral rotation has resulted in westward displacement of the south end of this block 340 km since about 20 mya (Magill and Cox 1981).

East of the Cascades and north of the pres-

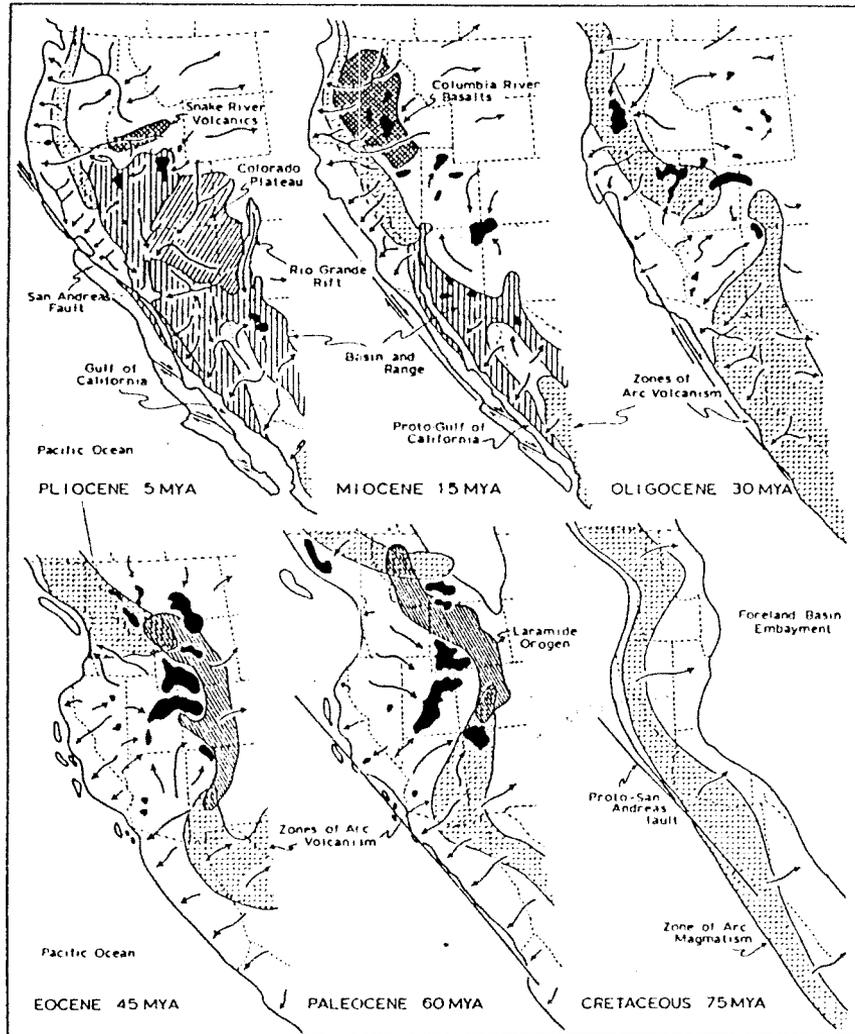


Figure 15.3 Diagrammatic representations of paleotectonic, paleogeographic and paleohydrographic features of western North America, Pliocene through Cretaceous. Sketches were modified from figures appearing in papers edited by Armentrout et al. (1979) and are not intended for use in navigation for travel in time.

ent Great Basin, rolling volcanic hills over much of what is now Washington and Oregon were buried by Middle Miocene rift volcanics constituting the Columbia River Basalts (McKee et al. 1977; Swanson et al. 1979; Fecht et al. 1982). Lavas later covered the Snake River Plain of southern Idaho (Fig. 15.3).

The Sierra Nevada borders Basin and Range on the west and extends southward through the Klamath-Cascade region to the Garlock Fault zone of southern California (Fig. 15.2). Similar to the Oregon Coastal-Klamath-Cascade Block, the Sierra Nevada region has experienced some rotation (Magill and Cox 1981) as well as westward displacement from its Early Tertiary position accommodated by the Garlock Fault (Davis and Burchfiel 1973; Wernicke et al. 1983a,b). During Miocene and Early Pliocene this highland (Hay 1976) was being eroded to moderate relief and sloped from the upwarped and extended Basin and Range into a depression termed the Great Valley of California (Axelrod 1955, 1957, 1962; Christiansen 1966; Cole and Armentrout 1979). As noted before, volcanism migrated stepwise from south of the Garlock Fault in Middle Miocene to the latitude of San Francisco by Early Pliocene, and now is limited to north of about 40° latitude (Snyder et al. 1976; Snyder and Dickinson 1979). Uplift and westward tilting of the Sierra Nevada to its present elevation of more than 4300 m began about 18 mya (Christiansen 1966; Noble and Slemmons 1975), experienced an acceleration pulse 10 mya (Hay 1976), but was mostly accomplished since 5 mya in the Pliocene-Pleistocene (Axelrod 1955, 1956, 1957, 1962, 1979; Huber 1981). Uplift proceeded from an origin in the south toward the north.

The Great Valley is an ancient, still largely intact forearc basin, preserved between the California Coast Ranges and the Sierra Nevada (Ingersoll 1982a). It passes south from the Klamath Mountains to the Transverse Ranges, with the broad central Stockton Arch separating it into the Sacramento and San Joa-

quin basins. It received both marine and continental sediments through Pliocene, filling from north to south (Cole and Armentrout 1979). The northern Sacramento Basin has existed as a nonmarine lowland since Oligocene, filled with terrestrial debris from the Klamath, Cascade, Coast Ranges and Sierra Nevada regions (Dickinson et al. 1979). The San Joaquin Basin remained beneath the sea through Pliocene. Pleistocene regression of the sea was associated with general uplift of the Coast Ranges and the entire Great Valley (Hamilton 1978).

The California Coast Ranges and Borderland areas, including the San Andreas Fault zone (Fig. 15.2), are remarkably complex (Hamilton and Myers 1968; Armentrout et al. 1979; Ernst 1981). The Northern California Coast Ranges are north of San Francisco, and the Southern Ranges pass south of that city to the Peninsular Ranges of Baja California (Crowell 1981). This region consists of Tertiary deposits superimposed on two markedly different basement complexes. A predominantly northeastern Franciscan Terrane represents materials likely accreted to the North American Plate from an early system(s) of subduction (B. M. Page 1981; see, however, Blake and Jones 1981). This complex constitutes the core of both the Northern and part of the Southern Coast Ranges. The southern Salinian Block forms the basement for much of the Southern Coast Ranges (Graham 1979; B. M. Page 1981, 1982). This block was thought by B. M. Page (1981) to represent a northward displacement of a former continuation of the Sierra Nevada Batholith. However, paleomagnetic and petrologic data now indicate that it originated in Late Cretaceous at paleolatitudes near present Central America. It was transported northward along with associated terranes to accrete to southern California in Eocene (McWilliams and Howell 1982; Page 1982). It then remained stationary until after collision (29 mya) of the East Pacific Rise with the Continent initiated uplift of the California Coast

Ranges and formation of the San Andreas Transform. The Salinian Block then again moved 60–100 km along the Transform (20–15 mya), with splinters moving further. By Late Miocene the region had again experienced subsidence, only to again be uplifted from Late Miocene to Recent (Hamilton 1978). Meanwhile, accelerated movement added 205–245 km over the past 5 my, with splinters moving perhaps an additional 115 km (Graham and Dickinson 1978).

The Southern Coast and Peninsular ranges were uplifted coincident with Pliocene-Pleistocene movements of Peninsular Baja California. The Transverse Ranges represent a microplate(s) that migrated west-northwest and was rotated and uplifted in apparent response to Middle Miocene extensional opening of basins to the west (Hall 1978, 1981). Uplift of the Transverse Ranges to their present elevation was in Pliocene-Pleistocene (Woodburne 1975; Dibblee 1975; Weldon and Meisinger 1982).

South and west of the Coast and Transverse ranges lie the California Borderlands, which include the Los Angeles and Ventura basins and numerous offshore depressions extending across the Continental Shelf. Prior to Middle Miocene, this region was largely covered by sea and received continental sediments from the east. Uplift or oceanic recession in Middle Miocene exposed structural blocks, but subsiding basins accumulated deep-sea deposits over shallow-sea and continental debris of Early Miocene. Uplift of blocks and eastern highlands provided sediments for rapid filling of basins from east to west (Campbell and Yerkes 1976). Other Middle and Late Miocene events included subsidence, crustal extension, and volcanism, uplift and major faulting of the Transverse Ranges (Cole and Armentrout 1979; Stuart 1979). Pliocene-Pleistocene north-south (or northeast-southwest) compression resulted in reverse oblique faulting. The area was again uplifted in Late Miocene, and this continues today.

Southeastern California, adjacent Arizona and northwestern Mexico (Fig. 15.2) lie within the fragmented transform boundary between the Pacific and North American plates (Crowell 1981). Rates and magnitudes of displacement along the San Andreas Transform since Eocene are thoroughly documented (Woodford et al. 1968; Clarke and Nilsen 1973; Howell et al. 1974; Stuart 1974; Ehlig et al. 1975; Bohannon 1975; Ehlert and Ehlig 1977; Farley and Ehlig 1977; Crowell 1975, 1979, 1981; Buesch and Ehlig 1982; Link 1982a–c). This zone has provided the medium through which numerous schollen, representing splinters of the once continuous Peninsular and Sierra Nevada batholiths, have been displaced northwestward from central Sonora to southern California (for example, the Orocochia, Chocolate and Transverse ranges; Crowell 1979; Livaccari 1979). These structures are rifted and fragmented by the San Andreas Transform, and blocks between faults have been squeezed obliquely upward to form highlands or downward to form basins (Yeats 1976, 1978; Blake et al. 1978). The transform boundary of the San Andreas complex merges with the divergent plate boundary that creates the Gulf of California south of the Salton Sea, where several active faults are present (Allen 1968, 1981; Crowell 1981). The fault zone then extends southeast into mainland Sonora for an undefined distance (Merriam 1965, 1968, 1972; Gastil and Krummenacher 1977).

Hamilton (1961), Karig and Jensky (1972) and Dokka and Merriam (1982) outlined development of the early Gulf of California region (30 to around 7 mya) as an extension zone inland from an offshore subduction alignment. Sea water covered parts of southwestern Arizona (P. B. Smith 1970; Shafiqullah et al. 1980) and western Sonora (Gomez 1971) in Late Miocene (Fig. 15.3). Miocene marine deposits (16–12 mya) are on Isla Tiburón (Stump, *in* Gastil et al. 1979). Upper Miocene marine fossils also are in diatomite west of San Felipe, Baja California del Norte and Miocene marine

strata (more than 12–13 mya but less than 16–20 mya) have been encountered in drill holes at Yuma, Arizona (Mattick et al. 1973; Eberly and Stanley 1978), and in western Sonora (Gastil and Krummenacher 1977; Gastil et al. 1979).

A controversy surrounds the Miocene Muddy Creek Formation near Lake Mead. It may be marine or marine/estuarine in origin (Blair et al. 1977, 1979; Blair 1978; Blair and Armstrong 1979) or nonmarine (Cornell 1979; Lucchitta 1979). Basalts overlying the Muddy Creek Formation and predating downcutting by the Colorado River near Lake Mead were deposited 5.8 mya (Shafiqullah et al. 1980). The extensive Imperial Formation in the Salton Trough marks definite marine conditions (Stump 1972) in the northwestern part of the Gulf depression (Gastil et al. 1979), and the contemporaneous Bouse Embayment (P. B. Smith 1970; Metzger 1968; Metzger et al. 1973; Lucchitta 1979) may have extended westward to approach the Death Valley Trough (Durham and Allison 1961; P. B. Smith 1960). Ingle (1973) and Shafiqullah et al. (1980) dated volcanics beneath both the Imperial and Bouse formations at 5.5–5.4 mya.

Interactions between the Pacific and North American plates shifted from west to east of the Baja California Peninsula after 5 mya, resulting in development of a spreading center and rapid peninsular separation from the Continent (Larson 1972; Karig and Jensky 1972; Mammerickx 1980; Hausback 1982). Northwest velocity of this peninsular splinter(s) has since varied because of irregular spreading centers and telescoping (Larson et al. 1968; Gastil et al. 1975). Displacement at the entrance of the Gulf of California totals 300 to perhaps 400 km (Bonneau 1971; Moore 1973; Gastil et al. 1981). Beck and Plumley (1979) and Karig (1979) suggested even greater movements based on paleomagnetic data.

What is now Basin and Range and Colorado Plateau (Fig. 15.2) were broadly uplifted during the Late Cretaceous to Eocene Laramide Orogeny (Coney 1973, 1976, 1978a,b; Damon

1979; Damon et al. 1981; Young 1979, 1982). Oligocene to present extension attributed to upwelling of asthenosphere to replace descending lithosphere of the Farallon Plate is believed responsible for (Dickinson 1979, 1981; Dickinson and Snyder 1979a) or a consequence of (Eaton 1979; Livaccari 1979; Ingersoll 1982b) early deformation of the Basin and Range (Fig. 15.3). Easterly to westerly crustal extension of 100–300% occurred over the past 30 my (Zoback et al. 1981; Wernicke et al. 1983a,b; Anderson et al. 1982). Perhaps 30% of the total extension has occurred since Middle to Late Miocene to Early Pliocene, when block-faulting produced existing parallel horsts and grabens (Zoback and Thompson 1978; Zoback et al. 1981; Nelson 1981; Anderson et al. 1983). Uplift elevated some graben floors from Early Tertiary levels of 300 m to their present 1500 m above sea level. Uplift was greatest centrally where basins now are 600 m higher than their counterparts along the eastern and western margins (Stewart 1978; Nelson 1981). Some southwestern basins experienced altitudinal depression. Death Valley, for example, has filled with 2.0 km of alluvium, yet its floor remains below sea level (Hunt and Mabey 1966; Hunt 1975). The previously mentioned shift of stress orientation at around 10 mya resulted in present differences in arrangement of basins and ranges in the Great Basin compared with that in southern regions.

Eastward compression of the Transverse Range before 5 mya was opposite the dextral rotation of the Colorado Plateau, jamming and largely neutralizing deformation to the south (Livaccari 1979). The Mohave Block and southern Basin and Range south of the Garlock Fault and Las Vegas Valley shear zone have since been relatively stable (Guth 1981; Zoback et al. 1981; Dokka 1983). Extension and shear north of the Garlock Fault and Las Vegas Valley shear zone, however, has accounted for east-west extension of at least 140 km between the southern Sierra Nevada and the western rim of the Colorado Plateau (Guth 1981; Royle 1983;

Wernicke et al. 1983a,b). For example, Stewart (1983) proposed detachment faulting that resulted in Late Cenozoic transport of the Panamint Range 80 km northwestward from the Black Mountains, forming the rifted area now occupied by Death Valley.

Extensional faulting in Miocene and into Pliocene and opening of the Rio Grande Rift (Elston and Bornhorst 1979; Kelly 1979; Chapin and Seager 1975; Chapin 1979; Gries 1979; Cape et al. 1983; Golombeck 1983) left the Colorado Plateau isolated by complexly faulted borderlands on the west, south and east (Hunt 1956; Kelly 1979; Shafiqullah et al. 1980; Humphrey and Wong 1983). Massive Pliocene-Pleistocene plateau uplift above surrounding Basin and Range was accepted by Eardley (1962), McKee and McKee (1972), Shoemaker (1975), Hamblin (1975) and others. Peirce (1976), Best and Hamblin (1978), Scarborough and Peirce (1978), Peirce et al. (1979), Young (1979, 1982) and Ulrich (1981) challenged this view on the basis of elevations of surrounding ranges and evidence for ancient development of a peripheral erosional scarp in Middle Tertiary, which indicate subsidence of surrounding regions rather than Plateau uplift.

Northwestern Mexico is dominated by the Sierra Madre Occidental (West 1964), which is bordered on the north and northeast by Basin and Range block faulting (or southern extensions of the Rio Grande Rift; Gries 1979) and west by a region of similar faulting (Fig. 15.2). Basin and Range formation progressed from the Rio Grande Rift around 27 mya (Chapin and Seager 1975; Chapin 1979), to 12–10 mya in Sonora (McDowell and Keizer 1977; Gastil and Krummenacher 1977), to around 7 mya in Baja California (Gastil et al. 1979, 1981; Cokka and Merriam 1982). Some vertical displacements on the west are greater than 1000 m and are dissected extensively by west-flowing rivers (King 1939).

Cenozoic history in northern Mexico involves a cycle of magmatism similar to that

described for western United States (Maldonado-Koerdell 1964). Volcanic activity moved eastward from the coast from the close of Cretaceous through Oligocene (Coney and Reynolds 1977; Gastil et al. 1979; McDowell and Clabaugh 1979; Clark et al. 1982), then reversed, so that by 20 mya volcanism again bordered the coast (McDowell and Keizer 1977; Shafiqullah et al. 1980; Gastil et al. 1981). Westward movement of magmatism corresponded with dilation of the Basin and Range and origin of the San Andreas Transform (Fig. 15.3). This volcanism formed the present Sierra Madre Occidental from 30 to 22 mya in the north (Karig and Jensky 1972; K. L. Cameron et al. 1980; M. Cameron et al. 1980) until 10–8 mya in the south (Watkins et al. 1971; McDowell and Keizer 1977; Mahood 1979; McDowell and Clabaugh 1979). The sequence presumably corresponded with north-to-south passage of the southern triple junction (Atwater 1970; McDowell and Clabaugh 1979; Keller et al. 1982), which now lies in the belt of active volcanism near and south of Mazatlán (Atwater 1970; Dickinson and Snyder 1979b). The Sierra Madre Occidental (Fig. 15.2) thus consists of a deeply eroded volcanic pile of Cretaceous-Early Tertiary rocks separated by unconformity from little faulted or tilted Middle Tertiary volcanics (McDowell and Clabaugh 1979; Cocheme 1981; Cocheme and Demant 1982a,b; Demant and Cocheme 1982; Keller et al. 1982; Gonzalez and Bartolini 1982). The present Sierra Madre Occidental stands similar to the Colorado Plateau, isolated on three sides by Basin and Range.

Paleohydrography

Rivers of our region are tightly constrained by structural geology. The tectonic history just outlined has resulted in complex paleohydrographic histories and has frequently obscured

evidence of drainage patterns. However, rivers respond in predictable ways to tectonic events and relationships of drainage history to tectonics, as outlined by Potter (1976), are applicable. Area cladograms (Figs. 15.4 and 15.5) provide a synopsis of geologic history of major drainage units in our region. Only broad paleohydrographic relations are discussed here, with details deferred for specific outlines of distributional relations of fish species and faunas.

Drainage in western North America after withdrawal of Cretaceous seas was largely east and/or north from western cordillera (Stokes 1979). Drainages of at least the region destined to become Basin and Range then were interrupted by the Laramide Orogeny (Coney 1976; Dickinson and Snyder 1978) to begin development of systems we see today.

As noted before, the Laramide Orogeny resulted not only in formation of the Rocky Mountain Axis, but also in broad uplift of at least parts of the Basin and Range and Colorado Plateau (Coney 1976, 1978a,b; Damon et al. 1981; Young 1982). Uplift stimulated a long period of erosion, resulting in development of a surface now represented by regional Eocene to Early Oligocene unconformities that extend from British Columbia to Mexico (Epis and Chapin 1975; Gressans 1981). Irregularities obviously existed, and Newman (1979) reviewed evidence for extensive development of closed basins in Late Cretaceous(?) to Eocene in what is now the Great Basin and the southern Basin and Range. Late Paleocene to Eocene intermontane basins that contained lakes existed in what is now Arizona and New Mexico (Eberly and Stanley 1978; Young and McKee 1978; Shafiqullah et al. 1980; Lucas and Ingersoll 1981; Young 1982), Nevada (Solomon et al. 1979; Fouch 1977, 1979), Wyoming, Colorado and Utah (the Green River Formation among others; Speiker 1946; Schaeffer and Mangus 1965; Fouch 1976; Mauger 1977; Buchheim and Surdam 1981; Smiley and Rember

1981) and eastern Oregon and Washington (Nilsen and McKee 1975). Most of these lacustrine habitats disappeared, however, by Eocene or Oligocene (Scarborough and Peirce 1978). Much of western Oregon and Washington, northern and southern California Coastal Ranges, and extreme northwestern Mexico were beneath or near sea level in Paleocene. Some allochthonous terranes of this region were yet to be emplaced. Parts of western Oregon and Washington yielded sediments eastward from coastal mountains (Nilsen and McKee 1979).

Headwaters of the Columbia River originate in the western Laramide region, and prior to Early Cenozoic drainage reversals passed north or northeast to Hudson Bay (McMillian 1973). This watershed extended in Late Miocene as far south as central Montana and South Dakota (Lemke et al. 1965) and perhaps to the upper Snake River and northern Bonneville regions (G. R. Smith 1975, 1981a).

Long before modern fishes appear in the fossil record, lands destined through rotation, extension and volcanism to become the lower Columbia River Basin produced Early and Middle Eocene alluvial fans termed the Tye Formation (Lovell 1969), which along with other fluvial sediments, indicate major streams flowing westward from Idaho and northern Nevada (Dott 1966, 1971). Late Eocene deltaic complexes in central Washington (Buckovic 1974, 1979) were from inland source areas of near 2100 m elevation (Axelrod 1968). The Eocene coastline was expanding through docking of allochthonous terranes such as the Oregon Coast Range (Magill and Cox 1981), volcanism and uplift and rotation (Hammond 1979).

What is now southwestern California (Figs. 15.2 and 15.3) accumulated Eocene deltaic gravels deposited by streams flowing west or southwest from Sonora (Fig. 15.3). Fluvial, lacustrine and marine sediments that broadly connected with Sonoran highlands east to west

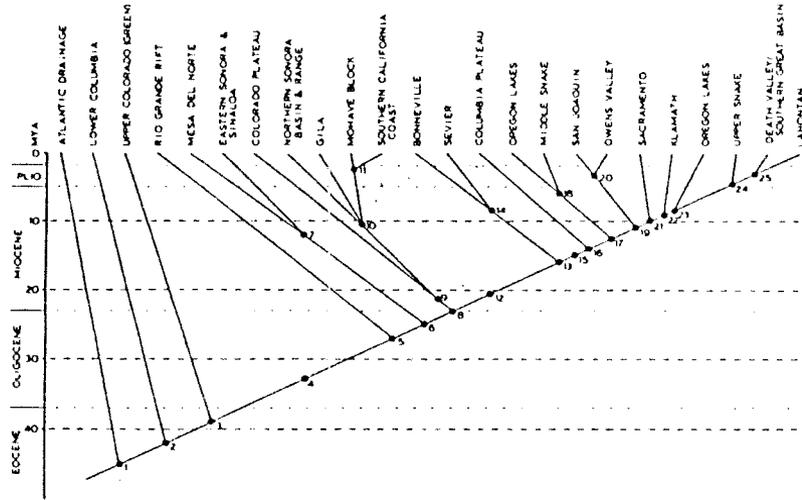


Figure 15.4 Simplified cladistic expression of probable area relationships of subregions east and north of present and proto-San Andreas Transform zone in western North America. Relationships are mostly inferred from timing and magnitude of major developments in structural relief. Areas are geographic/tectonic units that may have had varied hydrographic affinities through geologic time. Geological events, known and hypothesized interarea connections, and hydrographic relations are detailed in text. Nodes 1–25 denote the following: 1. end of Laramide Orogeny; 2. deposition of Tye Formation and associated deltaic sediments; 3. Wasatch-Uinta Disturbance; 4. establishment of Oligocene erosion surface; 5. initiation of Rio Grande Rift; 6. Sierra Madre Occidental volcanics (30–22 mya in north, 10–8 mya in south); 7. Basin and Range block faulting isolates Mesa del Norte; 8. collapse of Great Basin region; 9. development of southern margin of Colorado Plateau; 10. Basin and Range block faulting separates Gila River Basin from northern Sonora and Mohave Block; 11. uplift of southern California Coast and Peninsular ranges; 12. low-relief Great Basin surface; 13. Basin and Range block faulting in central Great Basin surface; 14. 45° shift in Great Basin stress axis; 15. extension of Basin and Range structure to area of Columbia Plateau and Snake River Plain; 16. Columbia Plateau basalts; 17. Snake River Plain volcanics; 18. Blue Mountains rotation and initial Modoc Plateau volcanics; 19. uplift of southern Sierra Nevada; 20. vicariance of upper San Joaquin and Owens valleys; 21. uplift and rotation of northern Sierra Nevada; 22. Cascade-Oregon Coast Range-Klamath rotation and volcanics; 23. vicariance of Klamath River and Oregon Lakes regions; 24. capture of upper Snake River by lower Columbia Basin; and 25. development of Sierra Nevada rainshadow.

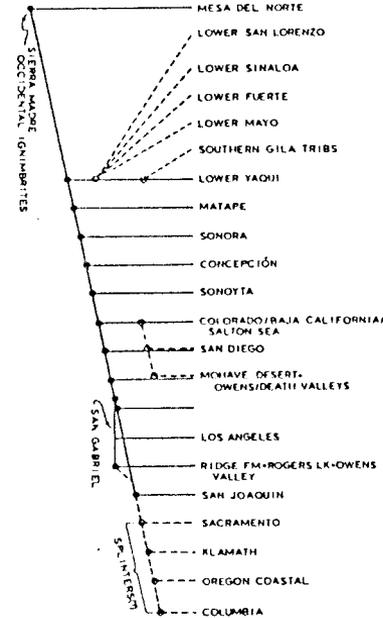


Figure 15.5 Diagram indicating possible biotic relationships among coastal drainages and regions resulting from transport of microplates along the western margin of North America. Dotted lines and open nodes are speculative; solid lines and nodes are based on geologic documentation provided in text.

are now displaced northwest to southern California, ranging from the Transverse Ranges (Woodford et al. 1968) south to near Isla Guadalupe (Doyle and Gorsline 1977) in both terrestrial and submarine deposition sites (Merriam 1965, 1968; Minch 1971, 1972; Sage 1973; Ehlig et al. 1975; Doyle and Gorsline 1977; Abbott and Smith 1978; Gastil et al. 1979, 1981; Abbott et al. 1982; others). There also is evidence for Eocene to Pliocene southwestward-

flowing drainages across western Sonora and from the Imperial Valley across the area of the Peninsular Range (Gastil et al. 1979). Westward-flowing drainages from the Mohave Desert and Sierra Nevada regions and eastward-flowing streams from offshore islands also contributed to alluvial fans along the California Coast (Nielsen and Clarke 1975; Graham and Berry 1979). The "San Joaquin River headed at least as far east as the present Mono Lake Basin, possibly farther north or east in Nevada, and its course across [the present] west slope of the Sierra Nevada was changed little since the Eocene . . ." (Huber 1981). This and other westward drainage from the Mohave Desert across the area now occupied by the Transverse Ranges may have persisted until interrupted by Pliocene uplifts (Woodburne 1975). A large westward-flowing system termed the Yuba River (Yeend 1974) also originated east of the present Sierra Nevada crest and deposited materials in what is now the central part of that range. Shallow seas in the Sacramento Trough and what is now the Northern California Coast Range also received continental materials from the east.

Through-flowing drainages of northwestern and central parts of Arizona passed northward toward Utah (Cooley and Davidson 1963; Young and Brennan 1974; Shafiqullah et al. 1978, 1980; Peirce et al. 1979; Scarborough and Peirce 1978; Young and McKee 1978; Nielsen and McKee 1979; Young 1982). Eocene drainage relations in northeastern Sonora presumably were also to the north and/or east (King and Adkins 1946).

Oligocene was marked by regression of coastal seas and deltaic and shallow-marine fluvial sedimentation along the California Coast (Fig. 15.3). The area of the present Transverse Range accumulated coarse basin-fill alluvium from both east and west (Bohannon 1975). The San Joaquin Trough was submerged, but the Sacramento Basin north of the Stockton Arch

was largely nonmarine and received fluvial sediments from rivers draining south and west (Dickinson et al. 1979). California was generally characterized by widespread, fluvial, synorogenic sedimentation from new source areas onto marine terraces (Nilsen 1982). Deposition of a Puget Delta was terminated by Early Oligocene eruptions of volcanics (Bucovic 1979) related to evolution and rotation of the Cascade Mountain Range (Hammond 1979). Reestablished volcanism deposited thick lenses of ash in preexisting lakes and formed other lakes, such as those of the John Day Basin of central Oregon (Robinson 1973).

Major Oligocene drainage in central and northern Arizona continued north and east into south-central Utah or into smaller closed basins (Young and Brennan 1974; Young and McKee 1978; Young 1982). Northward- or northeastward-flowing streams from central Arizona were in part interrupted by Late Oligocene (Peirce et al. 1979) to Miocene (Ulrich 1981) origin of the southern margin of the Colorado Plateau. Southward- or westward-flowing drainage remained in southern Arizona (Nilsen and McKee 1979) into the Miocene (Hunt 1969; see however Glazner 1982). Melton (1960) proposed a generally northeast-southwest trend in river channels of that area in pre-Miocene time, across what is now western New Mexico, east-central and southern Arizona and Sonora.

Formation of the Wasatch Front perhaps as early as Eocene (Cook and Berg 1961; Anderson and Mehnert 1979) and collapse of the Great Basin in the Late Oligocene isolated the upper Colorado River and Great Basin drainages. The Uinta Mountains became a drainage center for the Bear, Provo, Weber and Duchesne rivers. The Bear River may have been part of the Atlantic drainage via the Green and Platte rivers, while the Weber and Provo rivers entered the Great Basin and the Duchesne River flowed to the ancestral Colorado system (Stokes 1979). These divides were accentuated by fur-

ther uplift in Pliocene and Pleistocene (Best and Hamblin 1978).

North of the Basin and Range, the ancestral Columbia River maintained a course through the Cascade Mountain region during volcanism, faulting and folding associated with pluton intrusions and extruded volcanics of the Miocene (McKee et al. 1977; Swanson and Wright 1979; Camp and Hooper 1981; Camp 1981) (Fig. 15.3). East of the Cascades the drainage (including part of the Snake River Plain) was repeatedly overridden by volcanic flows 17–6 mya (Axelrod 1968; Suppe et al. 1975; McKee et al. 1977), resulting in mainly internal drainage (Fecht et al. 1982). The Miocene Columbia River Delta and other coastal structures were displaced northward, and basalts streamed through the lower Columbia River Gorge to extend west as a submarine flow. Depressions formed in Late Miocene-Pliocene by plateau subsidence and crustal faults were occupied by lakes and streams (Malde and Powers 1962; Malde 1965, 1972; Eaton et al. 1975; Armstrong et al. 1975), which were periodically filled by lavas. Late Miocene silicic volcanics progressed west to east across the Snake River Plain (Suppe et al. 1975) and flowed with reduced volume and extent into Late Pliocene. Lakes were common, yet rivers occupied essentially their present courses and have continued to do so for the past 14–12.5 my (Swanson and Wright 1979), maintaining integration by cutting and recutting of lava dams and filled canyons. The uppermost Snake River (above the Idaho-Oregon boundary) flowed southwesterly through southeastern Oregon across northwestern Nevada until it integrated with the lower Snake River in the Pliocene (Wheeler and Cook 1954; Malde 1965; Fecht et al. 1982).

Coastal Oregon, California and peninsular Baja California began to take on their present configuration at least by Miocene times (Fig. 15.3). Short precipitous streams developed along uplifted coastlines. Reactivation of the

San Andreas Transform and northwestern rafting of splinters of continental margin interrupted and further altered westward-flowing streams in the south and displaced alluvial fans and basin deposits northward (Bohannon 1975). No obvious major drainages existed in these areas in this time period (Nilsen and McKee 1979), perhaps because of truncated drainage areas and trends of increasing aridity.

Miocene through Pleistocene extension and faulting disrupted and obscured drainages throughout the Basin and Range. Massive accumulations of alluvium attest to extensive erosion throughout the region and resulted in the Late Miocene and Pliocene Baucarit and Maune sequences of Sonora and Sinaloa (King 1939; Hawley 1969; Clark 1976; Cocheme and Demant 1982a,b) and similar clastic alluvia in Arizona (Gilbert 1875; Nations et al. 1982). Extensive beds of lacustrine sediments, including evaporites, accumulated from Miocene through Recent in newly formed basins, and partially in old basins occupied by deformed earlier Tertiary deposits (Newberry 1870a et seq.; Hubbs and Miller 1948a; Feth 1961, 1964; Snyder et al. 1964; Hubbs et al. 1974; Stokes 1979; Nations et al. 1982). Internal drainages in grabens later began to coalesce. Superimposed channels were reoccupied (Melton 1960) and new waterways cut as structural troughs filled with alluvium from adjacent mountain ranges (McKee et al. 1967; Shafiqullah et al. 1978, 1980; Peirce et al. 1979). Ever-larger lacustrine habitats developed as drainage areas increased and precipitation and runoff were periodically adequate to maintain them.

The Humboldt Formation of northwestern Nevada (van Houten 1956) may be contemporaneous with outcrops of similar rocks in western Utah (Heylman 1965) and near Salt Lake (Stokes 1979) to document Miocene endorheic conditions in that region (Feth 1964). However, rivers flowed from northwestern Nevada to the Pacific over the present Sierra

Nevada axis in Miocene (Axelrod 1962). Miocene land surfaces destined to become the Sierra Nevada drained west to an ancestral Sacramento River (Dickinson et al. 1979). Pliocene uplifts added runoff to further the evolution of that drainage. Ancestral rivers now represented by the Yuba, Stanislaus, Tuolumne, Merced and San Joaquin flowed at gradients less than about 6.0 m/km (to as low as 1.0 m/km) into the Great Valley region (Wahrhaftig 1965; Christiansen 1966; Huber 1981). The San Joaquin Trough rose above the sea in Pleistocene to support a large lacustrine habitat (Feth 1964), which then disappeared to complete integration of the Sacramento-San Joaquin system (Figs. 15.2 and 15.3).

The upper Colorado River system must have originated before Miocene (Zettl 1975) as streams flowing from the uplifted Rocky Mountains over the gently sloping Colorado Plateau (see however Larson et al. 1975). Shoemaker (1975) placed drainage of the Plateau as entering the Basin and Range near what is now St. George, Utah, about 18 mya. However, it more likely deflected northeastward to pond in the Miocene Bidahochi Basin of Arizona, Colorado and New Mexico (Uyeno and Miller 1965) or through the Grand Wash area to terminate in the Hualapai (Red) Lake Basin of northwestern Arizona (Lovejoy 1980).

Integration of the upper and lower Colorado River systems over the Colorado Plateau and through Basin and Range has long been debated (Blackwelder 1934; Longwell 1946, 1963; Hunt 1956, 1969; McKee et al. 1967; Young 1970). It now is known to have occurred between 10.6 and 3.3 mya, both as a result of headward erosion and through reoccupation and reversal of flow in older channels (Damon et al. 1978; Lucchitta 1972, 1979; McKee and McKee 1972; Lovejoy 1980; Shafiqullah et al. 1980; Young 1982). The Colorado River reached the Parker, Arizona, area after deposition of the estuarine Bouse Formation (about 5.5 my old; Metzger 1968; Metzger et al. 1973; Shaf-

iqullah et al. 1980) and encountered the upper Gulf of California in Pliocene, resulting in rapid and extensive filling of the embayment and southward migration of the river's mouth (Merriam and Bandy 1965; Henyey and Bischoff 1973; Olmsted et al. 1973; Crowell 1981). Similar integration of internal drainages such as the Sevier River Basin, Utah (Rowley et al. 1981), also is apparent.

Gila River, now the major tributary to the lowermost Colorado, also became through-flowing in its lower portion between 10.5 and 6.0 mya (Eberly and Stanley 1978) following a period of discharge into closed basins (Nations et al. 1982). According to Shafiqullah et al. (1980) the Gila River began to enter the Gulf of California less than 5.5 mya. Other streams of the southern Colorado Plateau Borderlands (for example, the Verde and Salt rivers, Arizona) flowed south and/or west through structural troughs to enter closed basins or perhaps the sea by Late Miocene (Melton 1960; Deal et al. 1978; Eberly and Stanley 1978; Shafiqullah et al. 1980; Nations et al. 1981, 1982). The uppermost Gila River flowed south into Mexico for a time before final integration with its lower segment in Pleistocene (Melton 1960; Kottowski et al. 1965).

In Mexico, stream drainage east of the Sierra Madre Occidental continued eastward, but probably by Miocene and certainly by Pliocene times these watercourses terminated in closed basins of the Mesa del Norte (Burrows 1910; Brand 1937; Reeves 1969; Strain 1970). Drainage integration of streams to the Pacific must have resembled that of the Colorado River. Structural troughs and deeply cut channels exist that predate Basin and Range formation (Albritton 1958; Melton 1960; Shafiqullah et al. 1980; Bilodeau 1982a,b). Lakes and streams amalgamated to form complex modern drainages that remain characterized by inverted entry of tributaries (Hovey 1905, 1907) and apparent structural control of major channels (Hendrickson et al. 1981; Demant and Cocheme 1982; Cocheme and Demant 1932a).

Paleoclimatology

Much of western North America is now classed as desert; evapotranspiration greatly exceeds precipitation. Air movements over the Sonoran and Chihuahuan deserts (23°–30°N) are controlled by permanent high-pressure cells within which air descends from high altitudes (Vivo-Escoto 1964; Crosswhite and Crosswhite 1982). Adiabatic warming of 10°C per 1000 m results in hot, dry conditions. Aridity of the Chihuahuan Desert also is greatly influenced by its inland position (Medellin-Leal 1982).

North of 30° latitude the Mohave and Great Basin deserts become less influenced by high pressure and more by their inland positions relative to oceanic water sources and by rain shadows of the Sierra Nevada and Cascades to the west and Rocky Mountains to the east. Both northern deserts are seasonally cold due to winter invasion of polar air (Fowler and Koch 1982; Rowlands et al. 1982). The extreme aridity of Baja California results from the near-shore, cold California Current. Air aloft is hot and dry, moist air near the cool ocean surface is too small in volume to produce rainfall and surficial thermal inversion prevents convection that might result in precipitation (Crosswhite and Crosswhite 1982). Climatic conditions on highlands of the west are influenced by latitude, altitude and distance from and orientation to the sea, but are more mesic than lowlands, especially along coastlines and in the Pacific Northwest.

Climate has varied over geologic time as a result of: (1) changes in latitude of continents; (2) altitude changes; and (3) world-wide or broadly regional fluctuations associated with glaciation. North America has moved generally southwestward since Mesozoic for at least 6° in latitude (based on the fixed point of Death Valley, California), remaining within the temperate zone of westerly winds (Dickinson 1981). Regional tectonic and climatic events unrelated to latitude changes thus have been more

important in shaping Cenozoic climatic conditions.

G. R. Smith (1978, 1981b) and M. L. Smith (1981) reviewed Cenozoic climatic changes as pertain to fishes in western North America between 23° and about 44° N latitude. Most paleoclimatological interpretations, including theirs, are based on occurrences and distributions of fossil floras. Axelrod (1948, 1950, 1958, 1979) reviewed regional paleobotany and included broad paleoclimatic interpretations in his 1979 treatise. Modern vegetation was reviewed in contributions assembled by Bender (1982) and Brown (1982).

Warm, moist, subtropical climate prevailed at close of Cretaceous (Lowenstam 1963), and mesophytic tropical forests of ferns, gymnosperms and evergreen and deciduous angiosperms persisted through Paleocene and locally into Eocene (Brown 1962; Leopold and MacGinitie 1972; Axelrod and Bailey 1976; Ely et al. 1977; Wolfe 1978). Sufficient heterogeneity existed in the Great Basin in Middle Eocene for evolution of plants adapted to locally arid conditions. Climatic change during Oligocene was toward cooler, drier and more variable conditions (Barghorn 1953; Frakes and Kemp 1973; Wolfe 1978), and Madro-Tertiary floras (Axelrod 1958) spread over a semiarid interior (Axelrod 1950, 1979). Montane floras of the Great Basin resembled the present conifer-deciduous forests, of northwestern California, coast redwood and spruce-hemlock, with admixtures of shrubs and deciduous hardwoods (Axelrod 1966). From Eocene to Early Miocene times, with some exceptions, montane coniferous forests were above 1220 m elevation, conifers and mixed hardwoods lived at 900 m and deciduous hardwoods prevailed near 300 m (Axelrod 1950, 1966).

Remnants of subtropical vegetation were essentially replaced by temperate floras during Late Miocene through Pliocene (Dorf 1959) when rifting and extensional faulting were accompanied by further trends toward cooler drier climate (Dorf 1930; Chaney 1944; Axelrod

1950 et seq.; Smiley 1953; Hoover et al. 1982). Lowlands of the northern Great Basin were occupied in Miocene by an Arcto-Tertiary flora of temperate hardwood-deciduous and coniferous forest. More southern latitudes supported oak woodland, chaparral, thorn forest and semidesert Madro-Tertiary assemblages (Axelrod 1950, 1979). The northern assemblage indicates uniformly distributed precipitation of between 90 and 130 cm per year under a cool-temperate regime, while southern associations required between 40 and 65 cm per year, warm summers and mild winters. Miocene-Pliocene floras from New Mexico and Arizona indicate increasing aridity and modernization toward more xeric assemblages. Through Miocene to Late Pliocene, floral elements of the present deserts assembled on drier slopes and in lowlands (Axelrod 1950, 1956, 1979). This was in part a function of relative elevational change, where low-elevation or warm climate plants were enhanced in subsiding basins adjacent to forested highlands (Axelrod and Bailey 1976; Nations et al. 1981, 1982).

Local and regional uplift in Miocene through Pleistocene undoubtedly resulted in increased montane precipitation (for example, Larson et al. 1975) reflected in floras, and in increased rain-shadow effects promoting aridity in lowlands. Uplift of the Sierra Nevada and Cascades at end of Miocene and later accentuated inland drying trends. Compositions of Late Miocene and Early Pliocene Great Basin floras demonstrate the Sierra Nevada axis as a relatively ineffective rain shadow. Late Pliocene floras clearly show climatic influences of that range (Axelrod 1957, 1962; Hoover et al. 1982). Temperatures were higher and more constant over the year in Early Pliocene (Antevs 1952). By Middle Pliocene, winter and summer temperatures were distinctly different and precipitation was reduced. A cooling trend toward glaciation began in Late Pliocene.

Local Pliocene-Pleistocene montane glaciation began about 3 mya (Morrison 1964, 1965a;

Curry 1966; Merrill and P'ewé 1977). Paleobotanical and geologic evidence indicate a continuation of inland aridity (Mannion 1962; Snyder and Langbein 1962). The apparent inconsistency of vast Pleistocene lakes in the face of a continued trend toward aridity is explained not by glacially derived waters, but rather by modest increases in precipitation and cooler temperatures that reduced evapotranspiration rates (Morrison 1965a; Brackenridge 1978; Mifflin and Wheat 1979; Scott et al. 1982). These lakes fluctuated in a manner indicating increased climate variability as one approached the present (Meinzer 1922; Antevs 1925 et seq.; Snyder and Langbein 1962; Mifflin and Wheat 1979). Substantial short-term climatic fluctuations in Pleistocene are also well documented by development of soils (Morrison 1961a-d, 1964, 1965a-c) and by changes in distribution of fossil and relict biotic elements (Hibbard 1960; Milstead 1960; J. H. Brown 1971; M. L. Smith et al. 1975; Mehlinger 1977; van Devender and Wiseman 1977; Metcalf 1978; van Devender and Spaulding 1979; others). Origin and organization of vegetative communities of deserts were postglacial (Wells 1966, 1978, 1983; van Devender 1977; Axelrod 1979), reflecting conditions warmer and more arid than before recorded in the region.

Whether these broad patterns are applicable to Mexico is conjectural. However, much of Axelrod's (1979) treatise on the Sonoran Desert discussed fossil floras that had been displaced northwestward from Mexico to California; generalizations should thus apply. The gradient from cool in the north to warm at southern latitudes was low in Late Cretaceous and Early Tertiary (Lowenstam 1963; Frakes and Kemp 1973) and became increasingly pronounced to Recent (with obvious oscillations in Pliocene-Pleistocene) south to at least 25°N latitude. Interpretation of Late Cretaceous-Early Tertiary precipitation patterns indicates an arid zone in what is now Sonora, with increased

precipitation both north and south. Drying apparently radiated from this focal zone of aridity through Cenozoic (Axelrod 1979). However, evidence of relative climatic stability in north-central and central Mexico during Pleistocene climatic oscillations indicates amelioration of Tertiary trends in that region (Clements 1963; Bradbury 1971; M. L. Smith et al. 1975; Watts and Bradbury 1982).

ZOOGEOGRAPHY

Fishes of the Region

R. R. Miller's (1959a) "Origin and Affinities of the Freshwater Fish Fauna of Western North America" provides an excellent introduction and is largely paraphrased here, with modifications in numbers of taxa and some interpretations reflecting taxonomic changes and additions to knowledge in the intervening years. Sixty-nine families including some 334 species are native to nonmarine habitats of the region (Tables 15.1 and 15.2). Nine families and 107 species consist of primary or secondary fishes (Myers 1938, 1951; Darlington 1957), which we emphasize here. Primary fishes, with a few exceptions, are restricted to fresh waters throughout their life histories, and secondary species are largely so, but are salt tolerant and thus capable of crossing narrow brackish or marine barriers. A more flexible categorization of fishes for zoogeographic studies includes freshwater dispersants (primary and secondary fishes of Myers) whose distributions reflect restriction to freshwater habitats or dispersal over short distances through sea water, the last of which often may be more readily explained by plate tectonics (Rosen 1974, 1975a). Saltwater dispersants are fishes whose distributions may be explained by movements through the sea (Moyle and Cech 1982).

Of the other 60 families, 35 include predominantly marine dispersants that enter riv-

ers to a limited distance from the sea. Numbers of such species vary inversely with latitude. Included here are elopids, some clupeids, osmerids, ariids, atherinids, centropomids, lutjanids, mugilids, eleotrids, gobiids and others. Species representing the families Petromyzontidae, Acipenseridae, some Osmeridae and Salmonidae regularly complete parts of their life cycles both in fresh- and saltwater habitats at northern latitudes, and some species of each are now restricted to fresh waters. Species of four additional families of marine origins, now virtually limited to inland habitats, include a clupeid, an embiotocid, a gobioid and numerous cottids. One family, Gasterosteidae, includes a species that completes its life cycle either in fresh- or saltwater habitats.

Only about one-half as many families and one-fourth as many species of freshwater dispersants occupy western drainages as compared with eastern North America (R. R. Miller 1959a). However, endemism is high in these western families and in petromyzontids, salmonids and cottids. Species of restricted distributions, defined as isolated in a single spring, stream or lake basin, are a significant percentage of the fauna. Species common over wide geographic areas (even when in disjunct populations) are exceptional; some may prove on careful study to comprise more than one species.

Coastal Oregon and Northern California

Coastal Streams of Oregon

From the Necanicum River on the north to the Siuslaw River, Oregon coastal streams are separated from the Columbia River system by the Coast Range summit. South of the Siuslaw, northern tributaries of the Umpqua River have a similar relationship to the Columbia, but the Umpqua has cut through the Coast

Range so the North Umpqua drains from the Cascade Mountains and the South Umpqua flows through a valley between the Cascades and the Coast Range, also draining a portion of the Klamath Mountains on the south. The Coos River drains the Coast Range between the Umpqua and Coquille rivers, southern tributaries of which flow from the Klamath Mountains. The remaining coastal streams, from Sixes River to Chetco River, drain the Klamath Mountains, with some eastern tributaries of the Rogue River flowing from the Cascades.

According to Baldwin (1981), valleys of the Coast Range were eroded during a time of general Pliocene and Pleistocene uplift. These independent drainages have therefore been isolated from the Columbia and other systems at least since Early Pliocene. Early isolation apparently held until Recent, so that original fish colonists of coastal streams were mostly saltwater dispersants or freshwater forms with marine relationships and relatively wide distributions. The Rogue River continued to flow westward through the Klamath Mountains during Late Cenozoic uplift and has maintained ancient isolation from other coastal systems.

The Klamath River consists of discrete upper and lower segments separated by Klamath Falls. The lower portion taxonomically resembles Rogue River and other coastal streams. The upper supports a fauna sharply separated from the lower, and from those of both the Sacramento and Columbia rivers (Table 15.1). Physical evidence for drainage relationships is obscured by regional and local volcanism (Peacock 1931; Anderson 1941; Pease 1965; McKee et al. 1983).

Little ichthyological exploration was carried out in this region prior to the 1890s, a notable exception being Cope's (1879b, 1883b) reports on Klamath Lake fishes. C. H. Gilbert (1897) dealt with fishes of the Klamath River Basin, and Evermann and Meek (1897) reported on

Table 15-1. Freshwater Fishes Recorded from North America West of the Continental Divide, South of the Columbia River Basin, and North of the Río Grande de Santiago Basin

Taxa	Habitat											Drainage Occurrence													
	Euryhaline	Lowland	Upland	Montane	Big River	Stream	Creek	Lacustrine	Spring isolate	Oregon → North California Coastal	Klamath River	"Oregon Lakes"	Lahontan Basin	Bonneville Basin	North-Central Basins	Death Valley "System"	Sacramento River	Colorado River	South California Coastal	Sonoran Coastal	Río Yaqui → Río San Lorenzo	Sinaloa Coastal	Río San Pedro		
Petromyzontidae																									
<i>Lampetra ayrai</i>																									
<i>L. lethopluaga</i>						X	X																		
<i>L. minima</i>				X		X	X	X																	
<i>L. pacifica</i>						X	X	X																	
<i>L. richardsoni</i>						X	X	X																	
<i>L. tridentata</i>						X	X	X																	
Acipenseridae																									
<i>Acipenser medirostris</i>	X	X			X																				
<i>A. transmontanus</i>	X	X			X																				
Clupeidae																									
<i>Dorosoma smithi</i>	X				X																				
Salmonidae																									
<i>Oncorhynchus gorbuscha</i>	X	X	X		X	X																			
<i>O. teta</i>	X	X	X		X	X																			
<i>O. tshawytscha</i>	X	X	X		X	X																			
<i>O. nerka</i>	X	X	X		X	X																			
<i>Prosopium abyssicola</i>	X	X	X		X	X																			
<i>P. gemmiferum</i>																									
<i>P. spilonotus</i>																									
<i>P. williamsi</i>																									
<i>Salmo gairdneri</i>																									
<i>S. apache</i>																									
<i>S. chrysogaster</i>																									
<i>S. clarki</i>																									
<i>S. gairdneri</i>																									
Salmonidae																									
<i>S. gilae</i>						X	X																		
<i>Salmo</i> sp. (redband)						X	X																		
<i>Salmo</i> sp. (Yaqui)						X	X																		
<i>Salvelinus confluentus</i>						X	X																		
Osmertiidae																									
<i>Hypomesus transpacificus</i>	X	X			X																				
<i>Spirinchus thaleichthys</i>	X	X			X																				
<i>Thaleichthys pacificus</i>	X	X			X																				
Cyprinidae																									
<i>Acrocheilus alutaceus</i>					X	X	X																		
<i>Agozia chrysogaster</i>					X	X	X																		
<i>Camptostoma ornatum</i>					X	X	X																		
<i>Cadoma ornata</i>					X	X	X																		
<i>Dionda</i> sp.					X	X	X																		
<i>Eremichthys acares</i>					X	X	X																		
<i>Gila alboridensis</i>					X	X	X																		
<i>G. atraria</i>					X	X	X																		
<i>G. bicolor</i>					X	X	X																		
<i>G. borealis</i>					X	X	X																		
<i>G. coerulea</i>					X	X	X																		
<i>G. conspersa</i>					X	X	X																		
<i>G. copei</i>					X	X	X																		
<i>G. crassicauda</i>					X	X	X																		
<i>G. cypha</i>					X	X	X																		
<i>G. diazemia</i>					X	X	X																		
<i>G. elegans</i>					X	X	X																		
<i>G. intermedia</i>					X	X	X																		
<i>G. orcutti</i>					X	X	X																		
<i>G. purpurea</i>					X	X	X																		
<i>G. robusta</i>					X	X	X																		
<i>Gila</i> sp. (El Salto)					X	X	X																		
<i>Gila</i> sp. (Yaqui-Mayo)					X	X	X																		
<i>Hyporhamphichthys symmetricus</i>					X	X																			
<i>Hyporhamphichthys crameri</i>					X	X																			
<i>Isoichthys phlegmeonis</i>					X	X																			
<i>Lacina exilicauda</i>					X	X																			
<i>Lepidomeda albatris</i>					X	X																			
<i>L. altivelis</i>					X	X																			
<i>L. mollispinnis</i>					X	X																			
<i>L. vitata</i>					X	X																			

Table 15.1 (Continued)

Taxa	Habitat										Drainage Occurrence														
	Euryhaline	Lowland	Upland	Montane	Big River	Stream	Creek	Lacustrine	Spring isolate	Oregon → North California Coastal	Klamath River	"Oregon Lakes"	Lahontan Basin	Bonneville Basin	North-Central Basins	Death Valley "System"	Sacramento River	Colorado River	South California Coastal	Baja California	Sonoran Coastal	Rio Yaqui → Rio San Lorenzo	Sinaloa Coastal	Rio San Pedro	
Cyprinidae (Continued)																									
<i>Mela fulgida</i>			X			X			X										N**						
<i>Moxpa coriacea</i>						X													N**						
<i>Mylioparodon conocephalus</i>			X		X	X																			
<i>Notropis cf. calienis</i>			X	X	X	X																			
<i>N. formosus</i>			X	X	X	X																			
<i>Orthodon microlepidotus</i>			X																						
<i>Plagopterus argenteus</i>			X		X	X																			
<i>Pogonichthys cisoides</i>			X		X	X		X																	
<i>P. macrolepidotus</i>			X		X	X		X																	
<i>Pygochrotus grandis</i>			X		X	X		X																	
<i>P. lucius</i>			X		X	X		X																	
<i>P. oregonensis</i>			X		X	X		X																	
<i>P. umpiquae</i>			X		X	X		X																	
<i>Relictus solitarius</i>			X		X	X		X																	
<i>Rhinichthys cataractae</i>			X	X	X	X		X																	
<i>Rhinichthys dawsoni</i>			X		X	X		X																	
<i>R. evermanni</i>			X		X	X		X																	
<i>R. ocellus</i>			X		X	X		X																	
<i>R. (Aploche) sp.</i>			X		X	X		X																	
(Bonneville Desert)			X		X	X		X																	
<i>Richardsonius balteatus</i>			X		X	X		X																	
<i>R. egregius</i>			X		X	X		X																	
<i>Tiaroga cobitis</i>			X		X	X		X																	

Caetostomidae

<i>Caetostomus ardens</i>						X																				
<i>C. bernardini</i>			X		X	X		X																		
<i>C. columbianus</i>			X		X	X		X																		
<i>C. funeiventris</i>			X		X	X		X																		
<i>C. insignis</i>			X		X	X		X																		
<i>C. latipinnis</i>			X		X	X		X																		
<i>C. luazius</i>			X		X	X		X																		
<i>C. macrocheilus</i>			X		X	X		X																		
<i>C. microps</i>			X		X	X		X																		
<i>C. occidentalis</i>			X		X	X		X																		
<i>C. rimitulus</i>			X		X	X		X																		
<i>C. snyderi</i>			X		X	X		X																		
<i>C. laboensis</i>			X		X	X		X																		
<i>C. uarnerensis</i>			X		X	X		X																		
<i>C. longirostris</i>			X		X	X		X																		
<i>Caetostomus sp.</i>			X		X	X		X																		
(Surprise Valley)			X		X	X		X																		
<i>Caetostomus sp.</i>			X		X	X		X																		
(Yaqui-Guzmán)			X		X	X		X																		
<i>Caetostomus sp.</i>			X		X	X		X																		
(Yaqui-Mayo)			X		X	X		X																		
<i>Pantosteus clarkei</i>			X		X	X		X																		
<i>P. discobolus</i>			X		X	X		X																		
<i>P. polytrichus</i>			X		X	X		X																		
<i>P. plebeius</i>			X		X	X		X																		
<i>P. cf. plebeius</i>			X		X	X		X																		
<i>P. santanae</i>			X		X	X		X																		
<i>Chasmistes brevis</i>			X		X	X		X																		
<i>C. culius</i>			X		X	X		X																		
<i>C. liurus</i>			X		X	X		X																		
<i>Maxiostoma ausirinum</i>			X		X	X		X																		
<i>Yariyachem levanus</i>			X		X	X		X																		
Ictaluridae																										
<i>Ictalurus cf. latus</i>			X		X	X		X																		
<i>I. pricei</i>			X		X	X		X																		
Cyprinodontidae																										
<i>Cyprinodon diabolis</i>			X		X	X		X																		
<i>C. macularius</i>			X		X	X		X																		
<i>C. meeki</i>			X		X	X		X																		
<i>C. nevadensis</i>			X		X	X		X																		
<i>C. radiosus</i>			X		X	X		X																		

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Table 15.1 (Continued)

Taxa	Habitat										Drainage Occurrence														
	Euryhaline	Lowland	Upland	Montane	Big River	Stream	Creek	Lacustrine	Spring isolate	Oregon → North California Coastal	Klamath River	"Oregon Lakes"	Lahontan Basin	Bonneville Basin	North-Central Basins	Death Valley "System"	Sacramento River	Colorado River	South California Coastal	Baja California	Sonoran Coastal	Rio Yaqui → Rio San Lorenzo	Sinaloa Coastal	Rio San Pedro	
Cyprinodontidae (Continued)																									
<i>C. salinus</i>	X	X	-	-	-	X	X	-	X	-	-	-	-	-	N	-	-	-	-	-	-	-	-	-	-
<i>Cyprinodon</i> sp. (whitfin)	X	-	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	N	-	-	-
<i>Cyprinodon</i> sp. (Monkey Spring)	X	-	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goodeidae																									
<i>Charracodon lateralis</i>	-	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cremichthys baileyi</i>	-	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. nevadæ</i>	-	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Empetrichthys latos</i>	-	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>E. merrilli</i>	-	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poeciliidae																									
<i>Poecilia butleri</i>	X	X	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Poeciliopsis latidens</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. lucida</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. monacha</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. occidentalis</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. presidiensis</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. prolifica</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. virgosa</i>	-	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atherinidae																									
<i>Chirosolema jordani</i>	-	-	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae																									
<i>Gasterosteus aculeatus</i>	X	X	X	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Centrarchidae																									
<i>Ancistrilites interruptus</i>	-	X	-	-	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Percidae																									
<i>Etheostoma pottsi</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cichlidae																									
<i>Cichlasoma beanii</i>	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Embiotocidae																									
<i>Hysteroacarpus traski</i>	X	X	X	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae																									
<i>Cottus bairdii</i>	X	X	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. asper</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. asperimus</i>	-	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. bairdi</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. beldingi</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. echinatus</i>	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. extensus</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. gulosus</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>G. klamathensis</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. perplexus</i>	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. pinensis</i>	-	-	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. princeps</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. rotheus</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. tenuis</i>	-	-	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cobiesocidae																									
<i>Gobiosoma fluviatilis</i>	-	-	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Compiled from literature cited in text. Included are species known to reproduce in freshwater habitats; some families with marine representatives also are included in Table 15.2. Symbols: X = typical habitat; N = native occurrence; NI = possibly introduced; EX = extinct; - = not recorded; * = upper Klamath River (above Klamath Falls) or upper Colorado River (above Lees Ferry, Arizona) or upper Rio San Pedro (= Rio Mezquital); ** = lower Klamath River (below Klamath Falls) or middle Colorado River (Grand Canyon segment, including White River of eastern Nevada) or lower Rio San Pedro; and *** = lower Colorado River (including Gila River). Absence of an asterisk denotes occurrence throughout the system concerned.

Table 15.2 Fishes of Marine Derivation Recorded from Continental Waters of Oregon, California, Peninsular Baja California and northwestern mainland Mexico.

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloan Coastal
Squalidae							
<i>Squalus acanthius</i>	U	X	U	-	-	-	-
Carcharhinidae							
<i>Carcharinus leucus</i>	-	-	U	U	-	U	X
<i>C. porosus</i>	-	-	U	U	-	U	X
<i>Mustelus californicus</i>	-	X	U	U	-	U	X
<i>M. henlei</i>	-	X	U	U	-	U	-
<i>Negaprion brevirostris</i>	-	-	U	-	-	-	X
<i>Rhizoprionodon longurio</i>	-	-	U	-	-	-	X
Sphyrnidae							
<i>Sphyrna tiburo</i>	-	-	U	U	X	X	X
Pristidae							
<i>Pristis pectinatus</i>	-	-	-	-	-	-	X
<i>P. perotlei</i>	-	-	-	U	-	-	X
Rhinobatidae							
<i>Rhinobatos glaucostigma</i>	-	-	-	-	-	-	X
Torpedinidae							
<i>Narcine brasiliensis</i>	-	-	-	X	X	X	X
Rajidae							
<i>Raja binoculata</i>	U	X	U	-	-	-	-
Urolophidae							
<i>Urotrygon binghami</i>	-	-	-	X	X	X	X
Mylobatidae							
<i>Aetobatus narinari</i>	-	-	-	X	-	X	X
<i>Myliobatis californicus</i>	U	X	U	U	-	U	-
Rhinopteridae							
<i>Rhinoptera steindachneri</i>	-	-	-	U	X	X	X
Elopidae							
<i>Elops affinis</i>	-	-	X	U	X	X	X
Aibulidae							
<i>Albula vulpes</i>	-	U	X	U	X	U	X
Chanidae							
<i>Chanos chanos</i>	-	-	-	-	-	-	X
Clupeidae							
<i>Clupea harengus</i>	X	X	X	-	-	-	-
<i>Harengula thrissina</i>	-	-	X	X	-	U	U

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloan Coastal
Clupeidae (Continued)							
<i>Lile stolifera</i>	-	-	-	-	-	X	X
<i>Opisthonema libertate</i>	-	-	X	X	X	X	X
Engraulidae							
<i>Anchoa arenicola</i>	-	-	-	-	-	-	X
<i>A. compressa</i>	-	-	X	-	-	-	-
<i>A. curta</i>	-	-	-	-	X	X	X
<i>A. delicatissima</i>	-	-	X	-	-	-	-
<i>A. helleri</i>	-	-	-	X	X	U	U
<i>A. ischana</i>	-	-	X	X	X	U	X
<i>A. lucida</i>	-	-	-	-	-	U	U
<i>A. mundeoloides</i>	-	-	-	X	X	U	U
<i>A. panamensis</i>	-	-	-	-	-	-	X
<i>A. scofieldi</i>	-	-	-	-	-	-	X
<i>A. schultzi</i>	-	-	-	-	X	X	-
<i>Anchoviella analis</i>	-	-	-	-	-	X	X
<i>A. miaracha</i>	-	-	X	-	-	-	X
<i>Anchovia macrolepidota</i>	-	-	X	X	X	X	X
<i>Cetengraulis mysticetus</i>	-	-	X	U	X	U	U
<i>Engraulis mordax</i>	U	X	U	-	-	-	-
Osmeridae							
<i>Allosmerus elongatus</i>	U	X	U	-	-	-	-
<i>Hypomesus pretiosus</i>	X	X	X	-	-	-	-
<i>Spirinchus starksi</i>	U	X	-	-	-	-	-
Ariidae							
<i>Arius caeruleus</i>	-	-	-	U	X	X	X
<i>A. gualanensis</i>	-	-	-	-	-	-	X
<i>A. jordani</i>	-	-	-	-	-	-	X
<i>A. liroyus</i>	-	-	-	-	-	X	U
<i>A. secmani</i>	-	-	-	-	-	X	X
<i>Bagre panamensis</i>	-	-	X	U	X	U	X
<i>B. pinnimaculatus</i>	-	-	-	-	X	-	X
<i>Netuma kessleri</i>	-	-	-	-	-	-	X
<i>N. planiceps</i>	-	-	-	-	-	-	X
<i>N. platypogon</i>	-	-	-	-	-	-	X
<i>Sciadeichthys trocheli</i>	-	-	-	-	-	-	X

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloa Coastal
Synodontidae							
<i>Synodus scituliiceps</i>	-	-	X	U	X	U	X
Ophichthidae							
<i>Myrophis vafer</i>	-	U	U	U	-	U	X
<i>Ophichthus triserialis</i>	U	U	X	X	X	X	X
Scomberesocidae							
<i>Cololabis saira</i>	U	X	-	-	-	-	-
Hemiramphidae							
<i>Hyporhamphus roberti</i>	-	-	-	-	-	-	X
<i>H. rosae</i>	-	-	X	U	-	U	X
<i>H. snyderi</i>	-	-	X	X	-	-	U
Belontiidae							
<i>Tylosurus exilis</i>	-	U	X	U	-	U	X
Atherinidae							
<i>Atherinops affinis</i>	U	X	X	U	-	U	-
<i>A. regis</i>	-	-	-	U	-	X	-
<i>Atherinopsis californiensis</i>	U	X	U	-	-	-	-
<i>Eurystole eriarcha</i>	-	-	X	U	-	U	X
<i>Hubbsia gilberti</i>	-	-	-	X	-	X	U
<i>Hubbsiella sardina</i>	-	-	-	U	X	X	-
<i>Melaniris crystallina</i>	-	-	-	-	-	-	X
<i>M. evermanni</i>	-	-	-	-	-	-	X
<i>Nectargas nephente</i>	-	-	X	X	-	-	X
Sygnathidae							
<i>Pseudophallus starksi</i>	-	-	X	X	-	-	X
<i>Sygnathus leptorhynchus</i>	U	X	X	-	-	-	-
Merlucciidae							
<i>Merluccius productus</i>	U	X	U	U	-	-	-
Gadidae							
<i>Microgadus proximus</i>	U	X	U	-	-	-	-
Polynemidae							
<i>Polydactylus approximans</i>	-	-	-	-	-	-	X
Scomberidae							
<i>Scomberomorus maculatus</i>	-	-	-	-	-	-	X
Carangidae							
<i>Caranx hippos</i>	-	-	X	U	-	X	X
<i>C. marginatus</i>	-	-	-	-	-	-	X

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloa Coastal
Carangidae (Continued)							
<i>C. speciosus</i>	-	-	-	-	-	-	X
<i>C. vinctus</i>	-	-	-	-	-	-	X
<i>Citula dorsalis</i>	-	-	-	-	-	-	X
<i>Oligoplites altus</i>	-	-	-	X	-	-	-
<i>O. saurus</i>	-	-	-	X	-	-	-
<i>Trachinotus paloma</i>	-	-	X	X	-	X	X
Centropomidae							
<i>Centropomus armatus</i>	-	-	-	-	-	-	X
<i>C. nigrescens</i>	-	-	-	-	-	X	X
<i>C. robalitos</i>	-	-	-	U	-	-	X
<i>C. undecimalis</i>	-	-	-	X	-	-	X
Lutjanidae							
<i>Hoplopargus guentheri</i>	-	-	-	X	-	U	X
<i>Lutjanus arlatius</i>	-	-	-	-	-	-	X
<i>L. argentiventris</i>	-	-	-	X	-	-	X
<i>L. colorado</i>	-	-	-	X	-	X	X
<i>L. novemfasciatus</i>	-	-	X	X	-	X	X
<i>Rabirubia inermis</i>	-	-	-	-	-	-	X
Pomadasiidae							
<i>Conodon nobilis</i>	-	-	X	X	-	-	X
<i>Haemulon scudleri</i>	-	-	X	X	-	-	X
<i>H. steindachneri</i>	-	-	-	U	-	-	X
<i>Pomadasy axillaris</i>	-	-	-	U	-	X	X
<i>P. bayanus</i>	-	-	X	X	-	-	X
<i>P. branicki</i>	-	-	-	U	-	-	X
<i>P. leuciscus</i>	-	-	-	X	-	-	X
<i>P. macracanthus</i>	-	-	-	U	-	X	X
<i>P. panamensis</i>	-	-	-	U	X	X	X
Gerreidae							
<i>Diapterus peruvianus</i>	-	-	X	U	-	U	X
<i>Eucinostomus argenteus</i>	-	-	X	X	-	U	U
<i>E. melanopterus</i>	-	-	X	X	-	X	X
<i>Eugerres lineatus</i>	-	-	-	X	-	X	X
<i>Gerres cinereus</i>	-	-	X	X	-	X	X
Sciaenidae							
<i>Bairdiella armata</i>	-	-	-	-	-	-	X

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloan Coastal
Sciaenidae (Continued)							
<i>B. icistia</i>	-	-	U	U	-	X	X
<i>Cynoscion macdonaldi</i>	-	-	-	X	X	X	X
<i>C. nobilis</i>	U	U	X	X	X	X	-
<i>C. othonopterus</i>	-	-	-	U	X	X	X
<i>C. reticulatus</i>	-	-	X	X	X	X	X
<i>C. squamipinnis</i>	-	-	-	U	X	X	X
<i>C. xanthulus</i>	-	-	-	X	X	X	X
<i>Elattarchus archidium</i>	-	-	-	U	-	X	X
<i>Genyonemus lineatus</i>	U	X	U	U	-	-	-
<i>Larimus acclivis</i>	-	-	-	U	-	X	X
<i>L. effulgens</i>	-	-	-	-	-	X	X
<i>Micropogonias altipinnis</i>	-	-	-	U	X	X	X
<i>M. megalops</i>	-	-	-	U	X	U	-
<i>Ophioscion strabo</i>	-	-	X	U	X	X	X
<i>Umbrina xanti</i>	-	-	X	X	X	X	X
Embiotocidae							
<i>Amphistichus argenteus</i>	U	X	U	-	-	-	-
<i>Cymatogaster aggregata</i>	X	X	X	-	-	-	-
<i>Embiotoca jacksoni</i>	U	X	-	-	-	-	-
<i>Hyperprosopeus argenteum</i>	U	X	U	-	-	-	-
<i>Phanerodon furcatus</i>	U	X	U	-	-	-	-
<i>Rhacochilus vacca</i>	U	X	-	-	-	-	-
Mugilidae							
<i>Agonostomus monticola</i>	-	-	X	U	-	X	X
<i>Chaenomugil proboscideus</i>	-	-	-	U	-	X	X
<i>Mugil cephalus</i>	-	-	X	X	X	X	X
<i>M. curema</i>	-	-	X	X	-	X	X
<i>M. hospes</i>	-	-	-	-	-	-	X
Pholidae							
<i>Pholis ornata</i>	X	X	-	-	-	-	-
Eleotridae							
<i>Dormilator latifrons</i>	-	-	X	X	-	X	X
<i>Eleotris picta</i>	-	-	X	X	X	X	X
<i>Gobiomorus maculatus</i>	-	-	X	X	-	X	X

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloan Coastal
Gobiidae							
<i>Awaous transaeanus</i>	-	-	X	X	-	X	X
<i>Clevelandia ios</i>	U	X	X	X	-	-	-
<i>Evermannia zosterura</i>	-	-	-	-	-	-	X
<i>Eucyclogobius newberryi</i>	U	X	U	-	-	-	-
<i>Garmannia etheostoma</i>	-	-	-	-	-	-	X
<i>G. paradoxa</i>	-	-	-	-	-	-	X
<i>Gillichthys mirabilis</i>	-	X	X	X	X	X	X
<i>Gobionellus microdon</i>	-	-	-	U	-	X	X
<i>G. sagittula</i>	-	-	X	X	-	X	X
<i>Gobius manglicola</i>	-	-	-	-	-	-	X
<i>Lepidogobius lepidus</i>	U	X	U	-	-	-	-
<i>Quietula y-cauda</i>	-	U	X	X	X	X	-
<i>Sicyeium multipunctatus</i>	-	-	-	-	-	-	X
Hexagrammidae							
<i>Ophiodon elongatus</i>	U	X	U	-	-	-	-
Scorpaenidae							
<i>Sebastes auriculatus</i>	U	X	U	-	-	-	-
<i>S. flavidus</i>	U	X	U	-	-	-	-
<i>Scorpaena plummieri</i>	-	-	-	U	-	X	X
<i>S. russula</i>	-	-	-	-	X	-	X
Batrachoididae							
<i>Parichthys notatus</i>	U	X	U	-	-	-	-
Cottidae							
<i>Climacottus acuticeps</i>	X	X	U	-	-	-	-
<i>Leptocottus armatus</i>	X	X	X	-	-	-	-
<i>Scorpaenichthys marmoratus</i>	U	X	U	-	-	-	-
Gobiesocidae							
<i>Gobiesox adustus</i>	-	-	-	-	-	X	X
Stromateidae							
<i>Peprilus simillimus</i>	U	X	U	-	-	-	-
Bothidae							
<i>Citharichthys gilberti</i>	-	-	X	X	-	X	X
<i>C. sordidus</i>	U	X	U	-	-	-	-
<i>Cyclopssetta panamensis</i>	-	-	-	-	-	-	X

Table 15.2 (Continued)

Taxa	Oregon-California Coastal, North of Sacramento River	Sacramento-San Joaquin Estuary	Pacific Coastal California-Baja California South of Sacramento R.	Gulf of California Coastal, Baja California	Colorado River Estuary	Sonoran Coastal	Sinaloa Coastal
Bothidae (Continued)							
<i>Paralichthys californicus</i>	U	X	U	U	-	U	-
<i>Platichthys aestuarius</i>	-	-	-	U	X	U	-
Pleuronectidae							
<i>Hypopsetta guttulata</i>	U	X	U	U	-	U	-
<i>Lyopsetta exilis</i>	U	X	U	-	-	-	-
<i>Parophrys vetulus</i>	U	X	-	-	-	-	-
<i>Psettichthys melanostictus</i>	U	X	-	-	-	-	-
Achiridae							
<i>Achirus mazatlanensis</i>	-	-	-	U	-	X	X
<i>A. scutum</i>	-	-	-	-	-	-	X
<i>Trinectes fonsecensis</i>	-	-	-	X	X	X	X
Cyanoglossidae							
<i>Sympurus williamsi</i>	-	-	-	-	-	-	X
Tetraodontidae							
<i>Sphoeroides annulatus</i>	-	-	X	X	U	X	X

Compiled from Ganssle (1966), Messersmith (1966), R. R. Miller (1966), D. J. Miller and Lea (1972, 1976) and Castro-Aguirre (1978). Species that range from the northern Gulf of California southward to Central or South America, but are not recorded from the mainland coasts of Sonora or Sinaloa, are assumed to be present there, and those from Cabo San Lucas on the tip of Baja California are assumed to occupy both sides of the peninsula. Included are species not known to reproduce in other than marine habitats; some families with freshwater representatives are also in Table 15.1. Symbols: X = recorded; U = assumed occurrence because of geographic range; and - = not recorded.

fishes of the Siuslaw River, Woahink, Siltcoos and Tahkenitch lakes, and mentioned one species from the Umpqua River. An expedition that explored the length of the Oregon Coast in 1899 was reported on by Snyder (1908d), and he (1931) also dealt with salmonids of the Klamath River. Many additional locality records were added by Schultz and DeLacy (1935) who reported collections made by C. L. Hubbs, Schultz and the latter's students during the late 1920s and early 1930s.

Marine-related native species that inhabit or spawn in fresh waters of coastal streams are all from Holarctic families and include three species of Petromyzontidae, two of Acipenseridae, five common and two uncommon species of Salmonidae, two species of Osmeridae, one of Gasterosteidae and five of Cottidae (Tables 15.1 and 15.2). Some marine species that are often in freshwater near the head of tide or even a few kilometers above tide-water are *Hypomesus pretiosus*, *Cymatogaster ag-*

gregata, *Leptocottus armatus* and *Platichthys stellatus* (Table 15.2). An inland *Cottus*, four genera of Cyprinidae and one of Catostomidae apparently were added later from the Columbia Basin. One *Catostomus* from the Klamath entered the Rogue River, or vice versa. Dispersal of freshwater fishes into coastal drainages must have involved headwater transfers, the places and times of which are speculative.

On the north coast the Nehalem and major streams between it and the Columbia, including the Necanicum, support *Cottus rhotheus*, an inland species of the Columbia River (Snyder 1908d). Reimers and Bond (1967) discussed the presence of *C. rhotheus* above falls in tributaries of the lower Columbia and its availability for headwater transfers. Some sites above falls held no primary species, so in a transfer only *C. rhotheus*, the ubiquitous *Cottus perplexus* and salmonids would have gained access to the coast. *Cottus rhotheus* has limited salt tolerance (Bond 1963) so is an unlikely candidate for dispersal between river mouths.

A primary species is *Catostomus macrocheilus* in the Nehalem River. The course of the upper Nehalem is first east then north toward the Columbia before turning south and west toward the sea; stream capture involving an old tributary of the Columbia could be possible (Reimers and Bond 1967). Why only *C. macrocheilus* (and possibly *Cottus rhotheus*) made successful transfer and not upland forms such as *Cottus beldingi*, *Rhinichthys (R.) cataractae* and *R. (Apocope) osculus*, is unexplained. There are no native primary fishes in drainages between the Nehalem and Nestucca rivers. *Rhinichthys osculus* is the only such species in the Nestucca, Yaquina and Alsea rivers (Snyder 1908d).

Access to the Yaquina River for *Rhinichthys osculus* was doubtless from Marys River. *Rhinichthys osculus* in the Alsea River could have been derived from the Yaquina, Marys or Siuslaw rivers. Zirges (1973) examined dace from southern Willamette Valley and the middle and southern coast. Coastal populations had di-

verged from Willamette stocks in several characteristics, generally converging on appearance and increased body size of *R. cataractae*. Coastal populations may have been isolated so long that no conclusions as to their origins could be made from morphological comparisons.

A connection of Siuslaw River with the Willamette drainage is well documented by Baldwin and Howell (1949). The upper part of Long Tom River, now tributary to the Willamette, followed what is now Wildcat Creek westward in Pliocene-Pleistocene before being diverted eastward. Primary genera represented in the Siuslaw are *Ptychocheilus*, *Rhinichthys*, *Richardsonius* and *Catostomus*. Evermann and Meek (1897), noting differences between coastal and Columbia drainage representatives, described *Catostomus (siltcoosensis)* and *Leuciscus siuslawi*. Snyder (1908c) placed the former in synonymy of *C. macrocheilus* and the latter into *L. balteatus* (now *Richardsonius balteatus*), but included the *Ptychocheilus* with *P. umpqua*.

Spread of *Ptychocheilus*, *Catostomus* and *Richardsonius* into the three major lakes (Woahink, Siltcoos and Tahkenitch) south of the Siuslaw could have been natural through the low pass near Canary or possibly through temporary connections among waters impounded behind ocean dunes. It also is possible that these genera were introduced. Use of suckers and minnows for bait was once common in the area, and long, narrow plank boats called "minnow boats" were used "about the turn of the century" to gather bait on the Siuslaw for sale at the lakes (F. Judges, pers. comm., 1950). Whether this was practiced prior to explorations of Evermann and Meek is not known, but it is not mentioned in their 1897 paper.

Invasion of the Umpqua River by Columbia faunal elements could reflect the upper Umpqua having been a former tributary of the Willamette. Diller (1915) noted terraces indicating the Umpqua flowed north through the

early Pass Creek drainage to enter the Willamette drainage at the town of Divide before being captured by a westward-flowing stream. At present, run-off from heavy rainfall that fills the drainage ditch along the railroad at Divide can flow slowly east to Martin Creek, a tributary of the Coast Fork of the Willamette, through a valley that drops 15 m in 3.25 km or can flow more rapidly west to Pass Creek of the Umpqua drainage (Bond 1963). Baldwin (1981) mentions the possibility that rapidly eroding Pass Creek will eventually capture the Coast Fork of the Willamette.

Primary fishes native to the Umpqua drainage are *Hybopsis (Oregonichthys) crameri* (affinities uncertain, otherwise only in the Willamette Basin), *Ptychocheilus umpqua* (derived from *P. oregonensis*; Bond 1961), *Rhinichthys (R.) evermanni* (derived from *R. cataractae*; Bisson and Reimers 1977), *R. osculus*, *Richardsonius balteatus* and *Catostomus macrocheilus* (Snyder 1908d).

Coos River contains a form of *R. cataractae* quite distinct from *R. evermanni* (Bisson and Reimers 1977), *Rhinichthys osculus* and *Catostomus macrocheilus*. Snyder (1908d), Hubbs and Schultz (Schultz and DeLacy 1935) and Bond (1961) all failed to find *R. cataractae* in Coos River. It was first collected by Reimers in 1967 (Bisson and Reimers 1977).

Rhinichthys osculus and *Catostomus macrocheilus* are native to Coquille River, and probably gained access from Coos River. *Catostomus macrocheilus* extends to Floras Creek and Sixes River, which represents the southern extent of influence of the Columbia fauna on the coast (Reimers and Baxter 1976).

Rogue River has one native primary species, *Catostomus rimiculus* (Snyder 1908d). Rogue River is the southern limit of distribution of *Cottus perplexus*, a species of virtually every stream in western Oregon and Washington. A closely related species, *C. gulosus*, has a curious distribution in Washington coastal streams, in some lower Columbia tributaries,

in a few streams on the northern coast of Oregon, many streams of the middle coast and south to the Coquille River, but not from there to the Noyo River, California (Bond 1973; Moyle 1976a). Oregon coastal streams south of the Rogue River, Hunter Creek and Pistol, Chetco and Winchuck rivers, have no primary fishes or fishes of inland relationships.

Klamath River Basin

This drainage supports a number of unique fishes, mainly above Klamath Falls: *Lampetra minima* (now probably extinct), *Catostomus snyderi*, *Catostomus (Deltistes) luxatus*, *Chasmistes brevirostris*, *Gila* ("Klamathella") *coerulea*, *Cottus princeps* and *C. tenuis*. Species shared with adjacent drainages are *Lampetra lethophaga* (above Klamath Falls and in Pit River), *Catostomus rimiculus* (below the Falls and in Rogue River) and *Cottus klamathensis* (with distinct subspecies above and below the Falls and in Pit River; Daniels and Moyle 1984). Below the Falls are two nominal species of landlocked lampreys related to *Lampetra tridentata* (described as *L. folletti* and *L. similis*; see Vladykov and Kott 1976a, 1979a, 1982; see, however, Bailey 1982a). A slightly differentiated race of *L. tridentata* lives above Klamath Falls. Other native, but more widespread species are *Gila (Siphacles) b. bicolor*, *Salvelinus confluentus*, *Salmo gairdneri*, *Salmo* sp. (redband) and *Rhinichthys osculus*.

Several authors (C. H. Gilbert 1897; Rutter 1903; Snyder 1908b; Hubbs and Miller 1948a; Robins and Miller 1957; R. R. Miller 1959a, 1965; D. W. Taylor 1960, 1966, 1985; G. R. Smith 1978, 1981a; Taylor and Smith 1981) have discussed faunal relationships between the Klamath and upper Pit rivers and remarked on isolation of the former from the endemic fauna of the Sacramento system. They also noted an absence of lower Columbia River endemics in the Klamath, but Snyder (1908b) emphasized resemblance of *C. snyderi* of the Klamath to both *C. macrocheilus* of the Columbia drainage

and *C. occidentalis* of the Sacramento. He further suggested that the small-scaled suckers, *C. rimiculus* of the Klamath, and *C. microps* and *C. catostomus* (= *C. columbianus*, in part) of the Pit and Columbia rivers, respectively, are related. Hubbs and Miller (1948a) expressed the opinion that *C. rimiculus* was derived from *C. syncheilus* (= *C. columbianus*). G. R. Smith (1966) placed *C. columbianus* in subgenus *Pantosteus* and *C. rimiculus* into subgenus *Catostomus*, and demonstrated that *C. rimiculus* approached *Pantosteus* in characteristics of the parietal fontanelle and lower jaw. Koehn (1969) later demonstrated that blood proteins of *C. columbianus* most closely resembled those of *Catostomus* (s.s.) (G. R. Smith and Koehn 1971). *Catostomus* (or *Deltistes*; Seale 1896; R. R. Miller and Smith 1967; G. R. Smith 1975, 1978, 1981a) *luxatus* is most closely aligned with the fossil *Catostomus (D.) shoshonensis* (including *D. ellipticus*; G. R. Smith 1975) and *C. (D.) owyhee* of the Glenns Ferry Formation, Idaho. The further presence of *Chasmistes* in the Klamath River Basin demonstrates a relationship to the Great Basin and/or to the Snake River Plain. Recent records of that genus in Pyramid and Utah lakes, and fossil records at several sites including Fossil Lake in the Fort Rock Basin and from the Snake River drainage (R. R. Miller 1965; R. R. Miller and Smith 1981) are to be detailed later. *Gila coerulea* of the Klamath River is related to the fossil *G. (G.) milleri* of the Snake River Plain (G. R. Smith 1975) and perhaps to *G. (G.) atraria* of the upper Snake-Bonneville system (G. R. Smith 1978). Faunal analyses by G. R. Smith (1978) pointed out "intimate associations" of the Snake River and Klamath Basin to the Great Basin, which are detailed below. The absence of *Ptychocheilus* in the Klamath River Basin, despite its occurrence immediately north and south, was noted by Kimmel (1975) as possible evidence for early (Miocene) connections between the Snake River Plain and this system. Pliocene fishes (*Gila* and *Catostomus*) from near Alturas, Modoc County, California (upper

Sacramento River system), appear most similar to modern fishes of the Klamath system (G. R. Smith 1981a).

Northern California Coastal

Most streams in this region south of the Klamath River Basin and north of San Francisco Bay are small and support only seawater dispersants. Larger rivers, and creeks tributary to Tomales Bay, have freshwater fishes all apparently derived from the Sacramento River system.

Holway's (1907) contention that the Russian River was the ancestral home of the entire Sacramento-San Joaquin fish fauna stimulated early zoogeographic debate, and Snyder (1905, 1908a,d, 1913, 1916) summarized early knowledge of fishes of this region. A summary of other historical developments is provided in our later coverage of the Sacramento-San Joaquin fauna, as are occurrences of marine and estuarine fishes in coastal habitats.

Hesperoleucis symmetricus is the only widespread cyprinid in north-coastal California, occurring as a probably introduced population in Eel River (Moyle 1976a), then naturally from the Navarro River southward. We are not convinced that Avise et al. (1975) and Avise and Ayala (1976) demonstrated that *Hesperoleucis* and *Lavinia* are congeneric, and thus retain the former name. The nominal species (Snyder 1913) *H. navarroensis* from Navarro River, *H. parvipinnis* from Gualala River and *H. venustus* of Russian River and streams entering San Francisco Bay, are generally referred to subspecific rank, apparently following Murphy (1948) (Moyle 1976a, 1980a). Other Sacramento Basin cyprinids, *Ptychocheilus grandis*, *Lavinia exilicauda* and *Mylopharodon conocephalus*, have penetrated north-coastal drainages only to the Russian River system and appear undifferentiated.

Catostomus occidentalis is wide ranging and includes *C. o. humboldti* in the Mad, Eel, Bear and Navarro(?) rivers, and *C. o. occiden-*

talis in Russian River. It is apparently absent from the Gualala River and tributaries to Tomales Bay (Moyle 1980b). *Hysteroecarpus traski* in Russian River also is differentiated to the subspecific level (*H. t. pomo*) from Sacramento-San Joaquin and Clear Lake forms (*H. t. traski*; Hopkirk 1962, 1973; Baltz and Moyle 1981).

Moyle (1976a) discussed two possible routes for transfer of fishes from the Sacramento-San Joaquin system to Russian River: (1) through Clear Lake Basin, and (2) through tributaries of San Francisco Bay. Considering alignments of regional structure, estimates of coastal displacements and known elevational adjustments of aerial and submerged landforms, plus volcanic events documented to have caused drainage reversals (Anderson 1936; Walirshaftig and Birman 1965; Howard 1967; Sve and Dickinson 1970; Cole and Armentrout 1979), it is surprising that more fish species have not moved (or been moved) northward along the coast. The region also tends to include a hiatus in coastal distribution of some species of *Cottus* (Bond 1963; Moyle 1976a), yet it has been available for colonization as an area generally uplifting above the sea since Pliocene (Cole and Armentrout 1979). Perhaps regional marine transgressions in latest Pleistocene and Early Holocene excluded freshwater species. It is also tempting to entertain the speculation that allochthonous terranes along the coast are slowly colonized; comparisons of such terranes with range disjunctions might be informative.

Great Basin

The Great Basin (Fig. 15.2) includes more than 150 discrete drainages, only a few of which directly connect with the sea (G. R. Smith 1978). Many of these contained large lacustrine habitats in Pleistocene and earlier (Newberry 1870a et seq.; Russell 1883 et seq.), remnants of which still support fishes. Relationships of fish dis-

tributions and geologic history of this region have fascinated some of the most eminent North American geologists and biologists for more than a century.

Early exploration for wagon roads and in 1853 for a Pacific railroad route (Beckwith 1855) yielded some of the first fishes from this area (G. R. Smith 1983). Many of these were described by Girard (1857b). In 1851, Russell (1883, 1885, 1896) began his classic studies of the geology of Lake Lahontan, and E. D. Cope began researches on fossil and living fishes of the Great Basin and its environs about 1870 (Cope 1871b et seq.; Cope and Yarrow 1875). Jordan and Gill described fishes from Lake Tahoe (Jordan 1878a,b) and Jordan and Henshaw (1878) reported on collections of the Wheeler Surveys west of the 100th meridian (Wheeler 1875). Eigenmann and Eigenmann (1891, 1893) also dealt with components of this fauna, and C. H. Gilbert (1893) reported on fishes of the Death Valley Expedition, staged in 1891 by V. C. Bailey, C. H. Merriam and others of the U.S. Bureau of Biological Survey.

J. O. Snyder of Stanford University began field work in the northern Great Basin about the turn of the century, writing a comprehensive report on fishes of the Oregon Lakes region (Snyder 1908b) that combined results of an expedition led by B. W. Evermann in 1897 and of his own expedition of 1904. Snyder recognized the faunal relationships of Harney Basin to the Columbia River and pointed out that Goose Lake and Klamath basins had related fish faunas (see also Rutter 1903). His move into the Lahontan Basin in 1911 (Snyder 1912, 1914) culminated in a monograph on fishes of that system in 1918. His survey of the Bonneville Basin in 1915, with assistant C. L. Hubbs, was never published (Hubbs et al. 1974).

Studies of the Great Basin then expanded (reviewed by Morrison 1961a-d, 1964, 1965a-c). Meinzer (1922) mapped former lakes and discussed their climatological significance.

Jones (1914a et seq.), Antevs (1925 et seq.), Snyder and Langbein (1962) and Benson (1978), among others, also dealt with climatologic interpretations of lakes and lake stages. Broecker and Orr (1958), Broecker and Kaufman (1965) and many others (Scott et al. 1982), contributed radiocarbon dates. R. R. Miller (1946b, 1948) and Hubbs and Miller (1948a) synthesized data on fish distributions and the extent and interconnections of lacustrine habitats. Their maps have been updated and modified by Feth (1961, 1964), Snyder et al. (1964), Morrison (1965a), Flint (1971), Hubbs et al. (1974), G. R. Smith (1978, 1981a), R. R. Miller (1978, 1981) and Mifflin and Wheat (1979).

Inland Basins of Oregon ("Oregon Lakes")

Inland basins of southern and southeastern Oregon (Fig. 15.1) are a northwestward extension of the Basin and Range Province (Hubbs and Miller 1948a; Baldwin 1981) lying between the Cascade Mountains on the west and the Owyhee Upland on the east. To the north are the High Lava Plains in which two major basins, Fort Rock and Harney, are located (Baldwin 1981). Throughout the area there are roughly parallel uplifted and tilted grabens and horsts, all with a general north-south orientation (Russell 1884; Fuller and Waters 1929).

Fossil fishes of this region were dealt with by Cope (1883b, 1884, 1889), and little information has since appeared that aids in interpretation of older drainage relations. *Oncorhynchus* sp. from Pliocene beds indicates connections with the Columbia River (Cavender and Miller 1972). Late Pleistocene (Allison 1941, 1966) species now recognized (G. R. Smith 1981a) include *Gila* (*Siphateles*) *allarcus*, a relative of *G. bicolor* (Uyeno 1960; Uyeno and Miller 1963) and *Chasimistes batrachops* (also known as referred material from Inyo County, California, and Washoe County, Nevada; Miller and Smith 1981). *Salmo* sp. (similar to *S. clarki*), *Gila* (*Siphateles*) sp. and *Catostomus* (*Orestomus* or *Deltistes*) sp. are associated with Oregon C.

batrachops in the Fossil Lake area (Fort Rock Basin). The *Salmo* has recently been identified as *Salmo* sp. (redband) by Allison and Bond (1983).

The basin of Upper Klamath Lake, now draining south to the Klamath River, was once apparently without outlet (Russell 1884; Hubbs and Miller 1948a), and might then have been included in this regional category. The adjacent Goose Lake does not naturally overflow at present, but spilled during historic times into Pit River system (Sacramento Basin) (Baldwin 1981). The other basins have had no recent outlets and held large lakes in the distant past and during at least two periods in Late Pleistocene (Russell 1884; Waring 1908; Snyder et al. 1964).

The first of those periods, at the time of Tahoe Glaciation, ended 32,000 ya (Flint and Gale 1958; Hansen 1964). Some connections between basins could have formed during this time (Bills 1978) and Harney Basin was connected with the Columbia River drainage (Baldwin 1981). Lakes reached low levels or dried from 32,000-25,000 ya. During Tioga Glaciation, a second period spanning about 14,000 years, the lakes again filled. This period ended 12,000-10,000 ya (Flint and Gale 1958), and was followed by a rather arid period at its height 8000-4000 ya (Hansen 1947) when the lakes may have dried completely (Van Winkle 1914; Heusser 1966). In the past 4000 years lake levels have fluctuated (Phillips and Van Denburgh 1971) and some may have spread across their former beds (Allison 1979; Allison and Bond 1983).

Faunal relationships among these basins are not clear. In most instances reliable physiographic evidence of interbasin connections is lacking, although many share one or both of the persistent species *Gila bicolor* and *Rhinichthys osculus*. As G. R. Smith (1978) pointed out, many biological similarities within the Great Basin stem from local retention of these two extinction-resistant species.

The Fort Rock Basin has only three extant native species, despite connection with the Columbia system that must have persisted in Early Pleistocene. These are *Salmo* sp. (redband), *Gila bicolor* and *Rhinichthys osculus*, all inland forms. Pliocene *Oncorhynchus* noted before (Cavender and Miller 1972) and geological evidence of a drain to the Deschutes River (Allison 1940, 1979) support the Columbia River connection. Pleistocene fossils have largely been referred to Recent species, but presence of *Chasmistes batrachops* (Uyeno and Miller 1963; R. R. Miller and Smith 1981) argues for connections with drainages to the east, including one with Alkali Lake Basin that Bills (1978) suggested to exist about 30,000 years ago. Hubbs and Miller (1948a) proposed *Gila bicolor* could have entered the Silver Lake drainage via stream capture from the Sycan Marsh area. Such an avenue should have afforded access to *Salmo* and *Rhinichthys* as well.

Harney Basin shows evidence of at least two separate invasions of fishes. It once was connected through Malheur Gap via the Malheur River to the Snake River, and Bisson and Bond (1971) showed fish faunas of isolated or semi-isolated creeks and even some headwater streams of the Silvies and Donner und Blitzen rivers were related to middle or upper Snake faunas. Fishes typical of these streams are *Richardsonius balteatus hydrophlox*, a lightly prickled or unprickled form of *Cottus bairdi*, *Salmo* sp. (redband) and *Prosopium williamsoni*. Malheur Gap was dammed by lava flows that make up the Voltage Lava Field, probably in Late Pleistocene. Lake Malheur formed behind the dam and probably did not overflow either at Malheur Gap or Crane Gap (Piper et al. 1939). Fishes derived from Snake River were isolated and further hydrographic isolation took place within the Basin during Recent time. Lavas from Diamond Craters formed the Barton Lake subbasin and aided in isolation of Smyth and Riddell creeks. Desiccation 8000–4000 ya (Hansen 1947) no doubt cut most small

streams from their connections with receding lakes. Access for fishes among streams and lakes of the Basin has probably been variable but limited during the last 2000 years.

On the other hand, the fish fauna of main-stream Silvies River is more typical of the lower Columbia drainage and includes *Richardsonius b. balteatus*, *Acrocheilus alutaceus*, *Ptychocheilus oregonensis*, *Catostomus macrocheilus*, *C. columbianus* and a prickled form of *Cottus bairdi*, as well as the more generally distributed species *Gila bicolor*, *Rhinichthys cataractae* and *R. osculus*. This infers invasion of fishes after damming of Malheur Gap, either at a time of overflow at that point or of Crane Gap or by stream capture involving Silvies River and John Day or Malheur tributaries. Because there is no clear evidence of overflow (Piper et al. 1939), stream capture seems the most likely explanation. Specimens from Silvies River compared with samples from John Day and Malheur rivers showed greater morphological similarity to the former in discriminant function analyses (Bisson and Bond 1971). The site of a John Day–Silvies connection has not been identified. Additional information is, however, accumulating on the subject. Fish remains found by John Fagan at a tentatively dated site on the lower Donner und Blitzen River and identified by Ruth Greenspan (pers. comm., 1983), indicate that *P. oregonensis* and *C. macrocheilus* were in the area approximately 3000 ya.

Gila bicolor columbianus occurs in springs, lakes and larger streams of Harney Basin and in the Columbia drainage. There appears to be two sets of races of *G. bicolor* in Oregon drainages, one with gill raker counts of 16 or more and one with 16 or fewer. *Gila bicolor* of Harney Basin and the lower Columbia fit in the latter group along with those of Klamath, Fort Rock, Abert, Alkali and Summer Lake basins. Perhaps the Harney Basin *G. bicolor* invaded directly from one of the basins listed (Fort Rock and Alkali are nearest) or indirectly

from either to the Columbia and thence to Harney Basin.

Alvord Basin, south and east of Harney Basin, includes Virgin and Thousand creeks of Nevada, and Trout Creek, Alvord Lake and Borax Lake of Oregon, as well as several springs in both states. *Gila (Siphateles) alvordensis*, considered a sister species of *G. bicolor* of the Lahontan and associated basins by G. R. Smith (1978), is most widespread in the Alvord (Williams 1980; Williams and Bond 1983). *Gila (S.) boraxobius* is a dwarf, short-lived derivative of *G. alvordensis*; confined to warm waters of Borax Lake, the rim of which is about 10 m above the playa of Lake Alvord (Williams and Bond 1980). The representative of *Salmo clarki* that once lived in the Basin is apparently extinct through hybridization with introduced *S. gairdneri*. Behnke (1979) believed it most likely derived from the Lahontan Basin via Summit Lake, which could have spilled toward Virgin Creek during an early time.

A subspecies of *Salmo clarki* similar to the Alvord form exists in Whitehorse and Willow creeks, which flow into a shallow sandy basin east of Alvord Basin. Hubbs and Miller (1948a, following Russell 1903), advanced the opinion that Whitehorse Valley would spill into the Alvord Basin in times of high rainfall. Behnke (1979) disagreed, pointing out that Whitehorse Valley has a lower eastern rim toward the Owyhee River drainage. The western low point has an elevation of about 1326 m, whereas the eastern rim is about 1265 m (Army Map Service Series V502, Ed. 1-AMS, Sheet NK 11-4). As Behnke (1979) stated, *Salmo* of Willow and Whitehorse creeks were probably transferred by means of headwater connections. A few small lakes north of Alvord Lake seem not to have had native fishes in recent times (Hubbs and Miller 1948a).

Catlow Valley lies west of the southern part of the Harney and Alvord drainages and includes Guano Valley to the southwest. Major streams are Rock Creek, which drains the

northern part of Warner Mountains and Poker Jim Ridge, Guano Creek, draining the southern part of Warner Mountains, and Roaring Springs, Dry, Home, Threemile and Skull creeks, from western parts of Steens Mountain west of the Donner und Blitzen River.

Rock and Guano creeks yielded no native fishes in 1939 (Hubbs and Miller 1948a), but in a wet period of the mid-1950s *Gila bicolor* was in Rock Creek (possibly introduced) and Guano Lake. Specimens from Guano Lake were found partially decomposed after winter-kill. They could have originated in Piute Creek, which along with Fish Creek, Nevada, contains *G. bicolor eurysoma* (Williams and Bond 1981). A related subspecies of *G. bicolor* occurs in Roaring Springs and Home, Threemile and Skull creeks, along with *Salmo* sp. (redband). *Rhinichthys osculus* is in Skull Creek.

Although Hubbs and Miller (1948a) referred to "local testimony" that indicated all salmonids in Catlow Valley had been introduced, Wilmot (1974) and Behnke (1979) considered *Salmo* sp. (redband) native. The species is in the adjacent Harney and Warner basins. Hubbs and Miller (1948a) mentioned a possible overflow of Lake Catlow into Harney Basin and suggested *Gila bicolor* might have gained access via such a "very temporary" connection. Because the gap above Frenchglen stands at 1470 m, and the valley floor at Frenchglen less than 3 airline km distant is 210 m lower, any spill at this point would be precipitous. *Gila bicolor* would have had difficulty in ascending to Catlow Valley. Both forms of *G. bicolor* in the Catlow-Guano complex belong to the group with 16 or more gill rakers. They share this feature with the Warner Basin form, so they may be more closely related to that population than to coarser-rakered *G. b. columbianus* of Harney Basin.

Warner Valley has four indigenous species: *Salmo* sp. (redband), *Catostomus warrirensis*, *Gila bicolor* and *Rhinichthys osculus*. *Hesperoleucis symmetricus* is also present, but may have

been introduced (R. R. Miller 1959a). If native it was likely transferred from the Goose Lake drainage via stream capture (Hubbs and Miller 1948a). *Catostomus warnerensis* seems closely related to *C. tahoensis* of the Lahontan Basin and *Catostomus* sp. of Surprise Valley (G. R. Smith 1978). *Catostomus microps* of Pit River drainage, including Goose Lake, is related to this group (Moyle and Marciochi 1975). *Catostomus warnerensis*, like *C. microps*, is a small-eyed form. The lacustrine form of *G. bicolor* of Warner Valley is not separable from *G. bicolor* of Goose Lake at the 75% level using a combination of meristic and morphometric characters (F. Bills, unpubl. data). Cowhead Lake between Surprise and Warner valleys apparently drains toward the latter in wet periods (Hubbs and Miller 1948a), but the Cowhead Lake *G. b. vacceps* is distinct from that of Warner Valley (Bills and Bond 1980).

Although Hubbs and Miller (1948a) discounted a spill of Lake Meinerz of Long Valley into Warner Valley, or placed such a connection in "earlier pluvial" time, Snyder et al. (1964) indicated such an overflow on their map of Pleistocene lakes.

Hubbs and Miller (1948a) mentioned three endemic subspecies of *Rhinichthys osculus* in Warner Valley. One of these occupies Fosket Spring in Coleman Valley, truly one of the most restricted habitats in the entire region. However, as Hubbs and Miller stated, neither forms of *Salmo* nor of *Rhinichthys* give much help in assessing past water connections among basins.

Although now separated by a low ridge, Summer Lake and the Chewaucan-Abert Lake complex were once part of Lake Chewaucan (Huntington 1925; Hubbs and Miller 1948a). J. A. Davis (1982) provided recent data on Quaternary geology of this basin. The native fish fauna consists of *Salmo* sp. (redband), *Gila bicolor* and *Rhinichthys osculus*. The *G. bicolor* represents the group with 16 or fewer gill rakers,

so relationships would appear with those of Klamath, Fort Rock or Alkali basins, all of which are adjacent. Snyder (1908b) described *G. bicolor* of XL Spring as *Rutilus oregonensis*, and applied that name to populations in Fort Rock, Alkali and Warner basins as well as to those of Summer Lake (Ana Spring) and the Chewaucan River. Hubbs and Miller (1948a) considered *G. bicolor* of the last two waters racially or subspecifically distinct from that of XL Spring. Bills (1978) confirmed racial distinction of Chewaucan *G. bicolor* and agreed that populations of Ana Spring and River are subspecifically distinct. The form studied by Snyder (1908b) and by Hubbs and Miller (1948a) is extinct and replaced by a distinctly different form (Bills 1978). Ana Spring was dammed to form a reservoir. Game fish were stocked, but the native population of *G. bicolor* increased to the detriment of the sport fishery. The Oregon Department of Fish and Wildlife attempted to kill all fish in the reservoir in 1957, 1961 and 1970. A few *G. bicolor* escaped and also may have hybridized with additional fish introduced as bait. *Hesperoleucus symmetricus* was also introduced to Ana River in recent years.

Alkali Basin supports an undescribed subspecies of *Gila bicolor* in two springs northwest of Alkali Lake. One habitat was formerly termed Alkali Spring (Hubbs and Miller 1948a), but is currently known as Hutton Spring. The other, about a kilometer distant, seems to have no consistently-applied name. Snyder (1908b), as pointed out by Bills (1978), located Hutton Spring southwest of Alkali Lake playa, but local residents and government employees familiar with the area do not know of springs in that sector. Hubbs (1941) and Waring (1908) both refer to these springs as being on the northwest edge of the playa. The fish aligns with the group having 16 or fewer gill rakers, which argues for a connection with either the Chewaucan Basin as suggested by Hubbs and

Miller (1948a) or with Fort Rock Basin as stated by Allison (in Bills 1978).

Lahontan System

The Lahontan system of northwestern Nevada and adjacent California supported Late Pleistocene Lake Lahontan, equivalent in maximum size to modern Lake Erie (22,000 km²; Blake 1872a,b; Gale 1915; Hubbs and Miller 1948a; Morrison 1964, 1965a; Benson 1978), plus numerous smaller valleys that were variously interconnected. The region has long consisted of endorheic basins, and the great lakes of the immediate past may have been overemphasized as factors contributing to evolution and distribution of fishes (Taylor and Smith 1981).

Pyramid and Walker lakes are remnants of Lake Lahontan. Other lakes of the basin floor, such as Carson Sink, have dried or have been too fluctuant and/or saline to support fishes in historic time. Pyramid Lake has a maximum depth of about 90 m and is 40 km long. Its waters are noticeably saline as a result of evaporative concentration and are becoming more so with agricultural diversions of Truckee River. Declining water levels have been of major concern for many years (LaRivers 1962; Fowler and Koch 1982). Nearby Lake Winnemucca formerly received water from Pyramid Lake, but dried in 1938 when surface elevation of the latter dropped below its inlet level (LaRivers 1962). Walker Lake is 27 km long and around 40 m deep. Its recent history of declining water levels as a result of diversions from Walker River is similar to that of Pyramid Lake.

Lake Tahoe and Eagle Lake are quite different from the preceding waters. The former is 501 m deep and 36.4 km in maximum length. Eagle Lake has a maximum depth of only 23 m and is 20.8 km long. Their positions within coniferous forests are in marked contrast to

desert settings of most other Lahontan fish habitats.

Humboldt River is the largest remnant stream of the system, passing east to west across Lake Lahontan and other valley-fill sediments to traverse much of northern Nevada. Its major tributaries from mountains to the north approach and interdigitate with north-flowing tributaries of the Snake River (R. R. Miller and Miller 1948). Inflowing streams from the south are fewer in number, with Reese River originating in the Toiyabe Mountains, Nevada, as the most extensive tributary of the system. The Humboldt River desiccates in Humboldt Sink in the northern Carson Desert (LaRivers 1962).

Three eastward-flowing streams comprise most of the remainder of Lahontan riverine habitat. All originate at high elevations and have high gradient headwaters, then flow at low gradient over valley-fill and lacustrine sediments at lower elevations. Truckee River, a major western contributor to Lake Lahontan, originates in Lake Tahoe (1899 m elevation) on the east face of the Sierra Nevada, flows north then east in canyons cut through the Virginia Mountain Range, and again north to end at 1150 m in Pyramid Lake, Nevada. Carson River next to the south heads at greater than 3000 m near the Sierra Crest and flows north and northeast through the southern Virginia Range onto the Carson Desert to end in South Carson and Humboldt sinks. The most southerly tributary of the Sierran portion of the system is Walker River, flowing as two branches from the north and northeast Yosemite Rims of Mono County, California (more than 3000 m). These branches coalesce to enter Walker Lake after the West Fork crosses the Singatze Mountains.

Presence of the distinctive *Eremichthys acros* in the Lahontan region, the less differentiated but endemic species *Richardsonius egregius*, *Catostomus tahoensis* and *Chasmistes cujus*, sub-

specifically differentiated populations of *Rhinichthys osculus*, *Salmo clarki* and *Gila bicolor* and presumably less or scarcely differentiated *Prosopium williamsoni*, *Pantosteus platyrhynchus* and *Cottus beldingi* suggest long isolation, then variable, but repeated connections of the system to one or more adjacent basins. A less terable alternative is a vast differential in speciation rates. Variation in some of these forms has, however, scarcely been examined. Highland species such as *P. williamsoni*, *S. clarki*, *R. osculus* and *C. beldingi* could have arrived through stream capture over the rim, but as pointed out by Hubbs and Miller (1948a) other species are lowland forms not expected to traverse mountains. Populations of lowland species in high elevation habitats such as Lake Tahoe may reflect uplift (Hubbs and Miller 1948a), but Truckee River has no major barriers and *R. egregius*, *C. tahoensis* and *P. platyrhynchus* are common; *G. bicolor* has been taken in tributaries (P. B. Moyle, pers. comm., 1983).

Blake (1872a,b) first discussed the possibility for a northwestern outlet of Pleistocene Lake Lahontan to Alvord Basin of the Oregon Lakes region. King (1878) and Whitney (1882) proposed discharge southward into the Colorado River system (see also Keyes 1918). A southern transfer of fishes from the Lahontan to the Death Valley "system" is discussed later. Russell (1885) emphasized that the Lahontan Basin has an essentially unbroken rim. Hubbs and Miller (1948a) reexamined Russell's route around the Basin and similarly could find no evidence for a Pleistocene outlet.

Cope (1883b) considered the most probable zoogeographic connection for Lake Lahontan as through the Oregon Lakes region. Blackwelder (1948) speculated that an outlet existed in Middle Pleistocene via Pit River into the Sacramento or Klamath, or northward into the Columbia River. Hubbs and Miller (1948a) also espoused a close relationship between the Lahontan and upper Klamath River systems now obscured by uplift and lavas of the Modoc

Plateau, northeast California and southeast Oregon. That area now drains via Pit River to the Sacramento River system (Pease 1965; Moyle 1976a).

Fish species pairs or groups substantiating drainage relationships to the west include *Gila bicolor obesa* of the Lahontan system and *G. bicolor* subsp., plus *G. alvordensis* and *G. boraxobius* of the Oregon Lakes. Moyle (1976a) similarly noted that some *G. bicolor* of Pit River drainage were related to *G. b. obesa*. *Catostomus tahoensis*, an undescribed species of *Catostomus* from Surprise Valley, Nevada, *C. warnerensis* of the Oregon Lakes, *Catostomus funeiventris* of Owens Valley, California (G. R. Smith 1978) and possibly *C. microps* of the Pit River (Moyle 1976a) form a monophyletic assemblage. *Chasmistes brevirostris* of the Klamath River Basin and *C. cujus* are, however, less closely related than *C. cujus* and *C. liorus* of the Bonneville Basin (R. R. Miller and Smith 1981).

Modern fish faunas of the Lahontan system and the Bonneville Basin to the east are scarcely more similar than those of the Lahontan and Oregon Lakes despite their proximity and absence of intervening basins or high separating divides. *Richardsonius egregius* of the Lahontan and *R. balleatus hydrophlox* of the Bonneville and Columbia River basins are sister taxa (G. R. Smith 1978). G. R. Smith's (1966) variational study of *Pantosteus platyrhynchus* indicated that it is relatively uniform within the Great Basin, and those of the Lahontan system are more closely allied to similarly isolated populations in the northern Bonneville-upper Snake River basins. Hubbs et al. (1974) noted that *P. lahontan*, synonymized by G. R. Smith (1966) with *P. platyrhynchus*, may be a recognizable taxon, and Deacon and Williams (1984) retained it as a subspecies. As noted above, *Chasmistes cujus* and *C. liorus* of the Bonneville Basin are closely related (R. R. Miller and Smith 1981).

Eremichthys acros is restricted to Soldier Meadows, a closed basin in extreme north-

western Nevada. It represents an old endemic, aligned with *Rhinichthys*, but with a long, coiled intestine, cartilaginous sheaths on the jaws and other features, making its direct relationships obscure (Hubbs and Miller 1948b). The widespread *Rhinichthys osculus robustus* in the Lahontan system is sharply separable and not obviously related to subspecies of major surrounding basins and has further developed into other distinctive subspecies (Hubbs and Miller 1972; Hubbs et al. 1974). *Gila bicolor* has similarly differentiated into isolated subspecies in the north-central Great Basin discussed below, and also is represented by a widespread riverine form (*G. b. obesa*) and a lake-adapted form (*G. b. pectinifer*) within the system. The last was described as *Leucidius pectinifer*, distinguished as a distinct genus by Snyder (1918) on the basis of its profuse (29-36), elongated gill rakers and 5-5 pharyngeal teeth. It now is considered a subspecies of *G. bicolor* (Hubbs 1941; Hubbs and Miller 1942, 1948a; Shapovalov and Dill 1950; Hubbs et al. 1974), but alternately has been afforded specific status (R. G. Miller 1951; Hopkirk and Behnke 1966; Hopkirk 1973) or dismissed as a valid taxon (LaRivers and Trelease 1952; LaRivers 1962). Snyder (1918) took *G. b. pectinifer* only in lakes, and extensive series examined by Hubbs (1961) and Hubbs et al. (1974) confirmed this tendency. In some lacustrine environments (for example, Pyramid Lake and Lake Tahoe) this form and *G. b. obesa* coexist with varying degrees of introgression (R. G. Miller 1951; Hubbs 1961; Hubbs et al. 1974). Kimsey (1954), however, documented fusion of the two in Eagle Lake, California, into a population with bimodal, intermediate numbers of gill rakers and relative uniformity of other features.

Salmo clarki henshawi of Pyramid Lake and Lake Tahoe also is lake adapted, while an undescribed stream-adapted subspecies inhabits Humboldt River headwaters in eastern Nevada (Behnke 1981), and *S. c. seleneri*, isolated

(and likely saved from extinction) due to an early introduction above a waterfall (Snyder 1933, 1934; Busack and Gall 1981), is differentiated only slightly from *S. c. henshawi*. Populations below the falls were destroyed, presumably by introgression with introduced *S. gairdneri* (Busack and Call 1981). The Eagle Lake *S. aquilinum* has been variously classified as a subspecies of *S. clarki* (Snyder 1933), a hybrid between *S. clarki* and *S. gairdneri* (Hubbs and Miller 1948a), or as a subspecies of *S. gairdneri* derived from Pit River (Busack et al. 1980; Behnke 1981). Electrophoretic, chromosomal and meristic data form bases for the last conclusion. *Salmo rexalis* (Lake Tahoe) and *S. smaragdus* (Pyramid Lake) were described on the basis of introduced *S. gairdneri* (Behnke 1972, 1981).

That the modern Lahontan fauna includes an amalgamation of fishes of relatively recent derivation mixed with older faunal elements is strongly indicated by fossils. Beds near Honey Lake, California, include fossil fishes related to those of the Pliocene Glenns Ferry Formation on the Snake River Plain (G. R. Smith 1975), but that also resemble some species of the present Lahontan system (Taylor and Smith 1981). Included are: *Rhaidofario* cf. *R. lacustris*, which shows some characteristics like those of the Lahontan *Salmo clarki henshawi*; *Gila* (s.s.) sp., unlike *G. bicolor* subsp. that now inhabit the region and showing resemblances to the fossil *Mylopharodon haymanensis* (and to the genus *Lavinia* of the Sacramento River Basin); *Catostomus* sp. dentaries reminiscent of *C. cristatus* and maxillae like those of *C. (D.) shoshonensis* of the Snake River Plain; and bones referred to the genus *Chasmistes*, either *C. cujus* of the Lahontan Basin or any of several other Pliocene or Pleistocene forms from elsewhere in the west. Four of eight fossil molluscs from the Honey Lake beds similarly show relationships to southern Idaho. In contrast, Pliocene fish fossils from Mopung Hills, Nevada, between Carson and Humboldt sinks,

include kinds generally referable to modern species: *Salmo* sp. may be the same as *S. clarki henshawi*; *Gila* (*Siphateles*) sp. strongly resembles *G. bicolor*; *Catostomus* cf. *tahoensis* is clearly similar to *C. tahoensis*; and *Cottus* cf. *beidingeri* is almost certainly that species, which also is known from Pliocene(?) deposits on the east side of the Lahontan system (Jordan 1924a). *Salmo cyniclope* and *S. esmeralda*, fossil species from Miocene(?) beds (LaRivers 1964, 1966), another trout from the Miocene Truckee Formation (Bell, in Taylor and Smith 1981) and the species from the Mopung Hills site, all in Nevada, and from Pliocene Lake Idaho (*Salmo* sp.; G. R. Smith 1975), appear of the lineage that gave rise to most western *Salmo*, and attest to their remarkably long occupation of this region (LaRivers 1964; Taylor and Smith 1981). G. R. Smith (1978) also noted that *S. esmeralda* may be a relative of *S. clarki*. Molluscs from the Mopung Hills site were apparently lacustrine endemics, with no close relatives in the immediate area; only one widespread, living form was represented as a fossil (Taylor and Smith 1981).

Identity of some fossil cyprinids of the Lahontan region remains in doubt. Preservation only as lateral impressions of skeletons and body outlines on slabs of lake beds, plus possibilities for deformation after death of such features as positions of vertical fins and pelvic girdle, create problems of generic or subgeneric identifications. Thus the Miocene *Gila esmeralda* (LaRivers 1966; Lugaski 1977a) and Pliocene *Luciscus* (= *Gila turneri*) (Lucas 1900; R. R. Miller 1959a, 1965; LaRivers 1962, 1966; Lugaski 1977a) and *Gila traini* (Lugaski 1979), all from Nevada, were somewhat arbitrarily considered relatives of (and generally compared with) *G. (Siphateles) bicolor*. G. R. Smith (1978) considered *G. esmeralda* a synonym of *G. turneri*. G. R. Smith and Miller (1985) discussed similar Miocene cyprinids from the Clarkia Beds of north-central Idaho (presently Columbia River Basin) and referred them only

to "*Gila* sp.," commenting that, "Compared with the Pleistocene and Recent distribution, the Miocene distribution of the group [of generalized western cyprinids] was broader to the north and east." Other than fossils from Honey Lake just discussed, Pliocene to Recent fossils of this lineage from the Lahontan Basin preserved with evidence for critical characters have, however, been identified as allied with *G. bicolor* (R. R. Miller and Smith 1981; G. R. Smith 1978, 1981a).

Cyprinodontoid fishes also are known as fossils in the Lahontan region: *Fundulus nevadensis* (Pliocene) from northwestern Nevada (Eastman 1917; Bell 1974) and *F. lariiversi* (Miocene) from west-central Nevada (Lugaski 1977b). These, along with Mural's (1973) *Gasterosteus apodus* (= *G. doryssus*; Bell 1974) from northwestern Nevada and other *Gasterosteus*, *Fundulus*, *Cyprinodon* and *Empetrichthys* from the Mohave Desert and its environs (Hay 1907; Jordan 1908, 1924b, 1927; David 1945; R. R. Miller 1945c; Uyeno and Miller 1962) imply a terrain of gentle relief occupied by closed-basin lakes and otherwise drained by streams flowing to the Pacific prior to coastal and Sierra Nevada uplift (Axelrod 1948, 1958, 1962; Bell 1974; M. L. Smith 1981).

Ictalurus (Amiurus) hazenensis from diatomite of the Miocene Truckee Formation, western Nevada (Baumgartner 1982), is contemporaneous with abundant *Fundulus* and *Gasterosteus*. The ictalurid, a *Salmo* and *Gila* sp., are each known from single specimens. This portion of the Truckee Formation likely formed in several interconnected, variably saline lakes (Ruben 1971). *Ictalurus hazenensis*, *I. (A.) vespertinus* of the Miocene and Pliocene Snake River Plain (R. R. Miller and Smith 1967; G. R. Smith 1975; Kimmel 1975), and *I. (A.) peregrinus* (= *I. vespertinus*, *Fide*, Kimmel 1975) from Oregon (Lundberg 1975) are the only representatives of modern ictalurids known from northwestern North America.

Death Valley "System"

This fault-splintered zone of extended terrain of southern California and Nevada (Fig. 15.1) is characterized by remnant springs and marshes, often warm and saline, that rise along innumerable faults of desert mountains and valleys (Soltz and Naiman 1978). Large lakes long ago desiccated and low-elevation streams are scarce and ephemeral. The northwestern segment, Owens Valley, receives water from the Sierra Nevada and the White and Inyo mountains through streams that feed Owens River and Lake. Water removed by the Los Angeles aqueduct (Heinly 1910) dramatically modified this system. The largest segment includes Death Valley proper and supported Late Pleistocene Lake Manly, a water body 160 km long and 185 m deep (Hunt et al. 1966; Hunt and Mabey 1966; Hunt 1975). Surface tributaries to the sump of Death Valley include the Amargosa River and Salt Creek, both of which typically evaporate or subside into their beds before reaching the valley floor, plus a series of major springs and seeps. Springs of the Death Valley system yield water 8000–12,000 years old (Winograd and Pearson 1976) that flows from a vast area of southern and eastern Nevada through fractured carbonate rocks of Paleozoic age (Dudley and Larson 1976). Present aquatic habitats thus depend on interbasin water movement independent of surface topography (Naff et al. 1974; Winograd and Thordarson 1975). A southwestern segment is the Mohave River, which originates in the northern San Bernardino Mountains of California and passes east and north toward Death Valley. This stream percolates into its sandy bed after leaving the mountains and rises intermittently through its course to end in Soda Dry Lake.

Aquatic habitats and fishes of the Death Valley region have received a remarkable amount of study, which has been reviewed by R. R. Miller (1943a, 1946b, 1948), Hubbs

and Miller (1948a) and more recently by R. R. Miller et al. (1977) and Soltz and Naiman (1978). Hunt and Mabey (1966), Hunt et al. (1966) and Hunt (1975) reviewed geologic studies, which commenced in earnest with the monographic treatments of Russell (1885, 1889) and G. K. Gilbert (1897) (see also Harkewelder 1933).

Drainage relations of this now-arid region are and have been complex. Basins result from Miocene (and perhaps earlier) through Recent extensional events, complex events along the San Andreas Transform, movements of the Garlock and related faults and opening of the Gulf of California. Whole mountain ranges, such as the San Bernardino, San Gabriel, Panamint and Transverse ranges, have moved west and north. Changes in elevations and positions of these and the Sierra Nevada have provided geographically and temporally variable sources of water for lakes and streams during glacial events of Pleistocene and earlier wetter times. Remarkable volumes of sediment have been transported to fill intermontane basins. Evidence of connective events has thus been obscured and precision in dating is low. It is especially important to understand that available time has provided ample opportunity for aquatic connections through most unlikely areas and that bits of evidence for such events may not be contemporaneous.

Gale (1915) was first to propose with field evidence an integrated Death Valley system in Wisconsinan times, from Owens Valley along the eastern Sierra Nevada flank to Death Valley proper and including contemporaneous inflow of the Amargosa and Mohave rivers. R. R. Miller (1946b, 1948), Hubbs and Miller (1948a) and Morrison (1965c) accepted his hypothesis, which involved successive filling and overflow of Owens, Searles and Panamint lakes into Lake Manly. It is notable that sudden increases in water volumes in the Owens-China-Searles lakes alignment (G. I. Smith 1977, 1978a,b, 1979) may have resulted from diver-

sion eastward by volcanism of the San Joaquin River headwaters around 3.2 mya (Huber 1981). Hubbs and Miller (1948a, and references cited) further hypothesized an earlier connection of Mono Lake and Adobe Valley with Owens Valley, thus providing a plausible route for Lahontan fishes to the Death Valley region. Further passage of Panamint Lake into Lake Manly was questioned by Hunt and Mabey (1966) and Hunt (1975), but at least one Pleistocene overflow through Wingate Pass, possibly of a precipitous nature, was documented by Hooke (1972), R. B. Smith (1978), and G. I. Smith (1979 and in R. R. Miller 1981). An alternate pathway for water from Panamint Lake proposed by Hewett (1954) and espoused by R. R. Miller (1981) and D. W. Taylor (in Miller 1981) is through the east-west Leach Trough that follows the Garlock Fault toward Silver, Soda and Bristol (dry) lakes to enter a progenitor of the Gulf of California, which in Pliocene extended northwest at least to the Danby and Cadiz basins (P. B. Smith 1960). Lake Manly would have achieved similar connections, perhaps at a different time before Pleistocene, with the embayment or with what is now the lower Colorado River system (Metzger et al. 1973). Mohave River and its associated lakes were tributary to the Owens-Panamint aquatic alignment (R. R. Miller 1981). Hubbs and Miller (1948a) reviewed evidence for a headwater transfer from their "Las Vegas River" through Indian Springs Valley to the upper Amargosa River, as earlier proposed by Gilluly (1929) on the basis of physiographic evidence.

Fishes of disrupted drainages of the Death Valley region all are unique, with differentiation ranging from generic to subspecific levels. Four families are represented, with Cyprinidae including two species with five subspecies, Catostomidae with an endemic species and cyprinodontoids (Cyprinodontidae and Goodeidae) with two genera, six species and

13 subspecies. If native, *Gasterosteus aculeatus* from upper Mohave River (Bell 1982) adds an additional family, genus and species. That population is short-spined and melanistic, but otherwise resembles *G. a. williamsoni* of the adjacent Los Angeles Plain.

Fishes in the Death Valley region have generally been discussed in terms of Pleistocene dispersal and Pleistocene and Recent differentiation of taxa. Integrity of a Death Valley "system" has, however, recently been dismissed as too simplistic (R. R. Miller 1981), and far older occurrences and probable differentiation in the region have been forwarded for at least secondary fishes such as cyprinodontoids (G. R. Smith 1981a; M. L. Smith 1981; Parenti 1981a).

Gila bicolor is represented by *G. b. mohavensis* of the Mohave River drainage and *G. b. snyderi* of Owens Valley. *Gila b. mohavensis* is a lake-adapted form (gill rakers long, thin and numbering 18–29, average 24.0) restricted to Mohave River by desiccation of downflow lacustrine habitats. It is approaching extinction because of hybridization with introduced *Gila (Temeculina) orcutti* (Hubbs and Miller 1942). *Gila b. snyderi* also is influenced by hybridization with other subspecies transported to Owens Valley by fisherman (R. R. Miller 1973). This form closely resembles *G. b. obesa* of the adjacent Lahontan Basin, and differs markedly (for example, gill rakers numbering 9 to 15, average 12.1) from *G. b. mohavensis*. Pleistocene and Holocene remains of these or related *Gila (Siphateles)* sp. are known from Manix and Searles (dry) lakes in this region (Buwalda 1914; Blackwelder and Ellsworth 1936; Flint and Gale 1958).

The second cyprinid species, *Rhinichthys osculus*, includes *R. o. robustus*-like populations in Owens Valley, stocks referable to *R. o. nevadensis* in springs of Ash Meadows, and an unnamed subspecies in the Amargosa River (Deacon and Williams 1984). *Catostomus fu-*

meiventris occurs only in Owens Valley (R. R. Miller 1973), where it enjoys a wide distribution in almost all available habitats (Soltz and Naiman 1978).

Four species of *Cyprinodon* are separable into two lineages corresponding to the Owens Valley and Lake Manly segments. *Cyprinodon radiosus* of Owens Valley was almost destroyed by water developments and exotic, predatory fishes, but now persists in protected habitats within its native range (R. R. Miller and Pister 1971). *Cyprinodon nevadensis* (Eigenmann and Eigenmann 1889a; six subspecies, two extinct), *C. salinus* (R. R. Miller 1943b; including *C. milleri*, LaBounty and Deacon 1972; see R. R. Miller 1981) and *C. diabolis* (Wales 1930), form a second interrelated group distributed in Ash Meadows and southern Death Valley, Salt Creek–Cottonball Marsh, and the extremely isolated Devils Hole, respectively (R. R. Miller 1948, 1950a, 1961a, 1977, 1981; James 1969; Soltz and Naiman 1978).

Empetrichthys merriami, recently extinct (Minckley and Deacon 1968), formerly inhabited springs of Ash Meadows, Nevada. A second species, *E. latos*, had a subspecies in each of three now-dry springs in the isolated Pah-rump Valley southeast of Ash Meadows (*E. l. latos*, *E. l. concavus* and *E. l. pah-rump*; R. R. Miller 1948, 1950a). All natural populations are extinct, with only *E. l. latos* surviving in artificial refugia (Soltz and Naiman 1978). Immediate relationships of these fishes are to the genus *Crenichthys* of the White River and Railroad Valley to the east (Hubbs 1932; Uyeno and Miller 1962; Parenti 1981a).

Gila bicolor snyderi, *Catostomus fumeiventris* and *Rhinichthys osculus* cf. *robustus*, in Owens Valley, all with relationships to the Lahontan Basin (Snyder 1919c; R. R. Miller 1973), attest to past continuity between those two systems, likely through the Mono Lake area (Russell 1889) as hypothesized by Hubbs and Miller (1948a) and R. R. Miller (1973). The Mono Lake

basin lacked native fishes, perhaps because of volcanic catastrophe (Hubbs and Miller 1948a). G. R. Smith (1981a) considered *G. bicolor* in this region either as a Pliocene colonist that differentiated rapidly or as a relict of Pliocene north-south connections. *Gila b. mohavensis*, the only native cyprinid in the Mohave River drainage (Snyder 1919a; R. R. Miller 1936, 1938b), is the most southern penetrant of this northern fauna. If the recently discovered population of *Gasterosteus aculeatus* in Mohave River headwaters is native (Bell 1982), it must have been uplifted with the Transverse Range.

A Pleistocene fossil *Chasmodon* (cf. *batrachops*) near China Lake, California (R. R. Miller and Smith 1981), further substantiates a north-south distributional continuity east of the Sierra Nevada on the west side of the Great Basin. *Chasmodon batrachops* is otherwise known from Pleistocene sediments of the Fort Rock Basin, Oregon, and as referred fossil material from Washoe County, Nevada (R. R. Miller and Smith 1981).

Populations of *Rhinichthys osculus nevadensis* in the Lake Manly segment were originally thought to resemble those from Las Vegas Wash of the middle Colorado River drainage (R. R. Miller 1946b) and perhaps derived from headwater transfer between that wash through Indian Springs Valley to the Amargosa watershed (Gilluly 1929; Hubbs and Miller 1948a). R. R. Miller (1984) has described the Las Vegas Wash form as *Rhinichthys deaconi*, with relationships to spring-inhabiting populations to the north.

Cyprinodon clearly entered the Death Valley region from the south (R. R. Miller 1981). Among Recent species, *Cyprinodon radiosus* most closely resembles *C. macularius* from the lower Colorado River Basin (R. R. Miller 1948), but must have long been isolated. Marked differentiation of *C. nevadensis* and its allies in the Lake Manly Basin(s) may reflect long isolation from an ancestral form, more rapid ev-

olution in the Amargosa-Death Valley drainage or both (R. R. Miller 1981). *Cyprinodon salinus* and *C. diabolis* presumably evolved from *C. nevadensis* or its immediate ancestor in disrupted segments of the system. *Cyprinodon diabolis* arose in the last 10,000–20,000 years in a special, tiny, warm-water spring (Wales 1930; R. R. Miller 1948, 1950a, 1961a, 1977, 1981; Soltz and Naiman 1978). Origins of subspecies of *C. nevadensis* date to variable times before present depending on the sequence of disruption following high stages of Lake Manly around 12,000 ya (Hunt 1975). *Cyprinodon salinus* may have differentiated early as a stream-adapted form in tributaries to Lake Manly. If not, it also dates to less than 12,000 ya, coincident with desiccation of the lake. The Cottonball Marsh form, *C. s. milleri*, has been isolated from *C. s. salinus* for perhaps no longer than a few hundreds of years (Mehring, in LaBounty and Deacon 1972).

Despite evidence for recent and rapid phenotypic differentiation with little genetic change of species and subspecies (Turner 1974; Turner and Liu 1977; Soltz and Hirshfield 1981), cyprinodontoid fishes are old inhabitants of this region. A substantial fossil fauna of lowland fish genera, that is, *Fundulus*, *Cyprinodon*, *Empetrichthys* and one or more gasterosteids (*Gasterosteus*), occurs in Miocene and Pliocene deposits of southwestern United States (David 1945; R. R. Miller 1945c; Uyeno and Miller 1962; Bell 1973a,b, 1977; Mural 1973; Lugaski 1977b; Bell and Haglund 1982). Fossil *Fundulus* are especially widespread, ranging from what is now the Lahontan Basin near Pyramid Lake, Nevada, south throughout the Mohave Desert. The present distribution of this genus is coastal southern California, and Peninsular Baja California (Follett 1961). Fossil *Cyprinodon* (*C. breviradius*) are known only from the Death Valley region (R. R. Miller 1945c), from deposits thought to be Miocene in age (McAllister, in R. R. Miller 1981). *Empetrichthys erlisoni* occurs in Miocene lake beds in Los An-

geles County, California (Uyeno and Miller 1962; Crowell and Link 1982; Welton and Link 1982). The fossil *Empetrichthys* localities and some for *Fundulus* are, however, from deposits transported a substantial distance north and west from their original deposition sites.

These fossil occurrences linked with distributions of living species reflect a drainage pattern antedating movements of primary fishes into the region (M. L. Smith 1981) and support existence of a broad lowland drained by southwesterly flowing streams, as indicated by regional geologic evidence. Parenti (1981a) further emphasized the relict nature of this fauna by proposing *Empetrichthys* and *Crenichthys* to be egg-laying genera of the family Goodeidae (Empetrichthyidae of Miller and Smith, this volume), an otherwise live-bearing group presently restricted to central Mexico.

North-Central Great Basin

A series of contiguous endorheic basins in central and eastern Nevada and extreme western Utah constitute a zone of intimate contact among the Lahontan, Bonneville and middle Colorado River systems. Hubbs and Miller (1948a) and Hubbs et al. (1974) reviewed geological and ichthyological research in this area, and in the latter paper detailed the fish fauna. Four fish species comprise the native fauna, consisting of two widespread Lahontan forms, *Rhinichthys osculus robustus* and *Gila bicolor* and derivatives and two species of localized distribution, *Relictus solitarius* and *Crenichthys nevadae*. Of 21 basins studied by Hubbs et al. (1974), 10 supported fishes, 7 supported only a single species and only 3 were occupied by two species.

Both Lahontan fishes have differentiated into local subspecies (Hubbs and Miller 1972). Those for *R. osculus* are: *R. lariversi* (Lugaski 1972; = *R. o. lariversi*, *Fide*. Hubbs et al. 1974 and R. R. Miller 1984) from the Toiyabe Basin; *R. o. lethoporus* from Independence Valley in Clover Basin; *R. o. oligoporus* from Clover Valley also

in the Clover Basin; and *R. o. reliquus* from Gilbert Basin. All these forms were thought derived from *R. o. robustus* or an immediate ancestor, with possible exception of *R. o. reliquus*, which Hubbs et al. (1974) noted may be specifically distinct and a "relict of ancient and somewhat uncertain origin." Forms of *Gila bicolor* were thought derived from stream-adapted *G. b. obesa* of the Lahontan system. Included are *G. b. newarkensis* from Newark Basin, *G. b. euchila* from Fish Creek Springs also in Newark Basin, *G. b. isolata* from Clover Basin and aberrant forms from Diamond Basin referred to *G. b. obesa*. Hubbs et al. (1974) also referred to "several unnamed subspecies, still under study" from Railroad Valley, Nevada.

Relictus solitarius occupies springs and streams of Franklin and Waring basins, Nevada, and, unlike the other cyprinids, is scarcely differentiated among localities despite marked local isolation. Its relationships are remotely with *Rhinichthys*, but it equally could have been derived from the *Siphateles* lineage of *Gila* (Hubbs et al. 1974). Along with the monotypic cyprinid genera *Moapa* and *Eremichthys*, *Relictus* contributes toward a distinctive relict fauna inhabiting this portion of the Basin and Range region. *Crenichthys nevadae* of Railroad Valley (and *C. baileyi* of the White River) may also be assigned to this fauna.

Bonneville Basin

This vast area, lying mostly in northern Utah, is the largest interior drainage of the Great Basin (Fig. 15.1) and supported a Pleistocene freshwater sea of at least 51,700 km² and about 335 m depth (Hunt et al. 1953). High-water stages of Late Pleistocene Lake Bonneville cut deep terraces on surrounding mountains that stand in mute testimony to extensive, wave-washed beaches (Hubbs 1941). These terraces are now at variable elevations, both as a result of rebound of local terrains from loading and unloading of repeated filling and desiccation (Crittenden 1963a,b; Curry 1980) and

from local differentials in tectonic uplift (R. B. Smith 1978). Great Salt Utah and Sevier lakes are desert remnants of Lake Bonneville. Bear Lake, at higher elevation in coniferous forests of the Utah-Idaho border, was and remains tributary to the system.

Like the Lahontan Basin, this vast area has long been subject to isolation in bits and pieces, and may have enlarged in the Pliocene-Pleistocene to its present size by reduction of topographic divides (Tayor 1985). Miocene and Pliocene deposits in northwestern Utah are faunally similar to the Snake River Plain (McClellan 1973). Fishes (and molluscs) of similar age in northeastern Utah show far less resemblance to the Snake River fauna (Taylor 1985). Pleistocene fossils from the Bonneville system mostly are of the same species that occur today (citations below).

Great Salt Lake now comprises about 4360 km² and is 15 m in maximum depth. Salinities are too high to support fishes, except near immediate inflows of tributaries. Utah Lake is also broad and shallow, 360 km² and a maximum of 5 m deep, but its waters remain relatively fresh and support both native and introduced fishes (Sigler and Miller 1963). Sevier Lake in west-central Utah is ephemeral and when filled its waters are highly saline. Bear Lake is the only large lacustrine habitat of the system that supports a substantial ichthyofauna (McConnell et al. 1957). It lies at about 1800 m above sea level, is 32 km long and ranges to 63 m in depth.

Bear River originates east of the Wasatch Mountains, flows north, west and south to Bear Lake, then again turns north, west and back south around the Wasatch Range to enter Great Salt Lake at its northeast corner. Weber River begins in the Jinta Mountains, passes through the Wasatch Front and enters Great Salt Lake from the east. Additional inflow is from Jordan River, which flows north on Bonneville Lake beds to connect Utah and Great Salt lakes. Utah Lake receives the short, pre-

cipitous Provo and Spanish Fork rivers from mountains to the east. All these streams flow in disproportionately large valleys cut by outflows from montane glaciers of the Wasatch and Uinta highlands. Sevier River is the longest stream of the Great Basin of Utah, heading on the Colorado Plateau near the Utah-Arizona border, flowing north through successive structural troughs, then passing west and again south to desiccate in Sevier Lake (Fig. 15.1).

Unlike the Lahontan Basin, drainage relations of the Bonneville system include some clear-cut connections with adjacent drainages, especially with regards to the upper Snake River. G. K. Gilbert (1890) clearly demonstrated overflow of Lake Bonneville to the Snake River during what he considered the second of two high-water stages, which he further correlated with the last of two continental glaciations then thought to have occurred in west central North America. Morrison (1965a,c) summarized and revised older literature on this event and correlated Lake Bonneville stages with local montane glaciation. Scott et al. (1982) substantially revised Morrison's scheme on the basis of ^{14}C dating and amino-acid measurements of fossil shells. They documented two "deep lake" cycles, the latest between 24,000 and 11,000 ya and an earlier high stage about 150,000 ya. Overflow of Lake Bonneville was through Redrock Pass, Idaho, into a tributary of the upper Snake River during Wisconsinian time. Cook and Larrison (1954), Trimble and Carr (1961), Stearns (1962), Broecker and Kaufman (1965) and Malde (1968) documented catastrophic flooding that resulted in the Snake River. Soils developed before and between lake maxima indicate almost complete desiccation during interstadial periods. Lakes occupying the basin earlier in Pleistocene (Hunt 1953) had no apparent outlets, but also were separated by periods of drying during which thick soil profiles developed (Morrison 1964, 1965b,c). Addition of the Bear River watershed, which presently contributes about

14% of total inflow to the Bonneville Basin (Bright 1963), helps to explain Late Pleistocene overflow whereas earlier glaciations produced no such events (Morrison 1965c).

Bear River repeatedly changed its course in Pleistocene times due to block-faulting and volcanism (Morrison 1965c). It flowed north via the Portneuf River to the Snake prior to 34,000 ya, then was diverted southward into Gentile Valley by a lava dam. Successive lava damming resulted in Lake Thatcher, which filled to overflow and incised its southern rim, emptying into Cache Valley Arm of Lake Bonneville (Rubin and Berthold 1961; Bright 1963).

Probable connections of the Bonneville system and the Colorado River Basin via Green River include no such spectacular incidents. Headwater transfers doubtless occurred over broader divides where alluvial cones variably direct montane discharges between drainages (Hubbs and Miller 1948a) and stream captures between adjacent mountain streams are topographically evident (G. R. Smith 1966). Keyes' (1917, 1918) hypothesis that the upper Snake River flowed across the Bonneville Basin to join the lower Colorado River is, however, generally unsupported.

Commensurate with its size, the Bonneville system with 20 species has the largest fish fauna of any interior drainage in western North America (R. R. Miller 1959a; G. R. Smith 1978). Earlier treatments of the Bonneville ichthyofauna include Cope (1874a), Jordan and Gilbert (1881), Jordan (1891b), Snyder (1924), Tanner (1936), Hubbs and Miller (1948a), R. R. Miller (1959a), Hubbs et al. (1974) and G. R. Smith (1978, 1981b, 1983). Exchange of fishes between the Bonneville and upper Snake River systems during interconnective events has long been recognized (Jordan 1891b; Evermann 1892a; C. H. Gilbert and Evermann 1894). Twelve of the 20 species in the Bonneville system also are represented in the upper Snake.

Of the fishes studied, *Prosopium williamsoni*

may have entered the Bonneville Basin from its vast northern distribution on more than one occasion (Holt 1960). *Salmo clarki utah* of the Bonneville system is morphologically and biochemically nearest *S. c. bouvieri* of the Snake River (Loudenslager and Gall 1980; Behnke 1981). There are three races of *S. c. utah*, one widespread in the system, one in the Bear Lake segment and another (Klar and Stalnaker 1979) in the isolated Snake Valley segment. Fossils from Great Salt Lake (Stokes et al. 1964; G. R. Smith et al. 1968) indicate *S. clarki* achieved large size (greater than 70 cm standard length) in Lake Bonneville, as it did in Utah Lake within historic times (Cope and Yarrow 1875).

Gila atraria exhibits extensive local variation in body size and shape, coloration and meristic characters such as gill rakers (G. R. Smith 1978). Populations of the upper Snake River and Bonneville systems thus show little variation correlative with interconnective events. Distribution of *G. atraria* in the upper Snake River only above Shoshone Falls, a pattern similar to that of other presumed Bonneville fishes, implies its movement from south to north. Late Pleistocene fossils from Great Salt Lake terraces (G. R. Smith et al. 1968) and from Black Rock Canyon, Tooele County, Utah (R. R. Miller and Smith 1981), were clearly of *G. atraria*.

Gila (Snyderichthys) copei has a distribution including Wood River system, Idaho. Wood River is isolated north of lava flows of the Snake River Plain and enters the Snake River below falls that form a barrier to other Bonneville fishes. Its occurrence in Wood River could not be attributed to introduction by Hubbs and Miller (1948a), and R. R. Miller (1945b) considered the population differentiated from others. The species otherwise is known from uppermost Snake River and its tributaries in Wyoming (Simon 1946). Occurrence of *G. copei* above barriers may reflect a pattern of distribution older than those influenced by Late Pleistocene connections, yet R. R. Miller (1959a) considered it a Bonneville species that has

moved from south to north. In the Bonneville system it lives from Bear River south to headwaters of the Sevier River.

Richardsonius balteatus hydrophlox may have entered the Bonneville system from the north, since it also now occurs in parts of the Columbia River Basin above barrier falls that predate Bonneville-Snake River connections (Hubbs and Miller 1948a). The Pliocene *R. durranti* from the Snake River Plain is nearest *R. balteatus* (G. R. Smith 1975). *Rhinichthys cataractae* also most likely entered the Bonneville system from the north (G. R. Smith 1981a), since it otherwise inhabits northwestern North America only through the Columbia River Basin and its connectives. Jordan and Evermann (1896) acknowledged the relatively uniform morphology of Rocky Mountain populations of *R. cataractae* and those of the Columbia and Bonneville basins (as *R. c. dulcis*), and Simon (1946) referred all populations of the upper Missouri (excluding Platte River), Snake and Bear river systems of Wyoming to *R. c. ocella*.

Rhinichthys osculus, as in the Lahontan system and elsewhere, is not instructive due to lack of detailed taxonomic studies. It is represented in the Bonneville Basin by *R. o. adobe* described from the Sevier River drainage, populations from the northern Bonneville system and adjacent Columbia Basin referred to *R. o. carringtoni* and a number of other isolated races. It also presumably gave rise to an undescribed species of *Rhinichthys* (*Apocope*) known from the Bonneville Desert (G. R. Smith 1978; R. R. Miller, 1981). Simon (1946) attested to the common occurrence of *R. o. carringtoni* in the upper Snake and Bear rivers, Wyoming.

Pantosteus platyrhynchus of the northern Great Basin (including both the Lahontan and Bonneville systems) and uppermost Snake River show concordance in characters suggestive of recent genetic connections. G. R. Smith (1966) suggested that the Snake River was occupied by a form of *P. platyrhynchus* most closely allied to those of upper Missouri or Green rivers prior to overflow of Lake Bonneville. These

were presumably replaced by Bonneville stock. Populations of this species below Shoshone Falls are sparse, scattered and possess characteristics of fish from the Missouri River drainage, while those above the Falls are "undifferentiated associates of the Bonneville Basin populations" (G. R. Smith 1966). *Pantosteus platyrhynchus* from the Sevier River Basin, and some isolated stocks derived from that system, appear differentiated from those of the northern Bonneville region. Hybridization with introduced *P. clarki* has, however, been implicated in some detected morphological differences, at least in the Shoal Creek drainage (Koehn 1969).

Pantosteus discobolus in the upper Green River (Colorado River Basin), uppermost Snake River tributaries and the northeast Bonneville system (Bear and Weber rivers) reflects both drainage exchanges and major connections. Characters of these populations suggest recency of common ancestry.

Catostomus ardens, a species most intimately related to the *C. commersoni* complex of eastern North America (G. R. Smith et al. 1968; G. R. Smith 1978), shows a distinctive "Bonneville" distribution above Shoshone Falls in the upper Snake River and lives throughout the Bonneville Basin in larger streams and lakes. A Pleistocene *C. ardens* from the Great Salt Lake Basin closely resembled modern skeletal material (G. R. Smith et al. 1968). R. R. Miller (1959a) considered this species to have entered the Bonneville Basin from the north. The nominal *Catostomus fecundus* from Utah Lake (Cope and Yarrow 1875) was based on hybrids between *C. ardens* and *Chasmistes liorus* (R. R. Miller and Smith 1981).

Cottus beldingi and *C. bairdi semiscaber* in the Bonneville Basin are relicts isolated near the southern limits of their ranges. Both are widespread in tributaries of the upper Snake River Basin (Bond 1963; Bailey and Bond 1963).

Of the seven species shared by the Bonneville and upper Colorado River (*Prosopium wil-*

liamsoni, *Salmo clarki*, *Rhinichthys osculus*, *Pantosteus platyrhynchus*, *P. discobolus*, *Cottus bairdi* and *C. beldingi*), all are characteristic of or have populations that ascend to high elevation and thus are available for interbasin transfers through stream captures. Colorado River populations of *S. clarki* (*S. c. pleuriticus*), *R. osculus* (*R. o. yarrowi*) and *Cottus* (*C. bairdi punctulatus*, *C. beldingi annae*) are differentiated from those of the Bonneville and Snake River systems, although *R. osculus* tends to vary radically and distributions of the myriad of forms add little information (R. R. Miller 1959a). The other three species have differentiated only slightly if at all in the two systems (R. R. Miller 1959a; G. R. Smith 1966).

Fishes endemic to the Bonneville system include *lotichthys phlegythontis*, a diminutive cyprinid of uncertain generic affinities distributed in springs, marshes and smaller streams near Great Salt, Utah and Sevier lakes. The remainder are remnants of a Bonneville system lacustrine fauna: *Prosopium gemmiferum*, *P. spilonotus*, *P. abyssicola*, *Chasmistes liorus*, *Cottus extensus* and *C. echinatus*.

Prosopium gemmiferum is known only from Bear Lake (Snyder 1919b). It is so distinctive as to have been placed in the genus *Leucichthys* until Norden (1961) demonstrated its osteological alliance with *Prosopium*. Its relationships are otherwise unknown, but it may represent an old endemic. Its closest geographic relative is the Miocene-Pliocene *P. prolixus* of southern Idaho (G. R. Smith 1975; Kimmel 1975). A Pleistocene fossil 95% separable from *P. gemmiferum* (G. R. Smith 1981a) from the Great Salt Lake Basin (G. R. Smith et al. 1968) may represent an immediate ancestor from which *P. gemmiferum* rapidly evolved, or is a close relative (G. R. Smith 1981a). The age of the Bear Lake system is not known, but a succession of lakes from Miocene to Recent (Peale 1879) may have provided a continuous, albeit oscillating, lacustrine habitat (R. R. Miller 1965). *Prosopium spilonotus* and *P. abyssicola* also

are now restricted to Bear Lake. The former also occurs as fossils in Great Salt Lake Basin (G. R. Smith et al. 1968). Relationship of *P. spilonotus* is to *P. williamsoni* or its ancestral form (R. R. Miller 1965). Miller (loc. cit.) considered *P. abyssicola* autochthonous to the Bear Lake-Bonneville system and derived from an unknown ancestor.

Chasmistes liorus now lives only in Utah Lake, but referred fossils are known from Late Pleistocene Bonneville deposits in Tooele County, Utah (along with *Salmo clarki* and *Gila atraria*). Bright (1967) obtained material of a *Chasmistes* related to *C. liorus* or *C. muriei* of the Snake River Basin from Pleistocene beds of Thatcher Lake, Idaho (R. R. Miller and Smith 1981). Since a 1936 drought, *Chasmistes l. liorus* has been replaced through hybrid origin of *C. l. mictus* due to introgression of characters from *Catostomus ardens* (loc. cit.). Relationships of the Bonneville *C. liorus* are nearest *C. cujus* of the adjacent Lahontan Basin.

Cottus echinatus and *C. extensus* are respectively endemic to Utah and Bear lakes (Bailey and Bond 1963). They belong to the *C. bairdi* species group (Bond 1963) and presumably represent early invasions and lacustrine speciations from *C. bairdi* or its progenitor. *Cottus extensus* was sympatric with *C. bairdi* in Great Salt Lake Basin in the Late Pleistocene (G. R. Smith et al. 1968). According to the last authors *C. extensus* likely gave rise to *C. echinatus* in Utah Lake through several cycles of desiccation and isolation. *Cottus echinatus* was apparently forced to extinction by drought (Tanner 1936).

Sacramento-San Joaquin System

The complex Sacramento-San Joaquin system lies almost entirely within the state of California. The Sacramento River originates in Pit River near the Oregon-California border and flows south to and through the Great Valley. A now-closed basin, Goose Lake, spilled south

into Pit River in historical time. Most other major tributaries to the Sacramento drain westward from the Sierra Nevada.

The San Joaquin River flows north in the Great Valley from lower elevation and more arid southern California. Aridity results in pronounced isolation of headwaters, and the Kern, Tule, Kaweah and Kings rivers enter the mainstream only in exceptional runoff years. The Sacramento and San Joaquin rivers meet in the central Great Valley to form a common inland delta, then pass through the Suisun, San Pablo and San Francisco bays to the Pacific Ocean.

Some coastal streams of northern California south of Klamath River (Mad River south to creeks entering Tomales Bay) have been discussed before. The Pajaro-Salinas complex and the Clear Lake Basin lying within confines of the Sacramento watershed all support elements of the Sacramento River fauna (Moyle 1976a; J. J. Smith 1982; Taylor et al. 1982) and are included here.

Much of the Sacramento-San Joaquin fish fauna was described early. Baird and Girard (in Girard 1854) and Girard (1854) named *Gila crassicauda*, *Lavinia exilicauda*, *Hesperoleucus symmetricus*, *Mylopharodon conocephalus*, *Archoplites interruptus*, *Cottus gulosus* and *Leptocottus armatus*. Food fishes, *Spirinchus thalichthys*, *Orthodon microlepidotus*, *Pogonichthys macrolepidotus*, *Ptychocheilus grandis* and *Catostomus occidentalis*, were described by Ayres (1854, et seq.) from markets of San Francisco. Lockington (1878) further reported on food fishes from the area.

Zoogeography of this fauna stimulated early surveys and publications on variation and distribution. Campbell (1882) presented notes on McCloud River and its fishes. Jordan (1894) published on freshwater fishes from San Luis Obispo County, California. Clear Lake attracted early investigation (Jordan and Gilbert 1894) and has received substantial subsequent work (Coleman 1930; Murphy 1951; Hop-

kirk 1973; Taylor et al. 1982). Snyder (1905, 1908a,c,d, 1913) produced a series of papers on fishes of coastal streams from Oregon and northern California south to Monterey Bay. Branner (1907) noted drainage peculiarities reflected in freshwater animals of Santa Clara Valley. Rutter (1908) produced a summary of past and original data for the entire basin. Salmonid fishes of the region were and are a major natural resource (Evermann and Meek 1897), and *Salmo aguabonita*, plus forms such as the still-unnamed *Salmo* sp. (redband), have stimulated many workers (Evermann 1905; Needham and Gard 1959; R. R. Miller 1950b, 1972b; Schreck and Behnke 1971; Legendre et al. 1972; Behnke 1972, 1979, 1981; Gold and Gall 1975a,b; Gall et al. 1976; Gold 1977). Notes on distributional records and listings of California fishes contain many often obscure but important references, which were summarized by Moyle (1976a) and are mostly cited below.

Configuration of union of the Sacramento and San Joaquin rivers and the sea, an inland delta, than three downflow bays connected by narrow straits, results in complex interactions of tides, river currents and salinity (Kelly 1956). Salt water is kept from the Delta by river inflows, but relationships in bays are only generally those of ever increasing salinity as one approaches the Pacific. Mixtures of marine, euryhaline and freshwater fishes are common in this area (Table 15.2), as in other estuarine habitats of the California coast such as the Salinas (Hubbs 1947) and Navarro rivers (Moyle 1976a). Ganssle (1966) considered only *Hypomesus transpacificus* and *Spirinchus thalichthys* as "truly resident" of the Suisun and San Pablo bays. The latter also occupies Humboldt Bay and Eel River. *Spirinchus thalichthys* spawns in the lower reaches of rivers. *Clupea harengus pallasii* spawns in estuaries, and *Engraulis mordax* is abundant in the Sacramento-San Joaquin estuary in spring and summer (Ganssle 1966) and may be represented by an endemic subspecies (Roedel 1953).

A total of at least 48 species of marine fishes has been recorded in euryhaline waters of this part of the California coast (Table 15.2). Typical forms include *Hypomesus pretiosus*, *Atherinops affinis*, *Sygnathus leptorhynchus*, *Cymatogaster aggregata*, *Cleavelandia ios*, *Eucyclogobius newberryi*, *Gillichthys mirabilis*, *Clinocottus acuticeps*, *Leptocottus armatus* and *Platichthys stellatus* (Ganssle 1966; D. J. Miller and Lea 1972, 1976; Moyle 1976a). *Gasterosteus aculeatus* is marine, estuarine or freshwater throughout the area. *Fundulus parvipinnis* is at its northern limit in the Salinas River (see however Swift 1980f). Widespread anadromous forms include *Lampetra tridentata*, *L. ayresi*, *Acipenser transmontanus*, *A. medirostris*, *Oncorhynchus* spp. and *Salmo gairdneri*. An anadromous stock of *Salmo clarki* reproduces in the Eel River.

Among freshwater fishes, *Pogonichthys macrolepidotus* is perhaps the most salinity-tolerant cyprinid on the Delta (Messersmith 1966) and was formerly widely distributed. The species now is restricted to the Delta due to upstream alterations by man (Daniels and Moyle 1983). *Orthodon microlepidotus*, *Ptychocheilus grandis*, *Gila* (*Temeculina*?) *crassicauda*, *Catostomus occidentalis*, *Archoplites interruptus* and the freshwater embiotocid *Hysteroecarpus traski* are or were abundant on the Delta and in sloughs and other fresher parts of bays. *Archoplites interruptus* is extirpated from the Delta and is rare elsewhere. *Gila crassicauda* is likely extinct (R. R. Miller 1963a; Moyle 1976a). All the last fishes range widely through lowlands of the Great Valley and all but *P. macrolepidotus* are or were also in Clear Lake Basin (Hopkirk 1973; Taylor et al. 1982) and some coastal drainages (Moyle 1976a). A record of *P. macrolepidotus* from the Russian River (Pintler and Johnson 1958) was considered questionable by Moyle (1976a). *Pogonichthys ciscoideus* of Clear Lake was presumably derived from *P. macrolepidotus* (Hopkirk 1973). *Endemichthys grandipinnis*, described by Hopkirk (1973) from Clear Lake, was dismissed as a hybrid between *Lavinia*

exilicauda and *Orthodon microlepidotus* by Hubbs (1974), an action followed by most subsequent authors (see however Hubbs et al. 1979). Furthermore, the name *Endemichthys* is preoccupied according to Coad and Qadri (1978). We are prone to retain the taxon pending clarification of its status, but exclude it from Table 15.1.

Four Lahontan fishes are in the Sacramento River Basin. *Richardsonius egregius* was reported near Clear Lake (as *Phoxinus cleavelandi*; Eigenmann and Eigenmann 1889b) and in upper Feather (Rutter 1908) and Rubicon rivers (Kimsey 1950). *Catostomus tahoensis* and *P. platyrhynchus* also are recorded from the upper Feather River system (Rutter 1908; Murphy 1941; Kimsey 1950), and *Cottus beldingi* was reported from one stream in the same area (Rutter 1908). Moyle (1976a) further recorded *P. platyrhynchus*(?) from the Sacramento River mainstream, but he (pers. comm., 1983) considered the record questionable. G. R. Smith (1966) noted the Feather River occurrence of *P. platyrhynchus* as the only record of its genus on the Pacific Slope of the Sierra Nevada. Although he examined specimens collected by Rutter, we can find no mention of their variational status. The area was intensively used by gold seekers, lumbermen and ranchers in the 1800s, and Rutter (1908) noted that early salmonid introductions from the Lake Tahoe region could have been accompanied by other species. Other workers have considered this a distinct possibility (R. R. Miller 1946c [as *Pantosteus* sp.]; Hubbs and Miller 1948a; Kimsey 1950; Moyle 1976a). Early dates of collection for all four nevertheless argue against the introduction hypothesis, as do the number of species involved, but their rarity and (in part) local distributions argue for it (Hubbs and Miller 1948a). They could represent relicts of pre-Sierra Nevada uplift and drainage reversal at the Sierra crest, or their presence may record some later stream capture.

Goose Lake derived much of its fish fauna

from the Pit River. Native species now present are *Lampetra tridentata*, *Salmo* sp. (redband), *Catostomus occidentalis*, *Gila bicolor thalassina*, *Hesperoleucis s. symmetricus*, *Rhinichthys osculus* and *Cottus pitensis*. *Catostomus microps* was recorded from the basin (Schultz and DeLacy 1935; Bond 1961), but has not been taken there for at least 50 years. C. E. Bond (unpublished data) has intensively sampled the area and caught only *C. occidentalis*.

In discussing an hypothesized connection between the upper Pit River and Klamath basins, Robins and Miller (1957) included Goose Lake in the zone of interchange. However, there is little evidence of Klamath faunal elements in Goose Lake drainage. *Gila b. thalassina* of Goose Lake Basin has higher gill raker counts than either the Klamath or Pit River populations (F. Bills, unpublished data), which may align it with *G. b. pectinifer* or other Lahontan lacustrine forms (R. R. Miller, pers. comm., 1983). Neither *Cottus asperimus* (a close relative of *C. tenuis* of the Klamath) nor *C. klamathensis* are in the Goose Lake drainage, whereas *C. pitensis* is not in the Klamath drainage and landlocked *Lampetra tridentata* of Klamath River and Goose Lake drainages are racially or subspecifically distinct (C. E. Bond and T. Kan, unpublished data). *Lampetra tridentata* does not penetrate to the upper Pit River and *L. lethophaga* appears in the Pit drainage only below Goose Lake. Either the Klamath-Pit interchange was downflow from Goose Lake, or all Klamath forms that entered that basin were extirpated and their influence on Goose Lake forms not detected. If *G. b. thalassina* of Goose Lake originated in either the Klamath or Pit systems it has diverged from the presumed ancestral stocks in gill raker number and body shape.

Widespread species of the region may or may not be represented by distinct subspecies. The nonparasitic *Lampetra pacifica* is widespread at low elevation in the Great Valley and in coastal streams and is relatively uniform in

morphology (Vladykov 1973). *Orthodon microlepidotus* (throughout the Sacramento and San Joaquin rivers and their tributaries, in Clear Lake and the Pajaro-Salinas complex), *Ptychocheilus grandis* (entire system with exceptions of the remote Goose Lake and Kern River), *Mylopharodon conocephalus* (absent from Goose Lake and Kern River, and from coastal drainages except Russian River) and *Archoplites interruptus* (Sacramento-San Joaquin and tributaries, Clear Lake and Pajaro-Salinas system) all appear morphologically uniform throughout their ranges (Moyle 1976a). *Cottus asper* and *C. gulosus* (both in coastal drainages; and at low elevations in the Great Valley) exhibit substantial variability, as does *Cottus aleuticus*, which reaches southern limits of its range in coastal streams of San Luis Obispo County, California (Robins and Miller 1957); none has been carefully studied throughout its range. Interestingly, *Rhinichthys osculus*, a species notorious for local variability and thus a remarkably complex synonymicon (LaRivers 1962; Cornelius 1969), has not received taxonomic recognition in the Sacramento-San Joaquin region. It is in the main part of the system, Goose Lake and Pit River drainages, Pajaro-Salinas complex and a few coastal streams (Moyle 1976a).

In contrast to these taxa, the cyprinid genus *Hesperoleucus*, as noted in part before, is represented by nominal species (Snyder 1913) in the upper Pit River and Goose Lake (*H. mitrulus*), Navarro River (*H. navarroensis*), streams tributary to Monterey Bay (*H. subditus*), Gualala River (*H. parvipinnis*), Russian River and streams flowing into San Francisco Bay (*H. venustus*) and of the Great Valley and its tributaries (*H. symmetricus*). These are currently treated as subspecies of *H. symmetricus*. *Lavinia exilicauda* is similarly represented by *L. e. exilicauda* in main rivers of the Sacramento-San Joaquin complex, *L. e. chi* from Clear Lake, and *L. e. harengus* from Pajaro and Salinas rivers (R. R. Miller 1945d; Hopkirk 1973). *Gila*

bicolor also is represented by local differentiae: *G. b. thalassina* in Goose Lake and undescribed or poorly characterized forms in Hat Creek and in parts of the Pit River other than Hat Creek (*G. bicolor* subsp.). Forms reported from the Sacramento-San Joaquin Valley (*G. b. formosa*?; see Moyle 1976a and Hubbs et al. 1979) may have resulted from mislabeled specimens (P. B. Moyle, pers. comm., 1983). *Catostomus occidentalis* is the most widespread species of this region, inhabiting along with *Salmo gairdneri* (but in a far greater diversity of habitats) all parts of the Sacramento-San Joaquin complex and associated coastal watersheds. Four subspecies were recognized by Moyle (1976a): *C. o. occidentalis* in Sacramento and San Joaquin rivers and their tributaries, Russian River, Clear Lake and streams tributary to San Francisco Bay (Snyder 1905, 1908a); *C. o. mniotilus* in Pajaro and Salinas rivers (Snyder 1913); *C. o. humboldtianum* in the Eel, Bear and Mad rivers (Snyder 1908d); and *C. o. lacusanserinus* from Goose Lake Basin (Fowler 1913) and likely the upper Pit River. Martin (1967) demonstrated clinal tendencies in morphology of *C. occidentalis* from Goose Lake, down Pit River to the Sacramento. Hubbs et al. (1979) considered populations from tributaries to San Francisco Bay as another distinct, undescribed subspecies, and combined *C. o. lacusanserinus* with the typical subspecies. *Heterocarpus traski* also shows differentiation, occurring as *H. t. lagunae* in Clear Lake, *H. t. pomona* in Russian River and *H. t. traski* in the remainder of its range (Hopkirk 1962, 1973; Baltz and Moyle 1981).

Remaining species of this fauna are isolates, mostly in headwater areas, and generally are endemic or representatives of species from adjacent watersheds. *Lampetra lethophaga* is a nonparasitic form shared by the Klamath and Pit drainages; differentiated forms of *L. tridentata* occur in Klamath River and Goose Lake (C. L. Hubbs 1971; Kan 1975).

Salmo sp. (redband) also is restricted in dis-

tribution in northern California (McCloud and Pit rivers, Goose Lake and upper Klamath River). It also occurs in some Oregon Lake basins and in a restricted portion of the Columbia River system (Behnke in Moyle 1976a, 1981). *Salvelinus confluentus* in the McCloud River is the most southwestern outlier of a northern distributional pattern (Cavender 1978) and was presumably derived from the Columbia system.

Three catostomids occupy greatly restricted distributions in northern parts of the system. *Catostomus microps* is only in a few tributaries of Pit River (Moyle and Marciochi 1975; Moyle 1976a,b; Moyle and Daniels 1982). As noted before, *Catostomus tahoensis* occurs in upper reaches of the Feather River system, as does *P. platyrhynchus*; both are possibly introduced.

Cottus klamathensis, *C. pitensis* and *C. asperimus* are in the Pit River. The first is more widely distributed in the Klamath than in the Pit River. Robins and Miller (1957) and Daniels and Moyle (1984) considered the Pit River form (*C. macrops*) as subspecifically distinct. *Cottus pitensis* is widespread throughout Pit River system (Bailey and Bond 1963), whereas *Cottus asperimus* is restricted to its middle reaches (Daniels and Moyle 1978; Moyle and Daniels 1982).

In southern California, the nominal *Lampetra hubbsi*, described from a canal in Kern County (Vladykov and Kott 1976b) was recently discovered in the Merced River, California, and was further characterized by Vladykov and Kott (1984). *Salmo aguabonita* is native only to the uppermost Kern River Basin, southern California, from where it has been widely introduced elsewhere (Gall et al. 1976). It shares a Kern River distribution with *S. gairdneri gilberti* (Moyle 1976a).

Relationships of the Sacramento-San Joaquin fish fauna are ancient and complex. Four species, *Ptychocheilus grandis*, *Orthodon microlepidotus*, *Mylopharodon conocephalus* and *Archoplites interruptus*, had congeners in Miocene

Pliocene lakes of the Snake River Plain (G. R. Smith 1975, 1981a; Kimmel 1975). The fossil *Ptychocheilus arciferus* from Idaho is more closely related to *P. grandis* and *P. oregonensis* than to *P. lucius* of the Colorado River system (G. R. Smith 1975). *Orthodon hadrognathus* and *O. onkogathus* of the Snake River Plain have obvious relationships only to *O. microlepidotus*. The fossil *Mylopharodon lugermanensis* was more specialized than its recent sister species *M. conocephalus* (G. R. Smith 1975). *Archoplites taylori* from Miocene and Pliocene deposits of southern Idaho (R. J. Miller and Smith 1967; G. R. Smith 1975; Kimmel 1975) is one of several fossil centrarchids distributed widely over western North America in Miocene (Oligocene?) through Pliocene deposits. In addition to *A. taylori*, fossil *Archoplites* are known from Miocene of northwestern Idaho (G. R. Smith and Miller 1985) and eastern Oregon (R. R. Miller and Smith 1981). Kimmel (1975) further considered the Miocene *Cottus calcalus* from southern Idaho as likely related to *C. pitensis* (Pit River) or *C. gulosus* (lower Columbia River Basin, Oregon coast and southern California coast). These occurrences, along with a number of aquatic molluscs (D. W. Taylor 1960, 1966, 1985; Taylor and Smith 1981) support an aquatic connection to the Pacific of the upper Snake River across northern California. Other species in Idaho lake beds are represented by extant relatives in the Columbia River system, in the Klamath River Basin, in northern and northwestern North America (salmonids, one catostomid and most cottids) or in the eastern United States (one icthyurid) (G. R. Smith 1975, 1978; Kimmel 1975).

The four California species are further distributed as fossils within or near their present ranges: *Orthodon microlepidotus*, Pliocene through Holocene; *Mylopharodon conocephalus*, Early Pleistocene through Holocene; *Ptychocheilus grandis* (including *P. tularis*; Jordan 1927), Late Pleistocene through Holocene; and *Archoplites interruptus*, Miocene, Pliocene and

Holocene (Sinclair 1904; Jordan 1927; Casteel and Hutchison 1973; Casteel and Rymer 1975; Casteel and Adam 1977). Casteel and Adam (1977) further reported two distinct, but undescribed species from Pleistocene beds near San Francisco. One was a cyprinid reminiscent of some fossils from southern Idaho, and the other a catostomid of unknown affinities.

The equally (or more) distinctive *Pogonichthys macrolepidotus*, *Lavinia exilicauda*, *Gila crassicauda* and *Hysteroecarpus traski* are in Holocene deposits (mostly archaeological sites) of the Sacramento-San Joaquin area (G. R. Smith 1981a). They have not been recorded as fossils in other regions, nor have fossils known to us been referred to as relatives of these species. G. R. Smith (1975), however, noted similarities in osteology of *P. macrolepidotus* and the extinct *Idadon hibbardii* (Pliocene Snake River Plain). He further remarked that the *Idadon* lineage "is now either extinct or represented by a completely generalized form such as *Pogonichthys*." Taylor and Smith (1981) noted resemblances between Pliocene *Gila* spp. from Honey Lake and *Gila* (*Siphateles*) spp. from Mopung Hills with the genus *Lavinia*. *Hesperoleucus symmetricus* has not yet been recorded as fossils older than Late Pleistocene or Holocene (Casteel et al. 1977; G. R. Smith 1981a), and *Castostomus occidentalis*, as with many species just covered, is known only from Holocene deposits. An additional freshwater embiotocid, *Damalichthys saratogensis*, is known from Pliocene-Pleistocene strata of California (Casteel 1978).

Colorado River Basin

This vast watershed comprises nearly 650,000 km² of some of the most arid terrain in western North America. It begins in Wyoming and Colorado and collects water from parts of Utah, New Mexico, Nevada, Arizona and California in the United States, and Sonora and Baja California del Norte in Mexico (Fig. 15.1). The

now-isolated White River of Nevada entered the system in Pleistocene or Recent time (Hubbs and Miller 1948a), as likely did Rio Sonoyta of Arizona and Sonora (treated later). Now-closed basins of the Salton Sea, California, and Laguna Salada, Baja California del Norte, plus other smaller basins, have received Colorado River waters in the past as parts of the complex Colorado Delta system (Blake 1857; Sykes 1937).

As reviewed before, this river consists of discrete segments. The upper basin, Green River and the mainstream Colorado plus their tributaries, presumably terminated in closed basins prior to Pliocene. A contemporary middle segment now represented by the Little Colorado (Childs 1948), Virgin and White rivers, and perhaps in part by Bill Williams Basin, drained southwest from the Colorado Plateau. The lowermost portion consists of Gila River, which was incorporated after recession of the Miocene Bouse Embayment.

Fishes in this region attracted early attention because of their uniqueness. Baird and Girard (1853a-c, 1854) and Girard (1857a,b, 1859a) described a large percentage of the fauna based on specimens obtained during regional military operations and the U.S. and Mexican Boundary Survey. Taxa now recognized include *Agosia chrysogaster*, *Gila elegans*, *G. intermedia*, *G. robusta*, *Meia fulgida*, *Ptychocheilus lucius*, *Rhinichthys osculus*, *Tiaroga cobitis*, *Pantosteus clarki*, *Castostomus insignis* and *C. latipinnis*. Abbott (1861) characterized *Castostomus texanus* (= *Xyrauchen texanus*). Cope (1872a), described *Salmo pleuriticus* (= *S. clarki pleuriticus*), named *Lepidomeda vittata* and *Plagopterus argentissimus* (Cope 1874a) and Cope and Yarrow (1875) reported on fishes obtained from 1871 to 1874 during the Wheeler Surveys. Jordan (1878a, 1886, 1891a) reviewed most of Girard's nominal species and reported (1891b) on specimens he obtained from the upper basin in 1889. Kirsch (1889) reported on Gila River fishes from Ft. Thomas, Arizona. C. H. Gilbert

(1893) included a description of *Cyprinodon macularius baileyi* (= *Crenichthys baileyi*; Hubbs 1932) from the White River in his report of the Death Valley Expedition. Evermann and Rutter (1895) summarized information on fishes of the Colorado River Basin and C. H. Gilbert and Scofield (1898) published on collections from Arizona and from the Colorado Delta in Mexico.

After turn of the century, Chamberlain (1904 unpublished) sampled in southern Arizona (R. R. Miller 1961b; Minckley 1969a, 1973) and Snyder (1915) reported on fishes collected by naturalist-mammalogist E. O. Mearns (1894 unpublished) in rivers tributary to the Gulf of California. Ellis' (1914) *Fishes of Colorado* closed this period of active research. For the next two decades fishes of the Colorado Basin were scarcely mentioned in the literature.

In the 1930s, V. M. Tanner began his studies in Utah and Nevada, describing *Notolepidomyzon utahensis* (= *Castostomus* [*Pantosteus*] *clarki*, *Fide*. G. R. Smith 1966) in 1932, *N. intermedius* (= *C. [P.] clarki*, *Fide*. Smith) in 1942 and *Gila jordani* (= *G. robusta jordani*) in 1950. He also summarized information on Utah fishes (Tanner 1936). C. L. Hubbs began publication on Colorado River fishes about this time (Hubbs 1932, 1953, 1954, 1955; Hubbs and Miller 1941a, 1948a,b, 1953; Hubbs et al. 1943) and his work was carried on and expanded by R. R. Miller (1943a, 1946a, 1950b, 1952, 1955b, 1959a, 1961b, 1963b, 1972b, 1981; Miller and Winn 1951; Winn and Miller 1954; Miller and Hubbs 1960).

Subsequent works covering the Colorado River Basin, in addition to those already cited, included Beckman (1953) and Everhart and Seaman (1971) for Colorado; Simon and Simon (1939), Simon (1946) and Baxter and Simon (1970) for Wyoming; Sigler and Miller (1963) for Utah; LaRivers (1952), LaRivers and Trelease (1952), LaRivers (1962) and Deacon and Williams (1984) for Nevada; Koster (1957) for New Mexico; R. R. Miller and Lowe (1964) and Minckley (1971, 1973) for Arizona; Evermann

and Clark (1931), Shapovalov (1941), Shapovalov and Dill (1950), Shapovalov et al. (1959), Moyle (1976a) and Hubbs et al. (1979) for California; and Follett (1961) and Castro-Aguirre (1978) for the Colorado Delta. Contributions by Moffett (1942), Dill (1944) and Wallis (1951) on development on the nonnative fisheries of the lower Colorado River included valuable historic information, as did Evermann (1916) and Walker (1961) on the Salton Sea. Much information published on the Colorado River fauna since 1960 has dealt with its endangered status (R. R. Miller 1961b, 1963b, 1972a, 1979; Minckley and Deacon 1963; Minckley 1965, 1969b, 1973, 1983; Pister 1974, 1981; Deacon 1979; Deacon et al. 1979; Johnson and Rinne 1982; Minckley and Gustafson 1982; others).

Deltaic habitats of the Colorado River were severe, plagued by high siltation rates and variations in position of distributaries (Sykes 1937), remarkably high tides (to 9 m), an unpredictable tidal bore that passed many tens of kilometers upstream and seasonally high water temperatures and salinities that must have limited fish distributions. The Delta now is highly modified. The Colorado River is controlled by dams to a point that occasionally includes total cessation of flow. Sedimentation is curtailed by upstream entrapment of debris in reservoirs (Minckley and Rinne 1985), as is input of dissolved nutrients to both the Delta and the Gulf (Thomson et al. 1979; Paulson et al. 1980). Areas of estuarine sloughs and deltaic distributaries lined by riparian forests and scrublands as described by Sykes (1937) are replaced by hypersaline plains devoid of plants or supporting only halophytes (W. L. Minckley, unpublished data). Other places such as Laguna Salada and the Salton Sea receive waters enriched by domestic sewage and inorganic fertilizers from agricultural inflows, and are variably hypersaline as a result of evaporation rates greater than 12 m per year and salts leached from surrounding fields.

Few data are available on original or pres-

ent ichthyofaunas of the Colorado River Delta. Early workers (Orcutt 1890, 1891; C. H. Gilbert and Scofield 1898; Fowler 1913; Mearns 1894 unpublished; Jordan and Richardson 1907; MacDougal 1907; Grinnell 1914; Snyder 1915; Hubbs, in Follett 1961) recorded *Xyrauchen texanus*, *Gila* (*G.*) *elegans*, *Ptychocheilus lucius*, *Cyprinodon macularius* (in part as "*Lucania brcani*"), *Mugil cephalus* (in part as *M. mexicanus*), *Gill-ichthys mirabilis* (as *G. detrusus*) and *Paralichthys aestivalis* (Table 15.2). *Elops affinis* penetrates to Imperial Dam, Arizona-California, and formerly into the Salton Sea (Glidden 1941; Dill and Woodhull 1942; Shapovolov, in Follett 1961; Minckley 1973, 1979; Minckley and Brown 1982), and is locally common on the Delta (W. L. Minckley, unpublished data). *Mugil cephalus* moves upstream to Palo Verde Diversion, Arizona-California (Minckley and Brown 1982) and also was present in the Salton Sea before presumably being excluded by increasing salinity (Evermann 1916; Thompson and Bryant 1920; Coleman 1929; Dill 1944; Hendricks 1961). *Eleotris picta* was recorded by Hubbs (1953) from Winterhaven, California, but has not again been taken. Walker and Hubbs (in Follett 1961) added *Micropogonias megalops*, *Cynoscion xanthulus* and *C. macdonaldi* to this list. *Gila elegans*, *P. lucius*, *X. texanus*, a species of *Salmo* and *C. macularius*, in addition to marine fishes, entered Salton Sea when it received Colorado River water in 1904-1907 (Evermann 1916; Walker et al. 1961), and remains of the first three species in archaeological sites and other deposits indicate their former presence there and elsewhere in closed basins of the Delta (Hubbs 1960; Follett 1961; Wilke 1980). Marine, estuarine and freshwater deposits of the lower Colorado River have as yet yielded only Pliocene fossils of marine-to-brackish invertebrates, charophytes and the marine atherinid *Colpichthys regis*, which remains restricted to the northern Gulf of California (Todd 1976).

Castro-Aguirre (1978) reviewed continental

occurrences of marine fishes in Mexico and came up with an impressive list of species from lowermost Colorado River (Table 15.2). Thirty species, in addition to those given above, were reported as gleaned from earlier literature (Norman 1934; Fowler 1944; Berdegue 1956; Castro-Aguirre et al. 1970; Arvizu-M. and Chavez 1972) or based on original collections.

Freshwater fishes of the Colorado River are separable into three major categories: (1) "big-river fishes," largely endemic, that range throughout the system in larger streams; (2) endemic species that occupy smaller streams at low to intermediate elevations; and (3) high- or intermediate elevation components that are mostly shared with or have near relatives in adjacent drainages.

Big-river fishes share an array of morphological adaptations that make them collectively one of the most distinctive faunas in North America (Hubbs 1940a, 1941; Deacon and Minckley 1974). Many are large in size, most have leathery skins with reduced and embedded scales, all have expansive variably falcate fins and some develop an unique, hump-backed physiognomy and/or pencil-thin caudal peduncles. *Ptychocheilus lucius* is the largest North American cyprinid, approaching 2.0 m in total length, and *Gila elegans*, *G. (G.) cypha*, *G. (G.) robusta*, *Xyrauchen texanus*, *Pantosteus discobolus* and *Catostomus latipinnis* regularly exceed 40 cm in total length. All of the above, plus the smaller *Plagopterus argentissimus* and mainstream forms of *Rhinichthys osculus*, have modified skins and large fins. *Gila elegans*, *G. cypha* and *X. texanus* (especially the last two) have pronounced predorsal humps. Thin caudal peduncles are characteristic of *G. elegans*, *G. cypha* and some populations of *C. latipinnis* and *P. discobolus* (Hubbs 1940a, 1941; G. R. Smith 1966; Minckley 1973, 1980d; G. R. Smith et al. 1979).

Relationships of this fauna are to the north and northwest, to the south or are conjectural for some autochthonous forms. *Ptychocheilus*

lucius is obviously related to its congeners of the Sacramento-San Joaquin Basin and northward, but is highly differentiated and most closely aligned with the fossil *P. prelucius* in Miocene (Baskin 1975, 1978) Bidahochi lacustrine deposits of Arizona (Uyeno and Miller 1965; G. R. Smith 1981a). Fossils from that deposit also included an extinct, monotypic cyprinid genus *Evomus* (*E. navaho*) of unknown relationships, an extinct cyprinid species referred to *Gila* (?*G. cristifera*), but with characters reminiscent of the genera *Acrocheilus* and *Pogonichthys* and material referable to *Gila* cf. *robusta*. Some of the last fossils share features with modern, big-river forms (*G. elegans*, *G. cypha*), which led Uyeno and Miller (1965) to speculate that large, swift-water habitats were already present at the time.

Rhinichthys osculus of big-river habitats is likely derived independently from populations of smaller, higher-elevation tributaries (Minckley 1973) and is widely distributed both west and north of the river basin. *Catostomus latipinnis* also appears most closely related to species of the north and west on the basis of the cladistic analysis of G. R. Smith and Koehn (1971) and negative evidence (absence of fine-scaled *Catostomus* to the south). *Catostomus latipinnis* is known from Pleistocene beds of the Little Colorado River Basin (Uyeno and Miller 1963, 1965). *Pantosteus discobolus* was considered by G. R. Smith (1966, 1978) a sister species of *P. clarki* of the lower Colorado River Basin. It otherwise occurs in the upper Snake River and Bear and Weber rivers of the Bonneville system. Variation in this species may be more reflective of local ecological conditions than of phylogenetic consequence (G. R. Smith 1966).

A *Gila robusta* complex now occurs from the Colorado River Basin far south into Mexican drainages (R. R. Miller 1959a; G. R. Smith et al. 1979; Holden and Minckley 1980). *Gila elegans* and *G. cypha* are specialized derivatives of the *G. robusta* complex, which may have

arisen in response to special conditions in large, erosive, Colorado River habitats (G. R. Smith et al. 1979). *Xyrauchen texanus* also is endemic and its relations other than generally to the genera *Catostomus* and *Chasmistes* (Nelson 1948; Hubbs and Miller 1953; R. R. Miller 1959a) are unknown; R. R. Miller and Smith (1981) noted a closer relationship of *Xyrauchen* with the subgenus *Deltistes* of *Catostomus* than to other catostomid groups. A well-preserved Pleistocene fossil *Xyrauchen* from the Colorado Desert west of the Salton Sea is clearly *X. texanus* (M. A. Roeder, pers. comm., 1982). *Plagopterus argentissimus* is a member of the distinctive tribe Plagopterini.

Faunal endemism at intermediate elevations is due in large part to the tribe Plagopterini, comprised of *Meda fulgida* of the Gila River Basin, *Lepidomeda* spp. and *Plagopterus argentissimus*. This group is characterized by ossification and other spinelike modifications of the two anteriormost dorsal rays and pelvic rays (Cope 1874a; R. R. Miller and Hubbs 1960; Minckley 1969d). Miller and Hubbs postulated that the group arose from:

a species of *Gila* or from a similar, relatively unspecialized cyprinid genus; that *Lepidomeda* represents the ancestral type of the tribe; and that the more specialized genera, *Meda* and *Plagopterus*, arose from *Lepidomeda* in the same [Colorado River] river system.

Ancient origin for the group is indicated by presence of the genus *Lepidomeda* on both sides of the Colorado River, which must have formed a major barrier to these fishes after it achieved its present position, size and character. Each major tributary to the middle segment has one or more forms of *Lepidomeda* (R. R. Miller and Hubbs 1960): *L. vitata* in the Little Colorado above Grand Falls (R. R. Miller 1963b; Minckley and Carufel 1967); *L. m. mollispinis* and *L. m. pratensis* in Virgin River system; and *L. albivallis* and *L. altivallis* in springs along the course

of White River. Species of *Lepidomeda* other than *L. vittata* could well have differentiated in the Virgin-White rivers complex since Pleistocene (R. R. Miller and Hubbs 1960). *Meda fulgida* is isolated in Gila River Basin, likely from before its integration with the lower Colorado River mainstream. *Plagopterus argentinus*, unlike other plagopterines, exploits swift, seasonally hot and turbid rivers. It formerly occupied the Gila River from Tempe to near Yuma, Arizona, and now is isolated in the Virgin River mainstream, Utah-Arizona-Nevada (R. R. Miller 1961b; Minckley 1969d, 1973; Cross 1975; Deacon 1979).

The Virgin-White rivers system supports a significant number of additional endemic fishes (Cross 1975; Williams and Wilde 1981; Hardy 1982). *Gila robusta jordani* was distributed in Crystal and Hiko springs and Pahranaagat River downstream from Ash Springs (Tanner 1950; LaRivers 1962). The nominal *Pantosteus intermedius*, referred to *Catostomus (P.) clarki* by G. R. Smith (1966), also was widespread in the White River system. Two morphological types of *Pantosteus* sp. also occur in the Virgin River system (R. R. Miller and Hubbs 1960; Minckley 1973) and another is known from the Bill Williams River Basin (Minckley 1973). All were also referred to *C. (P.) clarki* by G. R. Smith (1966 et seq.). *Rhinichthys osculus* is locally differentiated as is typical of the species throughout its range, consisting of *R. o. velifer* in Pahranaagat Valley, *R. osculus* subspecies in White River, *R. o. moapa* in Moapa River, the more widespread *R. o. yarrowi* in Virgin River Basin (R. R. Miller and Hubbs 1960; Williams 1978; R. R. Miller 1984) and elsewhere in the upper Colorado River system, and others. *Moapa coriacea* is a thermal isolate in warm springs forming sources of the Moapa River (Hubbs and Miller 1948b; Deacon and Bradley 1972; Cross 1976), a tributary of Virgin River prior to closure of Lake Mead. Relationships of the monotypic genus *Moapa* are unknown, but appear to include features indicative of the same line-

age as *Agosia*, *Rhinichthys* and *Gila* (Hubbs and Miller 1948b).

Crenichthys baileyi also is represented by isolated subspecies (*C. b. baileyi*, *C. b. albivallis*, *C. b. grandis*, *C. b. moapa*, *C. b. thermophilus*) in remnant springs of the White River Basin (Williams and Wilde 1981) and by *C. nevadae* in the adjacent, now disjunct Railroad Valley (Hubbs 1932; Deacon 1979). W. L. Minckley (unpublished data) identified pharyngeal bones of *Empetrichthys* from the Pleistocene(?) Glendale Formation, southern Nevada (see Van Devender and Tessman 1975).

In addition to special fishes already discussed, the Virgin River is inhabited by *Catostomus latipinnis* and the distinctive *Gila robusta seminuda* (Cross 1975, 1978). The former in mainstream Virgin River is typical of the species as described by Baird and Girard (1854) from the Gila River Basin, but represented in tributaries by a coarse-scaled form (or separate species) (Minckley 1980d). The last may have been recorded by G. R. Smith (1978) as *C. insignis*. *Gila r. seminuda* shows characters indicating possible hybrid origin involving *G. r. robusta* and *G. elegans* (G. R. Smith et al. 1979).

The Little Colorado River now supports an undescribed *Catostomus* presumably derived from *C. latipinnis* (Minckley 1973); Pleistocene fossils from that basin were referred to *C. latipinnis* (Uyeno and Miller 1963). Minckley (1980d) hypothesized this form might also be represented in tributaries of the Virgin River Basin (see above). *Pantosteus discobolus* from Little Colorado Basin also is distinct from those in the mainstream Colorado River in having a thick body, short fins and remaining relatively small in adult size (Minckley 1973). The headwater form of *P. discobolus* isolated in Zuñi River (tributary to the Little Colorado) has been referred to *P. d. yarrowi*. Its distinctiveness is in part a function of introgression of genes from *P. plebeius*, presumably resulting from a Late Pleistocene stream-capture transfer of that species from the Rio Grande Basin (G. R. Smith

1966; G. R. Smith and Koehn 1971; G. R. Smith et al. 1983).

Records of *G. elegans* (as *G. robusta elegans*; Hemphill 1954) from the upper Little Colorado are doubtful. Rinne (1976) examined specimens from that system and referred them to a form of *G. robusta*, and G. R. Smith et al. (1979) cast doubt on the Zuñi River as a type locality for *G. elegans*. That species, along with *G. robusta* and *P. lucius*, penetrated the Little Colorado only to the base of Grand Falls in historic time (R. R. Miller 1963b; G. R. Smith et al. 1979).

With notable exceptions the Gila River ichthyofauna also includes a number of species at low and intermediate elevations that are found only there. Big-river fishes and *Meda fulgida* are joined by the endemic *Tiaroga cobitis*, a darter-like cyprinid of uncertain generic relations (Minckley 1980b), but likely a sister taxon of *Rhinichthys osculus*. The true *Pantosteus clarki* of the Gila system also occurs in Bill Williams drainage to the northwest (Minckley 1973), but does not range into Mexico except in the uppermost Santa Cruz River (Gila River Basin). *Gila (G.) intermedia* is a thick-bodied, coarse-scaled inhabitant of springs, marshes and creeks. It is restricted to the Gila River Basin.

The Gila River fauna also includes *Agosia chrysoaster*, which reaches the northern limit of its range in Bill Williams River and is the commonest fish in that (Kepner 1980, 1981) and the Gila watersheds (Minckley and Barber 1971; Minckley 1973; Kepner 1982). Relationships of *Agosia* are possibly with *Moapa*, although affinities also are demonstrable with *Gila* and *Rhinichthys* (Hubbs and Miller 1948b) and many phenetic features are reminiscent of species of the Mexican genus *Algausca* (D. A. Hendrickson, unpublished data). *Gila robusta* is widespread, occurring as a confusing array of body shapes ranging from a slim riverine form representing *G. r. robusta* to a thicker-bodied, creek-dwelling kind referred by Rinne

(1976) to *G. r. grahami*. *Catostomus insignis* is a northern representative of a widespread group of northwestern Mexico. *Poeciliopsis o. occidentalis* also is such a species, being the most northern representative of its Neotropical genus (Rosen and Bailey 1963) that once swarmed in streams of the Sonoran Desert in the Gila drainage (Hubbs and Miller 1941a; Minckley 1969c, 1973; Minckley et al. 1977; Meffe et al. 1983). *Cyprinodon macularius* is a Gila-lower Colorado River form (Hubbs and Miller 1941a; R. R. Miller 1943a; Turner 1983) related to the large pupfish fauna of the Mexican Plateau (R. R. Miller 1981).

Among fishes of our third category, *Salmo apache* is widely distributed in the upper Salt River of the Gila Basin and also occupies headwater creeks in the Little Colorado drainage (R. R. Miller 1950b, 1972b; Rinne and Minckley 1985). *Salmo gilae* also lives (or lived) in tributaries of Verde River, Arizona (where extirpated and reintroduced), and in uppermost Gila River headwaters in New Mexico. Relationships of these trouts remain conjectural (R. R. Miller 1950b, 1972b; Needham and Gard 1959, 1964; Behnke 1970, 1979, 1981; Schreck and Behnke 1971). However, recent biochemical studies indicated they are closely related to one another and are genetically nearer *S. gairdneri* than to the *P. clarki* lineage (W. Loudenslager, pers. com. n., 1982). We retain the opinion of Minckley (1973) that they are closely related to Mexican populations, and achieved their present highland distributions early in development of present drainage relations. The progenitor of *S. apache*: must have invaded the White Mountains of Arizona after their formation through volcanism in Late Cenozoic (Merrill and Péwé 1977). Rinne (1976) attributed absence of other than *G. r. robusta* in the Salt River to reinvasion after volcanism. *Salmo gilae* and other forms of *G. robusta* persisted in tributaries of the Verde and upper Gila rivers remote from White Mountain lavas (Minckley 1973; Rinne 1976). Movements between upper

parts of lesser rivers, such as of *S. apache* between the Salt and Little Colorado, may be attributed to local stream transfers.

The fish of most obvious northern derivation in the Gila River Basin is *Rhinichthys o. osculus*, represented perhaps also in the Bill Williams drainage. The species has not penetrated Mexican watersheds not connected with the Gila River. In the Little Colorado Basin this minnow has not been referred to any described subspecies, but resembles *R. o. yarrowi*. Minckley (1973) noted that a "northern form" and *R. o. osculus* "intergrade chaotically" in a band along the Mogollon Rim, which was attributed to repeated stream captures across that escarpment. The form of *R. osculus* upstream from Grand Canyon has been called *R. o. yarrowi* (Simon 1946; Sigler and Miller 1963; Hubbs et al. 1974), with relationships to Great Basin subspecies (Hubbs and Miller 1948a). Other forms identified from the Colorado River Basin include *R. deaconi* that occurred in the now-dry Las Vegas Wash, southern Nevada (R. R. Miller 1946b, 1984), and the isolated *R. o. thermalis* from Kendall Warm Spring, Wyoming (Hubbs and Kuhne 1937).

Other northern taxa known only from the upper Colorado River Basin differ at the subspecific level or are undifferentiated from counterparts in adjacent watersheds. *Salmo clarki pleuriticus* is in extreme headwaters of Green River, Wyoming (Simon 1946), tributaries of Green River as far south as inflow of the Colorado River, in the Dirty Devil River and in headwaters of Fremont River, Utah (Sigler and Miller 1963), and in remote creeks and lakes of Colorado and San Juan headwaters in Colorado (Ellis 1914); related subspecies are in all surrounding basins (R. R. Miller 1972b; Behnke 1981). *Prosopium williamsi* and *Cottus bairdi punctulatus* are at high elevations in Wyoming, Utah and Colorado; the latter also is in the uppermost San Juan River, New Mexico (Koster 1957). *Cottus beldingi* is represented in parts of the upper Col-

orado River Basin by *C. annae* (synonymized with *C. beldingi* by Bailey and Bond 1963). *Prosopium williamsi* and relatives of the two *Cottus* spp. are widely distributed in the Great Basin and upper Columbia systems (Bailey and Bond 1963; Scott and Crossman 1973). *Pantosteus platyrhynchus* in the upper Colorado Basin show features aligning them with populations of both Great Basin and upper Missouri River drainages (G. R. Smith 1966).

Southwestern California and Northwestern Mexico

Coastal mountains of southwestern California south of the Salinas River and those of northwestern Baja California give rise to short rivers that flow directly into the Pacific. Most of the remainder of Baja California is too arid to support permanent surface waters, exceptions being springs such as those near San Ignacio (Goldman 1951) and Río San Juan del Cabo that drains mountains of the tropical tip of the Peninsula (Tamayo and West 1964). The Basin and Range and Sierra Madre Occidental of the mainland, however, produce numerous rivers of diverse sizes and configurations. Those containing fishes are, from north to south, the Ríos Sonoyta, Concepción (= Altar or Magdalena), Sonora, Matape, Yaqui (with two major branches, the Río de Bavispe and Río Papigochic), Mayo, Fuerte, Sinaloa, Mocorito, Culiacán, San Lorenzo, Elota, Piaxtla, Presidio, Baluarte, Acaponeta and San Pedro (with an upper tributary, the Río Mezquital). An increasing rainfall gradient (Vivo-Escoto 1964) and greater contributions of high-elevation tributaries from the well-watered Sierra Madre result in increased river discharges with decreasing latitudes (Tamayo and West 1964).

These rivers pass to the sea over coalescing deltas, forming a coastal plain that becomes narrower north to south to the area of the Ríos Elota and Piaxtla, then again widens toward

mouths of the Río San Pedro and Río Grande de Santiago. Where relatively wide coastal plains exist, major rivers have changed their courses over time, allowing coastal distributions of some fishes to be readily explained. For example, the Río San Pedro was a tributary to the lowermost Río Grande de Santiago until about 500 years ago, when the latter shifted its mouth to enter the sea independently (Currey et al. 1969).

The large Ríos Yaqui, Fuerte and San Pedro watersheds extend eastward from arid or semi-arid lowlands to and through highlands of the Sierra Madre to the Mesa del Norte. These rivers are complexes of subbasins, with channels reflecting structural control in their long-reaches. This is especially evident in the Río Yaqui Basin, where long reaches flow a few degrees west of north, then short reaches breach mountain trend-lines from northeast to southwest (Hendrickson et al. 1981). Rivers draining northeast to southwest prior to Basin and Range formation (Melton 1960) are thought to have maintained their through-cutting capabilities as that event progressed, contributing deep-cut canyons (or barrancas) to the present physiography. Formation and expansion of north-south-oriented structural blocks and troughs provided valleys and highlands that now direct much of the surface drainage. The Río Fuerte and more southern watercourses assume more typical dendritic patterns as Tertiary lavas become thicker and the Sierra Madre Occidental heights (Fig. 15.2). Lava dams and diversions become more evident, and series of lacustrine deposits indicating consecutive natural lakes along river channels become common to the south (Barbour 1973b). Some rivers have barrier falls, effectively isolating upper and lower segments (for example, Albritton 1958).

Troughs followed by major rivers were subjected to alluviation and local (or regional) altitudinal adjustments that transferred major portions of drainages from one watershed to

another. The Río de Bavispe-San Bernardino trough, passing from Sonora into southeastern Arizona, is such a probable connection between the present Gila River and the Río Yaqui basins (Blasquez 1959). As compiled by Hendrickson et al. (1981):

Melton (1960) proposed that the upper Gila River followed the San Simon Trough southeast, received the Río de Bavispe or its precursor, then passed westward to connect with the Santa Cruz Trough of southern Arizona, through which it descended to the Phoenix basin. Continuing uplift in middle Pliocene severed the connection between the Gila and Santa Cruz rivers. The upper Gila River then flowed south into México (Kottowski et al. 1965), or was ponded in the vicinity of Safford, Arizona (Melton 1960), or upstream near the Arizona-New Mexico border (Cooley 1968). It eventually flowed northwest through the Safford Valley to possibly enter the Salt River northwest of Globe (Melton 1960) and again join the Phoenix basin. The Mexican headwaters continued to flow northward into the San Simon Trough or Sulphur Springs Valley, accounting perhaps for some of the vast deposition of the latter (more than 1,500 m; Meinzer and Kelton 1913). By early Pleistocene the Gila River had succeeded in cutting to the southwest, reoccupying the gorge through the Mescal Mountains and establishing connection to the Sea of Cortez, either directly or through the lower Colorado River. Melton (1960) proposed that drainages of northern México turned southward near this time to occupy the lower Río de Bavispe. This may have resulted from general upwarping to the north, which caused massive stripping of alluvium from former basin fills (Simon 1964; Cooley 1968). Antecedent channels north of Tertiary lavas of the Sierra Madre Occidental also were available to facilitate this transfer. Lava flow in the vicinity of the San Bernardino Ranch, Cochise County, Arizona, considered by Sauer (1930) as "... recent, almost current," plus uplift of the Chiricahua Mountain mass, also must have assisted in southerly diversion of those systems.

Integration of parts of the Mesa del Norte

into Pacific drainages also occurred through massive headwater erosion. Examples are the extensive Río Papigochic Basin of the Yaqui, the uppermost Río Fuerte, parts of the San Pedro Basin (Río Mezquital) and likely other headwaters that support fishes of eastern derivation. Uplift of Mesa del Norte stimulated increased precipitation, which accelerated erosion further to produce spectacular baranca topography along plateau margins (King 1939). Drainages and ancient lakes of the Mesa del Norte, parts of a formerly and presently integrated middle Río Grande system (including the Lago de Guzmán complex [Ríos Mimbres, Casas Grandes, Santa María and del Carmen], Río Conchos and associated closed basins and Ríos Nazas-Aguanaval) thus contributed watersheds and fishes to western México (Meek 1904; Belcher 1975; R. R. Miller 1978, 1981; Smith and Miller, Chapter 13).

Minor stream captures also are evident, not only in montane segments, but also on relatively undissected surfaces of the Mesa del Norte. Meek (1903) noted that Río Papigochic formerly drained through Laguna Bustillos (his Lago de Castillos) into Río Santa María, a feasible connection that is, however, not supported by the present fish fauna (R. R. Miller 1981). R. R. Miller (1959a) suggested a minor stream capture by the Papigochic from the Río Conchos 45 km south of Miñaca, Chihuahua, and also noted Río Papigochic would be a tributary of the Casas Grandes did it not abruptly cross the mountains northwest of Miñaca to enter the Yaqui complex. Hendrickson et al. (1981) pointed out an obvious capture of Laguna de los Mexicanos by the Papigochic, removing it from earlier probable connections to the Conchos or Santa María. Capture of the Guadiana Valley, formerly a tributary of Río Nazas, by the upper San Pedro is another incidence of Pacific drainage piracy from the Mesa del Norte (Tamayo 1949; Albritton 1958). Río San Pedro is exceptional among drainages south of the Fuerte since most do not penetrate as

deeply into that younger portion of the Sierra Madre Occidental.

Historically, Girard (1854) described *Gasterosteus williamsoni* and *G. microcephalus* (= subspecies of *G. aculeatus*) and *Fundulus parvipinnis* from the southwestern California region, on the basis of specimens obtained during early railroad surveys. Eigenmann and Eigenmann (1890) named *Phoxinus orcutti* (= *Gila* [Tene-culina] *orcutti*), and Snyder (1908c) characterized *Pantosteus santaanae*.

Coastal and inland fishes of Baja California were obtained mostly by naturalist-collectors such as Janos Xantus (Jordan and Gilbert 1882a; Madden 1949; R. R. Miller and Hubbs 1954) and L. Belding (Jordan and Gilbert 1882b), or were collected incidental to marine fishes or to terrestrial animals or plants. Vaillant (1894) named *Fundulus lima* from collections made by naturalist M. L. Diguët. Many records of entry of marine fishes into freshwaters of the region were similarly obtained (for example, Rutter 1896; Follett 1961; Castro-Aguirre 1978).

Fishes from drainages flowing into Gulf of California also were first described by Girard (1857b, 1959a) and by Baird and Girard (1853b,c, 1854) from specimens collected during U.S. and Mexican Boundary Surveys and later railroad surveys. Cope (1886 reported on a collection of *Salmo* from the Sierra Madre Occidental and E. W. Nelson revisited that site and an additional trout locality in Río Presidio Basin in 1898. *Salmo nelsoni* (= *S. gairdneri nelsoni*) from Baja California del Norte was named for the noted mammalogist (Evermann 1908; Needham and Gard 1959). Jordan (1888) described *Heros* (= *Cichlasoma*) *beani* and *Poecilia butleri* from Río Presidio near Mazatlán, and Rutter (1896) described and listed fishes caught in 1892 in Sonora by G. Eisen and in 1894 in Arizona and Sonora by W. W. Price. Jordan et al. (1895) summarized information on fishes of Sinaloa, with emphasis on marine forms. Meek (1902, 1903, 1904) was first to provide a thorough discussion of Mexican freshwater

fishes and their distributions. His 1904 contribution summarized earlier works, but was based mostly on personal collections while traveling by rail in 1901 and 1903. Absence of railroads across the Sierra Madre Occidental and through Sonora and Sinaloa resulted, however, in his providing little new information on faunas west of the Mesa del Norte.

Reports on fishes of the region became more frequent after Herre and Brock described *Ca-stostomus wigginsi* from Río Sonora (Herre 1936). Alvarez del Villar (1950a) produced a key to Mexican freshwater fishes, and compiled a comprehensive bibliography (1950b), including processed reports dealing with Mexican ichthyology. R. R. Miller began publishing on the fauna in the 1940s (1943a, 1945a; Hubbs and Miller 1941a,b; Miller and Simon 1943). Also active in that period was DeBuen (1940, 1947a,b). Miller has continued research (1959a, 1960b,c, 1966, 1968, 1976a,b, 1978, 1981; Miller and Winn 1951; Miller and Schultz 1959) and has recently been joined by others, usually dealing with a single species or genus. Reports of a regional nature are those of Branson et al. (1960) for Sonora, a review of freshwater fishes of Baja California by Follett (1961), a catalog of marine species in continental waters of Mexico by Castro-Aguirre (1978), a survey of the Río Yaqui Basin by Hendrickson et al. (1981), a review of Late Cenozoic fishes of warm deserts by M. L. Smith (1981) and reports of new records of native and introduced fishes by Hendrickson (1984). Alvarez de Villar (1970) provided a checklist of species and keys for identification of Mexican inland fishes, and in 1972 produced a coverage of the history of Mexican ichthyology.

South Coastal California and Baja California

South of the influence of the Sacramento-San Joaquin fauna, California coastal streams and those of Baja California support few fishes that

are not actually or potentially anadromous or principally marine. *Lan petra tridentata* and *Salmo gairdneri* comprise the first group. The former enters short coastal drainages northwest of Los Angeles, south through the Santa María and Santa Ynez systems to the Los Angeles Plain (Hubbs 1967; Moyle 1976a). The latter exists or formerly was present in coastal streams of southern California, south to headwaters of Río Santo Domingo of Sierra San Pedro Martir, Baja California del Norte (*S. g. nelsoni*; Needham and Gard 1959; Follett 1961). Sea-run *S. gairdneri* are known from the Tijuana River, California, and at sea from as far south as San Rosario, Baja California del Norte (Hubbs 1946, and in Follett 1961). An additional salmonid, *Oncorhynchus kisutch*, is known from near Islas Coronados, Baja California del Norte, and may have run into streams of northwestern Baja California in recent past (Schofield 1937; Castro-Aguirre 1978). Fossils from near 20°N latitude in the Mexican Plateau indicate *Oncorhynchus* ranged much farther south in Pleistocene (Cavender and Miller 1982).

Marine fishes that frequently enter freshwaters along the Pacific Coast of southern California (D. J. Miller and Lea 1972, 1976; Moyle 1976a) include *Elops affinis* (north to Ventura County, California), *Ambloplites rupestris* (north to San Francisco Bay) and *Cupea harengus pallasi* and *Hypomesus pretiosus* (coastal streams south to Los Angeles). *Cymatogaster aggregata* and *Lep-tocottus armatus* occur south to Bahía San Quintín, Baja California del Norte. *Eucyclogobius newberryi* lives south to Agua Hedionda Lagoon, California. *Clevalandia ios* and *Gillichthys mirabilis* range southward to Bahía Magdalena, Baja California del Sur; the latter also occupies the northern Gulf of California. *Syngnathus leptorhynchus* and *Atherinops affinis* also range south into Baja California del Sur. *Platichthys stellatus* enters mouths of streams south to the Santa Ynez River, California, and *Mugil cephalus* behaves similarly from San Diego south throughout Baja California.

Continental waters of Peninsular Baja California, as categorized by Castro-Aguirre (1978), have yielded more than 90 kinds of marine or euryhaline fishes (Table 15.2). Species only on the outer (Pacific) side of the Peninsula mostly are northern forms moving south in response to the cold California Current augmented by coastal upwelling (Hubbs and Roden 1954). Species occurring both on the outer and inner (Gulf of California) coastlines are biased toward the Pacific Coast by our arbitrary consideration of records from Cabo San Lucas as indicative of occurrence on both sides of the Peninsula. Most species recorded only from the inner coast are restricted to the Gulf or are tropical, ranging southward along the Mexican mainland.

Excluding species of the Colorado River, only six native fishes fulfill their life cycles in freshwaters of this region. *Gila orcutti* is native to the Los Angeles Plain, the upper Santa Clara River system and the San Luis Rey and Santa Margarita rivers, southern California (Greenfield and Greenfield 1972; Greenfield and Deckert 1973; Moyle 1976a; Swift 1980a). *Rhinichthys osculus* shares much of its range in southern California (Cornelius 1969) with *G. orcutti*, as does *Pantosteus santaanae* in streams of the Los Angeles Basin (Culver and Hubbs 1917; G. R. Smith 1966; Greenfield et al. 1970; Moyle 1976a). As pointed out by G. R. Smith (1966) and Cornelius (1969), populations of *P. santaanae* and *R. osculus* in southern California show little interbasin differentiation, implying short-term isolation within their presently disjunct ranges. Variation in *G. orcutti* has scarcely been studied (Hubbs and Miller 1942).

All these fishes obviously are isolated from other congeneric or conspecific populations. Their origins have been cited by G. R. Smith (1966) as evidence for connections of the Colorado River and Pacific Ocean. Plate tectonics of that region provide an alternate explanation for these distributional patterns, as is to be detailed later. *Gila orcutti* and *G. bicolor mo-*

havensis introduced into Arroyo Santo Tomás, Baja California del Norte, apparently did not survive (Follett 1961; R. R. Miller 1968). *Catostomus fumeiventris*, introduced into Santa Clara River, California, hybridized extensively with *P. santaanae* (Hubbs et al. 1943; Bell 1978); present status of that situation is unknown (see, however, Crabtree and Buth 1981; Buth and Crabtree 1982).

Of the last three species, *Fundulus parvipinnis* inhabits mostly marine habitats, but also lives in coastal marshes, estuaries and creeks from the lower Salinas River, California (where possibly introduced: D. J. Miller and Lea 1972; Swift 1980f), to Bahía Magdalena on the Pacific Coast of Baja California del Sur (R. R. Miller 1939; Follett 1961). Status of the two described subspecies (*F. p. parvipinnis* in vicinity of San Diego and *F. p. brevis* in southern Baja California) is conjectural (R. R. Miller and Hubbs 1954; Follett 1961; Hubbs et al. 1979). *Fundulus lima* from springs near San Ignacio, the only endemic freshwater fish species in Baja California, is an inland counterpart of *F. parvipinnis* (Myers 1927; R. R. Miller 1943c). The genera *Fundulus* and *Gasterosteus*, as already noted, are widely represented by fossils in the Great Basin and Mohave Desert regions, so present coastal distribution of *Fundulus* is relictual in nature (M. L. Smith 1981).

Gasterosteus aculeatus exists as three forms in this region (R. R. Miller and Hubbs 1969; Ross 1973). An unarmored form (*G. a. williamsoni*) is native to the Los Angeles Basin. Other populations are freshwater or marine, ranging southward to Bahía de Todos Santos, Baja California del Norte (Castro-Aguirre 1978). They are referred to *G. a. microcephalus* if with one to eight lateral plates and *G. a. aculeatus* if bearing 28 to 35 plates (R. R. Miller and Hubbs 1969). A Miocene fossil of the last is known from the California Coast (Bell 1977). These morphological types occur together as species in some places (Hagen 1967; Ross 1973), but numerous intermediate populations also exist

(R. R. Miller and Hubbs 1969; Moyle 1976a). Bell (1976) considered *G. aculeatus* a superspecies, so dynamic that subspecific names have little meaning.

Coastal Rivers of Northwestern Mainland Mexico

Streams of extreme northwestern parts of the Mexican mainland, Ríos Sonoyta, Concepción (= Altar or Magdalena), Sonora and Matape (Fig. 15.2), lack high-elevation watersheds and drain arid Sonoran Desert terrains. High evapotranspiration rates and infiltration into alluvial fill consume surface waters, and flows reach the Gulf of California only during rare periods of high runoff (Blasquez 1959). Fishes are in headwaters and consist only of freshwater dispersants.

Río Sonoyta, thought by Hubbs and Miller (1948a) to be a disrupted segment of the Colorado River diverted southward by Pinacate volcanics (0.4–0.5 mya; Lynch 1978), supports *Agosia chryso-gaster* and one or more distinctive populations of *Cyprinodon macularius* (R. R. Miller 1943a; Minckley 1973; Turner 1983). *Gila (Temeculina) ditaenia* characterizes the Río Concepción Basin, next to the south, where it lives with *A. chryso-gaster* and *Poeciliopsis occidentalis*. Recent records of *G. (T.) purpurea* from the Concepción system (Hendrickson 1984) may represent an introduction. An all-female *Poeciliopsis*, *P. monacha-occidentalis*, occurs from the Río Concepción southward and is discussed later. Contreras-Balderas (1969) miscited Branson et al. (1960) in reporting *Camptostoma ornatum* from the Río Concepción, and the error was perpetuated by Burr (1976).

The extensive Río Sonora, albeit small in discharge, supports six or seven fishes: *Agosia chryso-gaster*, *Gila purpurea*, *Camptostoma ornatum*, *Catostomus wigginsi*, *Ictalurus pricei*, *Poeciliopsis occidentalis* and the all-female *P. monacha-occidentalis* have been recorded. Lowland species such as *A. chryso-gaster* and both *Po-*

ciliopsis may have moved along the coast in better-watered times or may have been transported northward by tectonic movements. Occurrence of *C. ornatum* in the Río Sonora is the most western penetration of a Río Grandean faunal element into the region (Burr 1976, 1980a). We are not convinced of the presence of *I. pricei*, which was recorded incidentally by R. R. Miller and Lowe (1964). No native ictalurids from the Río Sonora Basin have been seen by us. Río Matape between the lowermost Ríos Sonora and Yaqui has records for only *G. purpurea*, *P. occidentalis* and the all-female *Poeciliopsis*, which may reflect a lack of collecting effort.

South of these desert rivers, the mouths of the large Ríos Yaqui, Mayo, Fuerte and others are frequented by a far greater number of marine than freshwater fishes (R. R. Miller 1966; Castro-Aguirre 1978; Hendrickson et al. 1981). About 20 essentially marine fishes have been taken from the lower Yaqui and absence of records for large species such as *Cynoscion* spp., which are abundant in the mouth of the Colorado (Table 15.2), point toward a need for additional sampling.

Of abundant clupeiform fishes of the Gulf of California, *Lile stolifera* enters Ríos Yaqui and Mayo (Gunter 1942) and engraulids (*Anchoa lucida*, *A. curta*) occupy the Yaqui Delta (Hildebrand 1943, 1944; Fowler 1944; Chirichigno 1963). *Elops affinis*, ariids (*Arius lipopus*, *A. caeruleus*), centropomids (*Centropomus robalito*, *C. nigrescens*) and lutjanids (*Lutjanus novemfasciatus*, *L. colorado*) also inhabit the Delta (Castro-Aguirre 1978; Hendrickson et al. 1981). *Mugil cephalus* and *M. curema* are present, *Chaenomugil proboscideus* has been taken from canals near Ciudad Obregón (Castro-Aguirre 1978) and *Agonostomus monticola* ascends the Yaqui to near Presa Novillo and attains foothill streams of more southern systems. With exception of the goby *Awaous transandeanus* that penetrates well into foothills, other marine fishes (*Dormitor latifrons*, *Eleotris picta*, *Go-*

biomorus maculatus, *Trinectes foncecensis*) are largely restricted to deltaic habitats. The sciaenid *Elattarchus archidiuum* enters lowermost Río Mayo (Castro-Aguirre 1978), and *Cynoscion macdonaldi* is known from the mouth of the Fuerte (Jordan and Evermann 1898).

South of Río Fuerte, lists of marine fishes entering freshwater habitats become larger, not in small part as a result of extensive early collecting in the estuary of Río Presidio near Mazatlán (reviewed by Castro-Aguirre 1978). This is in part reflected in 126 of the 178 species listed in Table 15.2 being recorded from "Sinaloa Coastal." Other factors are increasing diversity of the rich Gulf fauna as one proceeds southward (Thomson et al. 1979) and perhaps reduced numbers of lowland freshwater fishes. Marine fishes that penetrate far into freshwaters include *Awaous transaeneus*, *Eleotris picta*, *Dormitator latifrons* and *Gobiomorus maculatus*. *Lile stolifera*, *Elops affinis*, *Mugil* spp. and *Melaniris evermanni* occupy deltaic habitats. *Agonostomus monticola* and *Melaniris crystallina* extend far inland. The latter is freshwater in the northern portion of its range (R. R. Miller, pers. comm., 1983). The freshwater *Gobiesox fluviatilis* is known from the Ríos Fuerte, Piaxtla and Grande de Santiago (Briggs and Miller 1960; Burr and Buth 1977).

Among freshwater dispersants, single-basin endemism is rare in these larger coastal rivers, although inter-basin differentiation of widespread species has scarcely been examined. Headwater forms typically occupy mountain streams of two or more adjacent basins. As with fishes adapted to highlands in the Great Basin (G. R. Smith 1978), these species are positioned to move by headwater stream captures, and almost certainly have done so.

Among Mexican trouts, headwater *Salmo* sp. in the Río de Bavispe (Río Yaqui Basin) also occupy the adjacent Río Casas Grandes drainage (R. R. Miller 1959a; Contreras-Balderas 1978) and a similar form in the upper Río Papigochic (Río Yaqui system) also is represented in the Río Mayo (Hendrickson et al.

1981). These trouts were considered "almost identical" to *Salmo chrysogaster* of the Ríos Fuerte, Culiacán and San Lorenzo by Needham and Gard (1964). Other unique *Salmo* of undefined status are, however, known from the uppermost Río Presidio and Río San Pedro (Needham and Gard 1959, 1964). Nativity of *S. gairdneri* in Mexico south of the range of *S. g. nelsoni* is doubtful (Miller and Smith, Chapter 14), although introduced populations are certainly present. The Pleistocene fossil *Salmo australis* from Lake Chapala, Mexico, the most southern salmonid occurrence in North America, is not closely related to *S. chrysogaster*, and presumably represents a lineage achieving the Mexican Plateau during a period of cool oceanic surface waters (Cavender and Miller 1982). Fossil *Oncorhynchus* from near Lake Chapala (loc. cit.) supports this hypothesis. A Pliocene cyprinid near the genus *Gila* from upper Río Yaqui Basin, Chihuahua, Mexico, is one of the oldest primary fishes known from the region (M. L. Smith 1981).

Undescribed, endemic species of *Catostomus*, one from the uppermost Ríos Bavispe-Casas Grandes and another from the Ríos Papigochic-Mayo headwaters, share their respective distributions with the two *Salmo* of that region (Hendrickson et al. 1981). Another headwater endemic is an undescribed species of *Gila* (s.s.) in the upper Río Presidio (unpublished data), the relationships of which to *Gila* cf. *pandora* of the Río Tunal-Laguna Santiaguillo and *G. conspersa* of the Nazas-Aguanaval and the adjacent Río Mezquital Basin, are yet to be worked out.

Other species of western affinities distributed along the Sierra Madre Occidental-Mesa del Norte contact zone are *Pantosteus plebeius*, *Gila* (*Temeculina*) *pulchra* and *Gila* (*T.*) sp. Populations of the former range from the upper Río Grande, U.S.A., through the Guzmán, upper Río Conchos and Ríos Nazas-Aguanaval-Trujillo systems of the Mesa del Norte to the Pacific drainages of the Yaqui (uppermost Río de Bavispe), Piaxtla and Río Mezquital (G.

R. Smith 1966; Minckley 1980c). G. R. Smith (1966) reported Piaxtla and Mezquital populations meristically allied and different from all others. Ferris et al. (1982), however, demonstrated biochemical differentiation between these populations at a genetic level more distinctive than other "well-differentiated cypriniform subspecies." They expressed the opinion that neither could be an ancestor of the other, an observation reducing probability that Río Mezquital *P. cf. plebeius* was derived by stream capture of a former Río Nazas tributary (Meek 1904; Albritton 1958; R. R. Miller 1978). *Gila pulchra* occupies Río Conchos. The Yaqui Basin, that of Laguna Bavicora and the upper Río Mayo system support the related *Gila* sp. (Smith and Miller, Chapter 13). We have no explanations for the presence of *Gila* cf. *pandora* in the Río Tunal-Laguna Santiaguillo Basin of Mexico (M. L. Smith et al. 1984), hundreds of kilometers disjunct from *G. pandora* in the upper Río Grande system of the United States.

Codoma ornata, *Dionda* sp., *Cyprinodon* spp. and *Etheostoma pottsi*, with affinities to the Mesa del Norte and ultimately to faunas of eastern North America, are similarly distributed in upper parts of major river basins of the region (R. R. Miller and Smith, Chapter 14). *Codoma ornata* occupies the Nazas-Aguanaval, Fuerte and San Pedro (Mezquital) systems to the south, ranging east and north into the Ríos Conchos and Yaqui (Contreras-Balderas 1975, 1978; R. R. Miller 1976b, 1978). *Dionda* sp. is only in the uppermost Río Mezquital. Fishes of the genus *Cyprinodon* are most speciose and widespread in the Chihuahuan Desert region (R. R. Miller 1978, 1981). *Cyprinodon* of the western highlands of Mexico presumably achieved their distributions prior to regional uplift (Hendrickson et al. 1981). An undescribed species (whitefin) of the upper Río Papigochic (Yaqui Basin) is shared with the Río Santa María (Lago de Guzmán system) to the north, and *C. meeki* of the upper Mezquital (San Pedro system) is closely related to *C. nazas*

of the adjacent Nazas-Aguanaval and Laguna Santiaguillo systems (R. F. Miller 1976b, 1981; Minckley and Brown 1982). *Etheostoma pottsi* is restricted on the Pacific Slope to the Río Mezquital and has relatives in the Nazas-Aguanaval and other streams of the Mesa Central (M. L. Smith et al. 1984).

Some other fishes of southern Mexico enter our region only in the upper Río Mezquital. *Notropis* cf. *calientis* is such a species, otherwise ranging (as *N. calientis*) through the Río Lerma, upper Río Grande de Santiago and upper Panuco systems (R. R. Miller and Smith, Chapter 14). *Characodon lateralis* is shared by that drainage and the Parás Basin of Coahuila (as *C. garmani*) (Garman 1895; R. R. Miller 1961b; Fitzsimmons 1972) and possibly with southern basins in Jalisco as well (Pellegrin 1901). Good-eid fishes have inhabited the Mesa Central at least since Miocene times (Alvarez del Villar and Arriola-Longoria 1972; M. L. Smith 1981). *Chirostoma jordani*, another element from the Mesa Central (Barbour 1973a), was thought by Barbour (1973b) to have entered the Río Mezquital drainage via interconnected Pleistocene lakes. It also is in the now-isolated Laguna Santiaguillo lying between headwaters of the Ríos Nazas and Mezquital (Barbour 1973a,b; R. R. Miller 1981).

Notropis formosus and *Campeostoma ornatum* are two species characteristic of small to moderate-sized streams, clearly derived from the Río Grandean fauna. The former occupies the Río Yaqui Basin, in which it has differentiated into northern (Río de Bavispe) and southern (Río Papigochic) races (Contreras-Balderas 1975, 1978; treated as *N. lutrensis*). The species is further distributed in Lago de Guzmán tributaries and other close basins between that system and the Conchos drainage. Chernoff and Miller (1982a) reviewed the *N. formosus* complex, treating the nominal *N. santamariae* and *N. mearnsi* as junior synonyms and rejecting the presence of definable subspecies. *Campeostoma ornatum* also is distributed in the north in present and former Río Grande con-

nectives (Ríos Casas Grandes, del Carmen, Conchos, Nazas-Aguanaval), but also in Pacific drainages of the Ríos Sonora (as already discussed), Yaqui, Mayo, Fuerte and Piaxtla (Burr 1976, 1980a; Both and Burr 1978; Hendrickson 1984). While occupying a broad altitudinal range in the first three drainages (Hendrickson et al. 1981; unpublished data), it is more restricted to higher elevations in the last two. Its apparent absence in the Río Santa María is puzzling in light of its abundance in surrounding watersheds.

Fishes characteristic of larger aquatic habitats of eastern North America also exist through the Chihuahuan Desert region of the Mesa del Norte into the Mesa Central of Mexico. *Dorosoma smithi*, *Ictalurus pricei* and *Ictalurus* spp. are of such affinities and must represent a different crossing of the Continental Divide than do cyprinids just discussed. The former is known from the Piaxtla and Yaqui basins (Hubbs and Miller 1941b; Branson et al. 1960; R. R. Miller 1960c), with the approximately 600 km range disjunction attributed by Minckley et al. (1980) to a lack of collecting in that region. *Ictalurus pricei* lives in the Ríos Yaqui, Casas Grandes and Fuerte (R. R. Miller 1976b, 1978; Hendrickson et al. 1981). Hendrickson (1984) also obtained an *Ictalurus* likely referable to *I. pricei* from the Río San Lorenzo and anticipated additional localities for ictalurids in intervening river basins when collections became available. We follow Hendrickson et al. (1981) in tentatively referring *Ictalurus meeki* from the Yaqui Basin to *I. pricei*. The *Ictalurus* of the Río Mezquital is an unnamed species resembling *I. lupus* (Miller and Smith, Chapter 14; M. L. Smith et al. 1984). Relationships to *I. dugesi* of the Río Lerma (upper Río Grande de Santiago) and to an undescribed fossil species of that system (R. R. Miller, pers. comm., 1983) are unknown.

In addition to *D. smithi* and *Ictalurus* spp., *Moxostoma austrinum* (including *M. mascolae*; Both 1978) ranges south through the Conchos

and Mezquital to the Ríos Armeria, Ameca and Grande de Santiago systems (Robins and Raney 1957; Jenkins 1970, 1980a). Miocene to Pleistocene lacustrine beds in Jalisco have further yielded a mixture of eastern and western or Mesa Central fossil fishes, including two extinct salmonids (*Salmo australis* and *Oncorhynchus* sp.), two *Moxostoma*, minnows of the genera *Algansea* and *Yuriria*, extinct ictalurids of the *I. punctatus* group, goodeids, atherinids of the genus *Chirostoma* and an extinct centrarchid, *Micropterus relictus* (Alvarez del Villar 1966a, 1974; Alvarez del Villar and Arriola-Longoria 1972; M. L. Smith 1980, 1981; M. L. Smith et al. 1975; Cavender and Miller 1982).

Fishes of apparent western affinities enjoy wider and more congruent geographic distributions in northwestern Mexico than those from other regions. These include the *Gila robusta* complex, *Agosia chrysogaster*, the *Catostomus bernardini* group (including *C. insignis* from the Gila Basin, *C. bernardini* from the Río Yaqui, *C. conchos* from the Río Conchos; R. R. Miller 1976a; Hendrickson et al. 1981; Hendrickson 1984), and species and all-female forms of *Poeciliopsis*. Along with *Campostoma ornatum* and *Ictalurus pricei*, these form a broadly sympatric faunal assemblage from the Río Yaqui south through the Río Sinaloa system. The first four also range northward into the Colorado River system. Fishes referable to *G. robusta* range south to the Río Culiacán. Holden and Minckley (1980) erred in text by citing a record from the Río Culiacán (G. R. Smith et al. 1979) as being from the Río Piaxtla; their mapping of the locality was correct. *Agosia chrysogaster* ranges south to the Río Sinaloa (Minckley 1980a; Hendrickson 1984). Species of *Catostomus* resembling *C. bernardini* and *Poeciliopsis* spp. range far southward (to the Río San Lorenzo for the first [Hendrickson 1984], and to Central America [Rosen and Bailey 1963], for the last).

The wide, essentially continuous distribu-

tions of these species speak for their long occupation of this diversified region, remarkable abilities of dispersal or both. The cyprinoids all share the attribute of being highly adaptable, capable of reproducing at small or large sizes (for *Gila*, *Catostomus* and *Pantosteus*; G. R. Smith 1981b) or throughout the year (*Agosia chrysogaster*; Minckley and Barber 1971; Lewis 1978; Kepner 1982), and thus are capable of living from headwater streams to large lowland rivers. The livebearing *Poeciliopsis* presumably can disperse through estuaries, and includes species that resist severe conditions of inland streams, even under desert conditions (Hubbs and Miller 1941a; Constantz 1974 et seq.; Schoenherr 1974 et seq.; Meffe et al. 1983). The aggressive *Cichlasoma beanii*, often part of this assemblage in lowlands and distributed from the Río Yaqui south to the Río Ameca, Nayarit (Hendrickson et al. 1981), likewise must disperse through estuaries and dominates pools in streams of any size.

Fishes of the genus *Poeciliopsis* are wide-ranging in our region (Rosen and Bailey 1963). *Poeciliopsis occidentalis* is in the Basin and Range region of the lower Gila River drainage southward through the Ríos Magdalena, Sonora, Matape, Yaqui and Mayo, where it is often the only or the most abundant fish in small ephemeral reaches of desert streams. Since discovery of an "all-female strain" of *Poeciliopsis* (R. R. Miller and Schultz 1959), interest in the genus has been great, and it is now the most thoroughly studied group in northwestern Mexico. Research has been reviewed by Moore et al. (1970), Schultz (1977), Vrijenhoek (1978, 1979) and Vrijenhoek et al. (1977, 1978). Numerous unisexual strains are known and demonstrated to be of interspecific hybrid origin. Both diploid and triploid strains exist, the former reproducing by hybridogenesis in which females depend on sperm from males of a parental species, but while the paternal genome is expressed in all-female offspring phenotypes it is excluded from ova. Triploids

reproduce by gynogenesis, in which sperm initiates embryogenesis but no paternal genome is incorporated in progeny. Numerous strains arising from different interspecific crosses have been identified, and within many strains numerous identifiably distinct clones are known, progeny of different individual matings. In addition to *P. occidentalis*, species that have naturally produced all-female strains via various interspecific dihybrid and trihybrid combinations are *P. monacha* of the Ríos Mayo, Fuerte and Sinaloa; *P. lucida* from Ríos Mocorito, Sinaloa and Fuerte; *P. viriosa* from the Río Sinaloa south throughout our region to the Río Ameca; and *P. latidens*, distributed from the Fuerte south through lower reaches of streams to the Río Grande de Santiago. Also having a range equal to that of *P. latidens* and extending north into the lower Yaqui is *P. prolifica*, although it has not yet been implicated in natural hybrid crosses creating unisexuals.

It appears that unisexual strains in rivers north of the Río Mayo are ultimately derived from an original hybridization between *P. occidentalis* and *P. monacha* in the Río Mayo (Schultz 1977). Dispersal to these northern drainages from the Río Mayo is thus implied. The proportion of unisexuals in *Poeciliopsis* populations generally decreases with increasing latitude. Thus proportions of unisexuals near the border in the Ríos Magdalena, Sonora and Yaqui are low. Unisexuals are not known from the Gila River drainage (Moore et al. 1970).

The only other native poeciliid in our region is *Poecilia butleri*, distributed from the Río Fuerte south to Guatemala (R. R. Miller 1983).

DISCUSSION AND SUMMARY

Many have studied fish distributions in the west relative to geologic history (Cope 1883b; Snyder 1908a, b, 1914, 1918; R. R. Miller 1946b, 1948, 1961a, 1965, 1983; Hubbs and Miller 1948a;

R. R. Miller and Hubbs, 1960; LaRivers 1962; R. R. Miller and Smith 1967, 1981; Barbour 1973a,b; Hubbs et al. 1974; G. R. Smith 1975, 1978, 1981a,b; M. L. Smith et al. 1975; Taylor and Smith 1981; M. L. Smith 1981), and distributional patterns of fishes have in turn contributed to our understanding of that history. We also rely heavily in following discussions on knowledge of geology, and demonstrate from literature rooted in plate tectonic theory that many events dating to Oligocene, perhaps earlier, and certainly from Miocene to Recent, were influential in determining components of today's patterns.

Dispersal during wetter periods of Pleistocene and Recent has been justifiably emphasized in earlier literature. Elapsed time has been relatively short, and fish distributions plus geologic evidence for potential dispersal routes are yet to be obscured or erased. Biotic and geologic evidences of older events are attenuated by vagaries of time and superimposed upon by later phenomena. However, in many instances, empirical "hard-rock" evidence now is available from which to interpret far older area relationships. It also is useful to consider hypothetical paleogeomorphologies. Scenarios have been produced using geometries and velocities of interplate interactions known from paleomagnetism (Atwater 1970; Beck and Plumley 1979; Engebretson et al., *in* Page 1982), petrography (Kovach and Nur 1973; Dickinson et al. 1979a; Crowell 1931) and geophysical theory (Livaccari 1979; Zoback et al. 1981; Page 1981, 1982) to project expected responses of the earth's crust. We discuss these ideas for their plausibility, and propose them to have far-reaching consequences for reinterpretations of zoogeography of modern continental fishes. Such has only recently begun to be examined for modern fishes and other groups (Cox 1973; Cracraft 1974; G. M. Davis 1979, 1982; Kay 1980; papers in Nelson and Rosen 1981; Springer 1982).

Fossil Record

In considering the fossil record, we have often been frustrated by vaguely reported ages. Some confusion is attributable to recent changes in accepted geological time scales since times of publications. For example, the term Pliocene was formerly applied to the period 9–1.8 mya. In many cases we refined dates by reference to recent geologic literature. Dating of formations throughout the west is now comprehensive, and the data base is rapidly expanding. The geologic record is sufficiently resolved to allow much finer scales of temporal and spatial analyses of fossil distributions and we encourage paleoichthyologists to attempt further constraint of ages for material.

Most knowledge of Early Cenozoic freshwater fishes in western North America has been derived from the Eocene Green River Formation of Wyoming, Utah and Colorado, and contemporaneous deposits of Canada. Paleocene fossils referred to Ictaluridae are known from the west (Lundberg and Case 1970; Lundberg 1975), but other modern groups are rare if present through Oligocene times. Eocene faunas share relict non-teleosts (polyodontids, acipenserids, lepisosteids, amiids) with primitive salmonids, clupeids of lineages other than those giving rise to modern groups, hiodontids, primitive catostomids (genus *Amyzon*), ictalurids, percopsids, percoids and others of obscure relationships or actual or probable marine derivation (Cavender 1966, 1968; Lundberg 1975; Wilson 1977, 1978, 1979, 1980b, 1982; Grande 1979 et seq.; Grande et al. 1982). Oligocene faunas are rare, but in Nevada and Colorado include *Amyzon*, which along with amiid and ictalurid fishes also is known from the Late Eocene–Early Oligocene of Oregon (Cavender 1968). An extinct percopsid (*Tricophanes foliarum*) is associated with Oligocene *Amyzon* in Nevada and Colorado (Cope 1872b, 1884; Uyeno and Miller 1963). An Oligocene

umbrid (*Novumbra oregonensis*) lived in what is now north-central Oregon (Cavender 1969).

Many of these groups, largely extinct in western North America, have Recent representatives now restricted to east of the Continental Divide. This is true of all the non-teleosts except acipenserids, still represented by northwest-coastal species. Hiodontids persisted until Miocene (*Hiodon* sp.; G. R. Smith 1981a), and two species now live east of the Rockies. *Amyzon* is not known from Miocene or subsequent fossils unless represented by ictiobiin or cycleptiin derivatives in the east. Percopsids remain represented in the lower Columbia Basin by *Percopsis transmontana* and east of the Divide by *P. omiscomyces* (also in the north to the Yukon River system) and the related Aphredoderidae. Percid (or percoid) and priscacariid genera of the Green River and associated formations have no Recent relatives in the region unless they align with modern percids and centrarchids.

Modernization of the western ichthyofauna occurred in Oligocene, since Miocene deposits yield diverse fossils including hiodontids, salmonids, osmerids, umbrids, esocids, cyprinids, catostomids, ictalurids, atherinids, cyprinodontoids, gasterosteids, centrarchids, embiotocids and cottids. Of these, all but osmerids, umbrids, esocids and ictalurids remain abundant. Extirpation of non-teleosts and most of the last four families plus *Amyzon* must have been precipitated by the transition from Oligocene lowland rivers flowing over a broad erosional surface to diverse topography and disrupted drainages of Miocene, perhaps aided by magmatism. Oligocene cyprinid fragments are known from Washington and Oregon (T. M. Cavender, pers. comm., 1983), and most or at least many present genera of cyprinids and catostomids, which dominate the present fauna, were in areas of present occurrence by Miocene. Miocene-Pliocene forms are usually judged specifically distinct from Recent faunal

elements. Pleistocene taxa are not usually distinguishable at the species level from Recent taxa (R. R. Miller 1915; G. R. Smith 1981a).

Of the lesser groups, osmerids now are represented in the west only along the Pacific Coast. The Oligocene umbrid was similar to *Novumbra hubbsi* of coastal Washington (Cavender 1969; Meldrim 1980), which presumably is a relict of an earlier regional fauna (Schultz 1929). Other umbrids (genus *Umbra*) are in eastern North America and Europe. Esocidae are known from Paleocene of Canada, Miocene of Oregon and Pliocene of Washington, but not elsewhere in time and space of the west (Cavender et al. 1970; Wilson 1980b; G. R. Smith 1981a) except for *E. lucius* far to the north. Ictalurids continued to occupy the region in Miocene (Baumgartner 1982) through Pliocene to Early Pleistocene (R. R. Miller and Smith 1967; Lundberg 1975; G. R. Smith 1975, 1981a), then disappeared. *Ictalurus pricei* and *Ictalurus* sp. of Pacific coastal streams of Mexico are the only native ictalurids remaining in our region. Gasterosteids, although not speciose, exist as a phenomenal array of forms of *Gasterosteus aculeatus* (Hagen 1967, 1973; R. R. Miller and Hubbs 1969; Hagen and McPhail 1970; Hagen and Gilbertson 1972 et seq.; Ross 1973). Centrarchids are represented by "one or two genera and three or four species" (G. R. Smith and Miller 1985) at Miocene-Pliocene localities in Oregon, California and Nevada, plus fossil *Archoplites* spp. from Idaho, Oregon, Utah, Nevada and California (R. R. Miller and Smith 1967, 1981; G. R. Smith 1975, 1978, 1981a). *Archoplites interruptus* of the Sacramento-San Joaquin Basin is the only native centrarchid now west of the Rocky Mountains.

Characteristics of the Modern Fauna

Faunal lists of primary and secondary fishes for our portion of western North America (Ta-

ble 15.1) are summarized as numerical compilations of modern taxa in Table 15.3. The Sacramento-San Joaquin system supports the largest fauna, resulting from numerous marine-derived and anadromous forms, especially salmonids and cottids, and substantial numbers of cyprinoids. Other large faunas in the northwest similarly result from anadromous groups and cottids. Larger inland basins with complex interconnective histories, such as the Bonneville and Colorado, have relatively large faunas numerically dominated by cyprinoids. Cyprinodontoids become important in Mexican drainages. Smaller, drier, more isolated basins have fewer species than larger, wetter, less isolated or through-flowing systems (R. R. Miller 1959a; Hubbs et al. 1974; G. R. Smith 1978, 1981a,b; M. L. Smith 1981).

The modern fish fauna of western North America is characterized by endemic subfaunas in major drainage basins plus an interspersed of sparse but unique taxa in minor systems (Hubbs and Miller 1948a; R. R. Miller 1959a, 1965, 1981; Hubbs et al. 1974; G. R. Smith 1978, 1981a,b; M. L. Smith 1981). Major drainage basins have few fishes in common, and species that occur in more than one system

typically could move through seawater (petromyzontids, some salmonids, some cottids in the north and poeciliids and cichlids in the south) or occupy high-elevation tributaries or high latitudes with low relief. Montane species are subject to vicariance through stream captures or structural reversals, ways zoogeography may change without alteration of a species' habitat (G. R. Smith 1978). Or, species may disperse through headwater connections or watercourses shifting over broad divides. The last two mechanisms may have operated in determining present distributions in the north of inland genera of salmonids (*Salmo*, *Salvelinus*, *Prosopium*), some cyprinids (especially *Rhinichthys*), catostomids (especially *Pantosteus*) and freshwater-restricted cottids (*Cottus* spp.). Cyprinoid fishes penetrate far higher into montane habitats in the south due in part to latitudinal amelioration of minimum temperatures (G. R. Smith 1981a), which in part serves to explain broad distributions of *Campostoma ornatum*, the *Catostomus bernardini* complex, *Gila robusta* and relatives and others.

Modern genera and species that apparently demonstrate movement over the Continental

Divide include northern forms that may have dispersed stream to stream or through lakes, or in coastal seas. Most are far north of our area: *Coregonus clupeaformis*, *Prosopium cylindraceum*, *Salvelinus confluentus*, *S. namaycush*, *Thymallus arcticus*, *Esox lucius*, *Couesius plumbeus*, *Hybognathus hankinsoni*, *Rhinichthys cataractae*, *Richardsonius balteatus*, *Catostomus catostomus*, *Lota lota*, *Gasterosteus aculeatus*, *Pungitius pungitius* and *Cottus cognatus*. Other northern forms may either have dispersed or experienced vicariance in montane regions, or may represent relicts. *Prosopium williamsoni* occupies eastern drainages from the upper Missouri River region north into tributaries of Hudson Bay (Holt 1960). *Prosopium couleri* lives in a disjunct distribution in northwestern Washington and western Canada, then east in Lake Superior (Lindsey and Woods 1970). With respect to the last species, *P. gemmiferum* of Bear Lake, Idaho-Utah, shows no apparent relationships (R. R. Miller 1965) other than notably in its elongated jaws to *P. couleri* and to the Miocene-Pliocene *P. prolixus* of the Snake River Plain (G. R. Smith 1975). *Hybopsis* (*Oregonichthys*) *crameri* of the lower Columbia River and associated drainages is far disjunct from conceivable relatives, and may represent a relict or a taxon distinct from *Hybopsis*. *Rhinichthys cataractae* gave rise to *R. evermanni* of the Umpqua River, Oregon (Bisson and Bond 1971); its presence in the west may be ancient. Distribution of *Cottus bairdi* displays a broad central disjunction across Plains habitats, definitively separating western and eastern populations (Robins 1954).

Transdivide distributions in the north of *Salmo clarki*, *Rhinichthys cataractae*, *Catostomus macrocheilus* and *Pantosteus platyrhynchus*, plus western populations of *Cottus bairdi*, and in the south of *Salmo* sp. (Rio Yaqui), *Campostoma ornatum*, *Codoma ornata*, *Gila pulchra*, *Dionda* sp., *Gila temeculina* sp., *G. cf. pandora*, *Notropis cf. calientis*, *N. formosus*, *Pantosteus plebeius*, *Moxostoma austinum*, *Cyprinodon* sp.

(whitefin), *Etheostoma pottsii* and atherinids of the genus *Chirostoma*, must have involved stream captures, drainage reversals and structural integration of subbasins, in addition to dispersal. Events allowing lowland forms such as *Dorosoma smithi*, *Ictalurus* spp. and perhaps some poeciliids and cichlids to cross to Pacific drainages of Mexico will be dealt with below.

Unique species of western North America reflect isolation and continuity of drainage units in two major ways. First, endemic species may be allopatric differentiae of widespread genera, for example, regional species of *Ptychocheilus*, *Gila*, numerous *Catostomus* and *Chasmistes*. Special conditions may also have stimulated development of endemics, which are specialized derivatives of generalized groups; *Gila elegans* and *G. cypha* of the mainstream Colorado River seem to be examples (G. R. Smith et al. 1979). Second, some apparently endemic forms, such as the genera *Orthodon*, *Mylopharodon* and *Archioplites* now characterizing the Sacramento-San Joaquin system, represent relicts of formerly wider distributions. They earlier also occupied lakes of the Snake River Plain and adjacent areas. Other unique taxa may have long been isolated in their own drainage units, which either remained isolated or later were integrated into a larger system. Examples of the last may include *Moapa coriacea* and *Crenichthys baileyi* of the White River, Nevada, now part of the middle Colorado River system.

Tectonism and Fish Distribution

Barriers separating faunal areas are diverse in nature, but often are similar in position to tectonic boundaries between subplates. For example, the barrier zone between Great Basin and upper Columbia (Snake) watersheds along the southern margin of the Snake River Plain (G. R. Smith 1978) lies along a seismic boundary separating that region and the Great Basin (R. B. Smith and Sber 1974; Eaton et al. 1978;

Table 15.3 Summary of Families, Genera and Species of Freshwater Dispersant Fishes of Drainage Basins of Western North America

Basins	Oregon → North California Coastal	Klamath River	"Oregon Lakes"	Lahontan Basin	Bonneville Basin	North-Central Basins	Death Valley "System"	Sacramento River	Colorado River	South California Coastal-Baja California	Sonoran Coastal	Río Yaqui → Río San Lorenzo	Sinaloa Coastal	Río San Pedro
Families	8	8	4	4	4	2	4	10	7	8	4	9	7	10
Genera	13	13	9	10	10	4	5	21	18	11	5	14	12	15
Species	28	29	15	13	20	4	9	41	32	12	7	27	17	19

Compiled from Table 15.1.

R. B. Smith 1978). Other seismic alignments corresponding to limits of faunal regions include the Wasatch Mountain Front, margins of the Colorado Plateau, a separation of the Great Basin from the southern Basin and Range, zones separating the Great Valley (Sacramento-San Joaquin Basin) from surrounding regions, the San Andreas Fault zone and others. Major faunal areas thus tend to correspond with major (aseismic) subplates. Systems that cross seismic zones, such as the Columbia and Colorado rivers, have composite faunas (R. R. Miller 1959a; Hubbs and Miller 1948a; R. R. Miller and Hubbs 1960; G. R. Smith 1978).

Direct effects of tectonism on differentiation and distribution of faunas occur by separation of formerly continuous habitats or joining of isolated habitats. Evidence for direct effects include concentrations of derived endemics in areas of recent tectonism (Taylor 1966; G. M. Davis 1979) and the corollary of relicts isolated (or persisting) in areas of long-term aseismicity, both of which are demonstrable for western fishes. Indirect influences are manifest through environmental changes. For example, exclusions of fishes from vast areas recently changed to deserts by the Sierra Nevada rainshadow are indirect results of tectonism.

Vicariance is an evident factor in distributional and evolutionary history of fishes in our region. Numerous fossil and recent species pairs and groups clearly adhere to the classic allopatric speciation model (G. R. Smith 1978). This has been largely attributed to dispersal and subsequent isolation through indirect effects of tectonics, especially increasing regional aridity (Hubbs and Miller 1948a; R. R. Miller 1948, 1959a, 1961a, 1965, 1981; G. R. Smith 1978, 1981a,b; M. L. Smith 1981). Vicariant or disjunct species and/or populations may, however, also imply earlier more widespread continuity of ancestral forms (Taylor 1966).

D. W. Taylor (1960, 1966), R. R. Miller (1959a, 1965), G. R. Smith (1975, 1978, 1981a,b), R. R. Miller and Smith (1981), and Taylor and Smith (1981) have documented fossil and Recent zoogeographic tracks linking aquatic faunal elements of the Snake River Plain westward south of the lowermost Columbia River to the Pacific Slope through regions of the: (1) Sacramento and (2) Klamath rivers, and (3) from the Snake River-northern Great Basin south on the east side of the present Sierra Nevada to the Mohave Desert ("Fish hook pattern"). Fossil fishes involved in these tracks include ancestors of modern species that now are largely allopatric from congeners (G. R. Smith 1966, 1975, 1978, 1981a; G. R. Smith and Koehn 1971; R. R. Miller and Smith 1981). Included genera and subgenera are *Chasmistes*, *Catostomus* (s.s.), *C. (Deltilistes)*, *Ptychocheilus*, *Gila* (s.s.), *Gila (Siphoteles)*, *Richardsonius*, *Mylopharodon*, *Mylocheilus*, *Orthodon*, *Acrocheilus* and *Archoplites*.

Estimates of timings of connections within this regional pattern have been justifiably vague. The Snake-Sacramento track is overlain and thus must be older than the Fish hook pattern (Taylor 1966), and G. R. Smith (1975) concurred with its greater age because of greater phenetic divergence evident in Sacramento River relict taxa than elsewhere. Geologic evidence for such a drainage connection includes convincingly positioned remnants of stream channels of appropriate size, original grades and original directions of flow (Wheeler and Cook 1954; Axelrod 1958, 1962; Christiansen 1966), fluvial sedimentation in the northern Great Valley since Oligocene from appropriate source areas (Dickinson et al. 1979) and likelihood of physical absence of highland barriers in the northern Sierra Nevada until much later times (Christiansen 1966; Hay 1976). The Snake-Klamath and Fish hook patterns are evident mostly in faunal distributions. Direct geologic evidence is sparse, hinging mostly on north-south-oriented structure. We reiterate regional geologic history (in part, Fig. 15.4) to

set a stage for tectonic interpretations that in part explain present distributional patterns.

Late Eocene-Early Oligocene were times of widespread erosion and tectonic quiescence after Laramid compressional tectonism (Gressens 1981). Following collision of the North American Plate and the East Pacific Rise in Late Oligocene (around 29 mya), intracontinental rotation and shear produced expansion of the region west of the northern Laramide Axis and Colorado Plateau, which resulted in development of extensional structure after about 27 mya (Zoback et al. 1981).

The elongate Cascades-Oregon Coast Range-Klamath Mountains subplate, an allochthonous terrane through which the Columbia River now passes and including parts of the Rogue, Umpqua, Klamath and northernmost Sacramento (Pit) rivers, was oriented essentially east to west in Eocene. It had rotated 46° dextrally by end of Oligocene, remained quiescent for a time, then an additional 27° rotation in the last 20 my resulted in 340 km of western displacement at its southern tip (Magill and Cox 1981). This complex has scarcely changed in elevation since Miocene times (Wells and Peck 1961), and is separated from the northern Sierra Nevada block by a shear zone (L. Wright 1976) that presumably acted as a hinge during displacements. Extension occurred sparingly within the Cascades (Hammond 1979) and Sierra Nevada (Hamilton and Myers 1966), mostly in Basin and Range (Oregon Lakes region; Simpson and Cox 1977; Magill and Cox 1981), and perhaps in rift formations of the Columbia Plateau now covered by lavas. Rotation of this subplate was contemporaneous with 210 km of westward displacement of the Sierra Nevada at its southern end since 20 my (Magill and Cox 1981), accommodated for by extension in Basin and Range to the east. Block faulting in the Great Basin, beginning around 17 mya and well established by 10 mya, resulted in formation of north-northwest-trend-

ing mountains and valleys conducive to development of parallel drainage trends, as tracked by the shank of the Fish hook zoogeographic pattern. Length of the shank may, however, have been modified by displacement of 130-190 km along shear zones in the regional alignment (Stewart et al. 1968; Stewart 1978).

The Sierra Nevada was relatively stable and undergoing erosion in Early Miocene. Uplift and westward tilting began from south to north about 18 mya, accelerated 10-9 mya, then waned to again pursue present elevations 4.5-1 mya (Christiansen 1966; Noble and Slemmons 1975; Hay 1976; Huber 1981). Eastern margins of the Sierra Nevada developed as an escarpment through block faulting 9-3 mya, while western slopes remained more entire. Large structural units such as Walker Lane east of this escarpment provided continuity lacking in smaller Basin and Range structures.

We compare in Figures 15.6 and 15.7 generalized range maps of selected species with diagrammatic palinspastic reconstructions of the region concerned. In each instance a case may be made for formerly continuous distributions prior to post-Oligocene rotations and accommodative extension. In addition, adjustments of extended terrains back to estimated positions at various times in Basin and Range formation detract considerably from linearity and geographic extent of all three zoogeographic tracks, especially in earliest extensional stages. A Snake-Sacramento track must have been severed more than 10 and perhaps about 17 mya due to development of extensional structures associated with rotation of the adjacent Cascade-Oregon Coast-Klamath Mountains subplate and western displacement of the Sierra Nevada. The Klamath River area was removed from a Snake-western Lahontan Basin track more than 10 mya through continued rotation, and emplaced westward. Basalts of the Modoc Plateau originating 5-10 mya (McKee et al. 1983) further isolated that system. The Fish

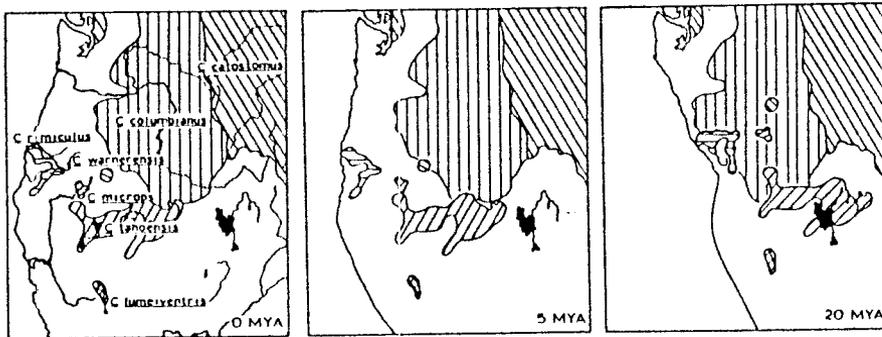


Figure 15.6 Diagram of present distributions of seven catostomid fishes (genus *Catostomus*) in western North America held fixed in size relative to rotation of the Cascade-Oregon Coast Range-Klamath Subplate and the Sierra Nevada. Great Salt Lake is held immobile as a reference point, and extension behind (east of) the rotating and westward displacing blocks was progressively reduced at a time-dependent rate. See text for details and Figure 15.4 for further explanation.

hook pattern may have been severed about 10 mya by a 45° shift in patterns of faulting that disrupted earlier Great Basin alignments (Zoback et al. 1981), or persisted until later when broken by indirect tectonic effects (desiccation) less than 4.5 mya with rise of the Sierra Nevada.

Tectonism also provides substantial infor-

mation on isolation of the Lahontan and Bonneville faunas, often cited as being unique despite absence of spectacular divides. G. R. Smith (1981a), although certainly not minimizing tectonism, emphasized hydrographic connections and dispersal in Pleistocene, and subsequent disruption through desiccation in explanation of present distributional patterns.

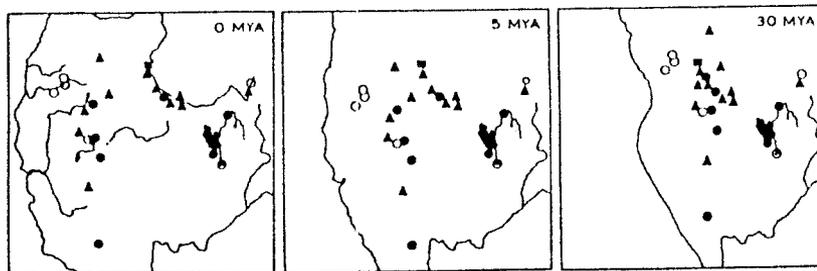


Figure 15.7 Diagram of fossil and recent records for the catostomid genus *Chasmistes* in western North America relative to extension between the Wasatch Front-Colorado Plateau margin and the Sierra Nevada axis. Great Salt Lake is held immobile as a reference point and extension was progressively reduced at a time-dependent rate. Fossil records of ages known to be younger than diagram dates were retained as indications of minimum ages of occupation; see text for details and Figure 15.4 for further explanation. Symbols: (○) modern records; (●) Pleistocene; (▲) Pliocene; and (■) Miocene (from Taylor and Smith 1981).

Vertical displacements potentially isolating the Great Basin from the Colorado Plateau and Sierra Nevada regions occurred from around 27–10 mya (Christiansen and McKee 1978). Basin and Range topography did not exist in the region 20 mya based on thickness distributions of volcanic tuffs (Stewart 1978). Extension, spreading from a central region toward the east and west margins, may have preceded block faulting (Scholtz et al. 1971; R. B. Smith and Sbar 1974; Stewart 1978). Large basins were nonetheless established 14–10 mya, and perhaps as early as 17 mya, on both sides of the upward-arched central region (Robinson et al. 1969; Nelson 1981). Block faulting oriented north-northwest around 17–10 mya surely controlled drainage development, which must have been disrupted by the 45° shift to north-south structural alignment about 10 mya.

Evidence seems adequate to hypothesize a broadly distributed ancestral fauna consisting of the genera *Salmo* (or near relative), *Gila* (*Siphateles*)-like and *Rhinichthys* (*Apocope*)-like cyprinids, and *Catostomus* (s.s.) in streams flowing through low relief of the Great Basin region around 17 mya. Barriers existed between the Great Basin-Snake-Sacramento (including Klamath) drainages, Great Basin-Colorado River system and Great Basin-southwestern lowlands, the last occupied by cyprinodontoids and gasterosteids. A barrier must also have existed, and likely had long been present, between the lower Columbia and Snake-Sacramento systems, preventing interchanges of umbrids, esocids, percopsids, *Chasmistes*, *Mylopharodon*, *Archoplites* and others (in part, G. R. Smith 1981a). Albeit negative data, absence of genera such as *Ptychocheilus*, *Mylopharodon*, *Mylocheilus*, *Acrocheilus*, *Archoplites*, the extinct *Idadon* and others in modern or fossil faunas of the Great Basin may similarly indicate long isolation between it and the Snake-Sacramento track. Some northwest Lahontan fossil localities that have yet to have their early drainage relations described may confuse the last relationships.

Basins today containing lakes and most of the fishes of these systems are in peripheral zones of most recent tectonism. Central zones of early tectonism have long been aseismic and are fishless or support highly differentiated relictual taxa such as *Relictus solitarius* and *Moapa coriacea*, as well as oviparous good-eids (*Crenichthys nevadae*, *C. baileyi*). *Eremichthys acros* is similarly unique, but is toward the western margin of the Lahontan Basin. *Iotichthys philegethontis* is distributed in the eastern Bonneville system. Synapomorphies linking *Chasmistes cujus* and *C. liorus* from the Lahontan and Bonneville basins, respectively, indicate their close relationships (R. R. Miller and Smith 1981), fitting observations that derived endemics inhabit zones of most recent tectonism.

Many differences between the Bonneville and Lahontan faunas relate to complex connections between the former and the upper Snake River, and in turn interrelations of those basins to the northeast. The extreme upper Snake River Basin communicated early with northern or eastern drainages as evidenced by fossil cottids, *Myoxocephalus* and *Kerocottus*, and perhaps *Prosopium prolixus*, in southern Idaho (G. R. Smith 1975, 1978, 1981a). Smith considered *Myoxocephalus idahoensis* of the Snake River Plain a sister taxon of *M. thompsoni* of Great Lakes, Hudson Bay and Great Bear Lake drainages. Modern taxa of northern and eastern affinities in the Snake and Bonneville (especially the Bear River segment) systems further emphasize such a connection: *Prosopium* (four species, three endemic), catostomids (*Catostomus catostomus*, *C. ardens*, *Pantosteus platyrhynchus*) and cyprinids (*Richardsonius*, *Rhinichthys catractae*). Their presence is best explained by Miocene access used by ancestral forms, or by later, complex connections (G. R. Smith 1981a); molluscan distributions show similar relationships (Taylor 1985).

Of 12 species shared by the Bonneville and Snake River basins, two (*Gila atraria*, *G. copei*) may have moved south to north while *Catos-*

lunus ardens and *Richardsonius balteatus hydrophlox* might have moved north to south (R. R. Miller 1965). Distributions of *Protopium williamsoni*, *Salmo clarki*, *Rhinichthys cataractae*, *R. osculus*, *Pantosteus discobolus*, *P. platyrhynchus*, *Cottus bairdi* and *C. beldingi*, all of which achieve highlands and thus move over divides, and many of which are indicated by fossils to have occupied the region since at least Pliocene, provide little information on timings or directions of interchanges. They could, however, as readily have achieved their distributions by vicariance of older broad distributions as an alternative to such things as overflow events from lakes. All of the last eight species except *R. cataractae*, for example, are also in the upper Colorado River to which there is little evidence of direct connection with adjacent lake basins.

Excluding the last eight species, early isolation of the upper Colorado River Basin on the aseismic Colorado Plateau is substantiated by modern *Ptychocheilus lucius* and Miocene *P. preluccius* (Bidahochi Formation) being closely related and clearly separated from their congeners (G. R. Smith 1975). Fossil *Gila cristifera*? and *Evomus navaho* of the Bidahochi Formation have no apparent relatives other than a generalized western cyprinid prototype (Uyeno and Miller 1965). The modern *Catostomus latipinnis* is cladistically near *C. macrocheilus* of the Columbia system (G. R. Smith and Koehn 1971), and *Xyrauchen texanus* shows similarities with subgenus *Deltistes* of *Catostomus* (R. R. Miller and Smith 1981) also distributed to the north and west. Fossil catostomids older than Pleistocene are unknown from the Colorado River Basin. Large cyprinids of the *Gila robusta* complex are, however, known from the Bidahochi, as well as being widely distributed southward.

Long separation of future upper and lower Colorado rivers was assured by formation of margins of the Colorado Plateau greater than 20 mya, and such an erosion scarp also allowed development of drainage channels with

habitats that must have stimulated evolution of a distinctive middle Colorado River fauna (R. R. Miller and Hubbs 1960; G. R. Smith 1978; others). Cyprinids of the tribe Plagopterini are centered here (*Lepidomeda* spp. and a remnant population of *Plagopterus argentissimus*) and likely originated from a *Gila copei*-like ancestor. *Pantosteus* spp. also differentiated along this margin (referred to *C. [P.] clarki* by G. R. Smith 1966) as has a form of *Catostomus* related to *C. latipinnis*, and *G. robusta* (*G. r. seminuda*, *G. r. jordani*). *Cremichthys baileyi* subsp. of the White River may be remnants of an earlier fauna, and the cyprinid *Moapa coriacea* is either a relict representative of an early Basin and Range fauna isolated on the southern end of central upwarping, or was derived from the south.

The lowermost Colorado River Basin is comprised mostly of the Gila River, a stream of independent history since at least Middle Miocene (Eberly and Stanley 1978; Nations et al. 1982). Earlier formation of Basin and Range physiography in the south allowed this drainage to complete a cycle of integration that remains in progress in the younger Great Basin. Endorheic basins in structural troughs were largely integrated by Pliocene. Endemics of the Gila River thus may trace their origins to *in situ* allopatric divergence. *Pantosteus clarki* represents its group as an apparent sister species of *P. discobolus*, *Meda fulgida* and *Plagopterus argentissimus* represent the plagopteriins, and the distinctive *Tiaroga cobitis* may be an autochthon, derived from a *Rhinichthys (Apocope)*-like ancestor. Other components have nearest relatives to the north, *Salmo apache*, *S. gilae*; south and/or east, *Agosia chrysoyaster*, *Catostomus insignis*, *Cyprinodon macularius* and *Poeciliopsis occidentalis*; or both north and south, *Gila intermedia*. Integration of the Colorado River over the Plateau margin to the Gulf of California in Late Miocene allowed upper basin fishes to invade south (R. R. Miller 1961a). Species of the middle and lower reaches, with

possible exception of *Plagopterus* and perhaps *Gila robusta*, scarcely dispersed. Southern and/or eastern forms were allowed access through basin transfers (Rio Yaqui, Gila) or tectonic movements on the west.

Evolution and distribution of montane or potentially montane fishes may have been more closely allied to mountain building and continuity of high-altitude terrains that supported aquatic habitats than to continuity of individual drainage basins, and thus are direct results of tectonic activities. Extension zones producing lowlands act as barriers as effective to these species as mountains are to cyprinoids such as *Gila*, *Catostomus* and *Chasmistes*. This seems true in some of the more widespread taxa, such as the *Salmo clarki* group, some forms of the *Rhinichthys osculus* complex, some inland *Cottus* and especially in the genus *Pantosteus*. The last is the best documented (G. R. Smith 1966) and is discussed as an example.

Pantosteus consists of a generalized form, *P. plebeius*, which occupies the southern Rocky Mountains (Rio Grande) and Sierra Madre Occidental axis far south into Mexico, a compact group of specialized forms (*P. clarki*, *P. discobolus*, *P. platyrhynchus*) concentrated along or on the Colorado Plateau and extending westward to the Sierra Nevada, and *P. santaanae* of the Los Angeles Basin, southern California. *Catostomus columbianus* from the northwest is problematical, resembling *Pantosteus* in morphology but *Catostomus* (s.s.) biochemically (Koehn 1969; G. R. Smith and Koehn 1971); we place it with the latter. As typical of fluvial fishes, fossils are rare, consisting only of the Pliocene *P. arenatus* from the Snake River Plain, osteologically a *Pantosteus* considered a near relative of *C. columbianus* (R. R. Miller and Smith 1967; G. R. Smith 1966, 1978).

Despite elevational adjustments, rotation and marginal retreat through faulting and erosion, the Colorado Plateau has remained a stable highland since more than 20 mya, drained by (pre-Miocene to Recent) disrupted, ponded

and reintegrated rivers on its surface and along its margins (Zelt 1975; Shoemaker 1975; Lovejoy 1980; Young 1982). The uppermost Rio Grande also is old, with the river as we know it flowing in a rift that originated about 27 mya (Chapin and Seager 1975; Cape et al. 1983) and leading southward toward highlands of Mexico that are similar in age to the Colorado Plateau. The northern Sierra Madre formed 30–22 mya in the north and 10–8 mya in the south (Karig and Jansky 1972; McDowell and Keizer 1977). Origins of these highlands also stimulated increased precipitation and runoff, providing cool, hard-bottomed streams suited for production and harvest by fishes of diatomaceous films (a major food source of *Pantosteus*) and highly oxygenated water, the need for which is demonstrated by morphology (G. R. Smith 1966) and perhaps hemoglobin structure (Powers 1972) in these specialized animals.

Evolution within *Pantosteus* must have been coincident with development of Miocene relief. Such would allow time for ancestors of *P. plebeius* to achieve the Rio Mezquital of Mexico and to explain presence of *P. santaanae* in southern California, which we attribute below to crustal displacements. Populations of *Pantosteus* further show evidences of introgressive hybridization and stock replacement among Bonneville, Snake, Colorado and Missouri Basin populations (*P. discobolus*, *P. platyrhynchus*; G. R. Smith 1966). Isolation of taxa in developing watersheds resulted in early differentiation, followed by secondary contacts and hybridization to produce a reanastomosing evolutionary pattern that we interpret as demanding long-term occupation of the area. With relative stabilization of drainage relations, distinct taxa evolved, only to again be influenced by interconnective events. Such an event in Pleistocene involving introgression of traits from *P. plebeius* into a local form of *P. discobolus* to produce *P. d. jarrwii* in the Little Colorado River headwaters has been detailed by G. R.

Smith et al. (1983). Selective introgression following hybridization may be a common mode of evolution in this and other western fishes (G. R. Smith 1966; Echelle and Echelle 1978; G. R. Smith et al. 1979; R. R. Miller and Smith 1981).

A faunal association in areas now comprising the Mohave Desert and environs south and west of the Great Basin and Colorado Plateau was markedly different from those just discussed, including Miocene *Fundulus*, *Cyprinodon*, *Empetrichthys* and *Gasterosteus* (David 1945; R. R. Miller 1945c; Uyeno and Miller 1962; Mural 1973). This assemblage extends north and inland to near Pyramid Lake, Nevada (Bell 1974), where joined by Miocene *Salmo*, *Gila* and *Ictalurus* (Baumgartner 1982). Other freshwater fish fossils are otherwise yet unknown from the region until Pleistocene (M. L. Smith 1981). Miocene-Pliocene floras and reconstructed gradients of fossil streams indicate extension of Coastal Plain conditions into the Great Basin (Axelrod 1958, 1962; Huber 1981), and such is accommodated in Miocene by direct geologic evidence. Northward extension of this fauna into what is now the western Lahontan Basin may be explained in part by postdeposition displacements along Walker Lane, the Oregon-Nevada Shear Zone, and other lineaments (R. B. Smith 1978). Some fossil and modern elements must similarly have been displaced northward from some distance to the south. Populations of *Fundulus parvipinnis* and *F. lima* now occur in south coastal California and springs of Baja California. *Cyprinodon* is concentrated in Death Valley, the lowermost Colorado River and far south and east in Mexico. *Empetrichthys* and the related *Crenichthys* are in Death Valley region and east in the middle Colorado River drainage; other goodeids are in central Mexican highlands. *Gasterosteus* is along the coast and, although possibly introduced, also in the upper Mohave River. Modern fauna of the region also includes *Gila (Siphateles) bicolor* subsp., *Ca-*

lostomus fumeiventris and *Rhinichthys osculus* subsp. All but one subspecies of the last, presumably with affinities to the Colorado River Basin, have relationships to modern fishes of the Lahontan Basin and represent southern outliers of the Fish hook pattern. Fossils presently include only Pleistocene representatives of *Gila (Siphateles)*.

Origins of cyprinodontoids of the Death Valley region have been of major interest and have stimulated repeated attempts to reconstruct connections among closed-basin lakes to facilitate dispersal from the east and south, largely in Pleistocene or later. Parenti (1981a) vastly expanded potentials for interpretation in proposing primitive goodeids now represented by *Empetrichthys* and *Crenichthys* were part of a Late Cretaceous-Early Tertiary biota better represented in fossil and living faunas by primitive dicotyletonous forests. Disjunctions in ranges of cyprinodontoid fishes, north to south for the goodeids and east to west for *Fundulus* and *Cyprinodon*, were proposed to reflect disruption of continuous distributions by intervention of Eocene-Oligocene and later aridity. Present world distributions of cyprinodontiforms were further interpreted by Parenti (1981a) as Pangean in part, and considered Late Triassic in age, coincident with a time when the Laurasian and Gondwanian landmasses had begun to separate.

If the fossil *Cyprinodon brevirostris* from near Death Valley (R. R. Miller 1945c) is of Late Miocene (McCallister in Miller 1981), minimum regional age for the genus is established. This substantially predates and excludes from consideration as dispersal routes most lacustrine habitats for which surface evidence remains. It similarly negates the importance of Pliocene and later events pertaining to origins other than for extant species. *Cyprinodon* now lives in some of the most tectonically active regions of southwestern United States, reflecting in part the correlated presence of springs in such zones. These areas are, however, inboard on

the continent from migrating terranes, and there is no evidence that this genus ever achieved the Pacific Coast. Its present-day proclivity for low-gradient habitats is pervasive (R. R. Miller 1981) and presumably held in the past.

We expect that *Cyprinodon* was distributed in eastward-flowing, low-gradient streams penetrating in Oligocene times south of the Laramide Axis to near the western continental margin. Tectonic events would have transferred headwaters and fishes of these systems to internal or Pacific drainages. Development of shear and extension zones produced western, northwestern and northern structural orientation. If the genus was thus not already present on land surfaces now comprising the Death Valley region, which were then located to the east and south, a parsimonious explanation for origin of *Cyprinodon* is provided by formation of near coastal and inland shear zones from Miocene to Recent (Haxell and Dillon 1973; Page 1982). A long zone of right-lateral wrench-faulting developed in Mexico (in part, Merriam 1972), extending northward into the Great Basin (Longwell 1974) and northwest as the San Andreas Transform. Schollen ranging to blocks as large as the Transverse Range were displaced north-northwestward along this splintered alignment. Movements of more than 300 km are indicated for schollen along and across the Salton Sea region (Crowell 1981; Ehlig 1981). Springs rising directly or indirectly along such fractures now support most fishes of the Death Valley region. Transport of fishes on schollen or in spring zones associated with migrating schollen seems reasonable, and potentials for passive or active dispersal through this mechanism have existed for longer than 20 my. Origins of some schollen in southwest Arizona and northwestern Mexico (Livacari 1979) are obviously concordant with the derivation of *Cyprinodon*.

Another plausible alternative is dispersal of *Cyprinodon* through shallow marine incursions

inland to or near the Death Valley area (P. B. Smith 1960, 1970; Watkins 1975; Gastil et al. 1979; M. L. Smith 1981). Estuarine parts of such a system may have supported the taxon (R. R. Miller 1981). Conditions such as tides higher than 9.0 m that likely exclude *C. macularius* from the upper Sea of Cortez (W. L. Minckley, unpublished data) would not have occurred prior to formation of a large volume, but constrained Gulf of California Rift. Traces of westward-flowing streams in the Imperial Valley and Mohave Desert (Woodburne 1975; Gastil et al. 1979) must predate the Peninsular and Transverse ranges, and indicate at least moderate highlands immediately west of the embayment that would have prevented western dispersal. These drainages were interrupted by Pliocene uplift and emplacement of intervening schollen.

Transport of fossils through displacement is certain, and it is evident that fossil *Cyprinodon* and *Fundulus* from Death Valley were interred east and south of their present positions. Possibilities for similar displacement of fossil *Fundulus* and *Gasterosteus* in west-central Nevada have been mentioned. Fossil *Empetrichthys erdisi* are in Miocene components (Link 1982b) of the Ridge Formation now emplaced north of Los Angeles, California, derived from the Orocochia Mountains now lying northeast of the Salton Sea (Eaton 1939; Farley and Ehlig 1977; Ehler and Ehlig 1977; Link 1982b,c). We have been unable to determine the probable position of the Orocochia Mountains at deposition time of Ridge Formation sediments, but they were even further south and east of their present position (Haxell and Dillon 1973).

Origins of oviparous goodeids and perhaps *Fundulus* and *Cyprinodon* conceivably relate to even older and more extensive movement of terranes along and within the southern and western margins of North America. Large masses of continental margin were lost from central Mexico between the Late Cretaceous

and Miocene (Karig et al. 1978). Paleomagnetic reconstructions indicate these may now be represented more than 2000 km north by the southern California batholith, including coastal areas south of Los Angeles and all of Baja California (Beck and Plumley 1979). Rocks forming San Miguel Island near Los Angeles were deposited in Eocene near 15°N latitude, 3800 km south of their present position (Champion et al. 1981). B. M. Page (1981, 1982) documented similarly long displacement of the Salinian Block, and loss of some of its splinters perhaps to as far north as Oregon or Alaska. Combined with evidence for Middle Cenozoic east-west displacement of about 260 km across the Transverse Volcanic Belt of central Mexico (Gastil and Jensky 1973), transport from centers of present abundance and species diversity becomes an apparent possibility for early goodeids, *Fundulus*, perhaps *Cyprinodon* and other enigmatic taxa such as *Dorosoma smithi*, *Moxostoma* spp., *Ictalurus* spp. and the fossil *Micropterus relictus*. Recent additions and positional adjustments in known distributions of fossil and modern goodeids (M. L. Smith, pers. comm., 1983) may, however, support Parenti's (1981a) hypothesized continuous pre-Miocene distribution (Fig. 15.8).

We suggest examination of possible relationships of western American *Fundulus* to those of southern and central Mexico (*F. grandis*, *F. grandissimus*, *F. persimilis*). R. R. Miller (1955a) anticipated such congruence in his "tentative phylogenetic sequence" by grouping some of these with *F. parvipinnis* and *F. lima*. Cladistic relations of western *Cyprinodon* also may in part lie further south than before appreciated (for example, *C. meeki* of the Río Mezquital); however, these last fishes also may demonstrate reticulate evolution (Echelle and Echelle 1978) that bodes ill for cladistic methodology.

The most clear-cut example of probable transport of fishes by documented tectonic displacement involves *Gila orcutti* of the Los

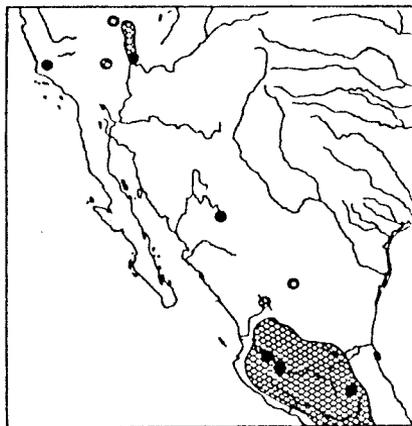


Figure 15.8 Geographic distribution of fossil (●) and modern (■) goodeid fishes; modified from Parenti (1981a), M. L. Smith (1980, 1981, and pers. comm., 1983), and Uyeno et al. (1983). See text for further explanation.

Angeles Basin. Palinspastic coastline reconstruction places present distribution of *G. orcutti* in juxtaposition with those of its closest relatives, *G. ditaenia* (Río Magdalena) and *G. purpurea* (Ríos Matape-Sonora-Yaqui), in northwestern Sonora (Fig. 15.9). Rocks and other sediments along the coastline derived from northwestern Sonora confirm drainage continuities prior to northward translocation. If relationships of the subgenus *Temeculina* of *Gila* are as postulated by Barbour and Miller (1978) with the genus *Alganssea* of the Mexican Mesa Central, a zoogeographic track of that group is concordant with shear and displacement alignments discussed for western cyprinodontiform fishes. Possible relationships of *Alganssea* and *Agosia* (D. A. Hendrickson, unpublished data) also may apply. If one includes *G. crassicauda* of the Sacramento-San Joaquin Basin in *Temeculina* (Barbour and Miller 1978) the pattern extends to the modern north-

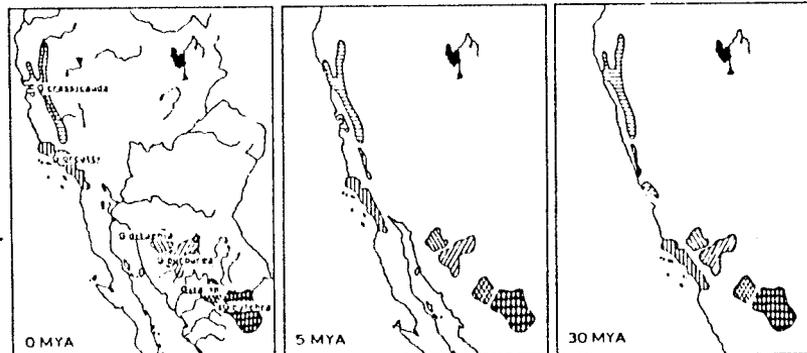


Figure 15.9 Diagrams of present distributions of six cyprinid fishes (genus *Gila*, subgenus *Temeculina*) of western North America held fixed in size relative to displacement of microplates along the present and proto-San Andreas Transform zone. Great Salt Lake is held immobile as a reference point. Same extension between the Colorado Plateau margin and the Sierra Nevada axis and across Sonora was reduced at a time-dependent rate. See text for details and Figure 15.5 for further explanation.

ern boundary of regional transform tectonics (compare Figs. 15.5 and 15.9).

Pantosteus santaanae, which shares a distribution in the Los Angeles Basin with *Gila orcutti*, has less definitive palinspastic congruence with probable ancestors. However, it is clearly a relative of *P. plebeius* (G. R. Smith 1966) that partially shares a present distribution with subgenus *Temeculina*, and may thus reflect the same tectonic history. The absence of members of the genus *Pantosteus* in intervening drainages detracts from this interpretation.

A viable alternative for origin of *Pantosteus santaanae* may involve the lower Colorado region and conditions that existed prior to Basin and Range formation and integration of the upper, middle and lower parts of the Colorado River. The region should have early been occupied by a primitive, *P. plebeius*-like form. Basin and Range faulting south and west of the Colorado Plateau isolated stocks perhaps now represented by problematic populations (Minckley 1973) of the White, Virgin and Bill

Williams rivers. *Pantosteus santaanae* shares some characters with these populations as well as with southern populations of *P. plebeius* (G. R. Smith 1966). Invasion of stocks giving rise to *P. clarki* as a sister taxon of *P. discobolus* (G. R. Smith 1978) may be reflected in characters of these fishes, and could as well have resulted in extirpation of remnant stocks in the Gila River. Precedent for stock replacement after such invasion has been indicated for the upper Snake River system (C. R. Smith 1966).

Emplacement of a primitive *Pantosteus* in coastal California through events associated with schollen migration is feasible and may be supported by presence of *Rhinichthys osculus* in the Los Angeles Basin. Cornelius (1969) demonstrated morphological alliance of the last with the middle Colorado River and not with the Sacramento-San Joaquin Basin or northeast through Owens Valley to the Lahontan Basin. *Rhinichthys o. nevadensis* in Ash Meadows of the Death Valley region (R. R. Miller 1946b; Hubbs and Miller 1948a) and *Rhinichthys deaconi* in Las Vegas Wash (R. R. Miller

1984) may reflect the same processes. *Rhinichthys osculus* further does not occupy Mexico south of the Gila River Basin. Inconsistencies between this hypothesis and those just forwarded for *Cyprinodon* may in part be reconciled by typical differences in habitat preferences, lowland versus upland, respectively, for that taxon and the pair of cyprinoids.

Application of principles of vicariance biogeography (Rosen 1975a,b; Nelson and Platnick 1981; Nelson and Rosen 1981) to analysis of some situations just described was in part attempted by comparison of hypothesized area relations (Fig. 15.4) with two available species-level cladograms (Figs. 15.10 and 15.11). There are no phylogenies yet available for comparison with area relationships in Figure 15.5.

A cladogram of G. R. Smith and Koehn (1971), based on morphological and biochemical data for *Catostomus* (excluding *Pantosteus*) depicts the group as paraphyletic. *Pantosteus* forms a sister group to *C. rimiculus* (Fig. 15.10). Only 13 of 23 species of our region were included, making interpretation tenuous, but there is a lack of obvious congruence of the overall phylogeny with area relationships. Congruence of disjunct parts of the phylogeny suggest, however, that both area relationships and phylogeny may be at least partially correct. We thus altered the cladogram through internal rotations without change in relationships or in concept relative to implied or proposed times of origin to see how much change was required to produce a reasonable "fit" with geologic history.

If we accept area relationships as true, greatest correspondence is obtained by alteration of the phylogeny to hypothesize early divergence of two lineages, one being the left limb in Figure 15.10 including the *C. commersoni* line and a second giving rise to the *C. occidentalis*-*C. tahoensis*-*C. rimiculus* group and its early-differentiated sister group, *Pantosteus*. Consideration of the basal trichotomy as an early event produces initial congruence: basal divergence of the eastern *Catostomus*

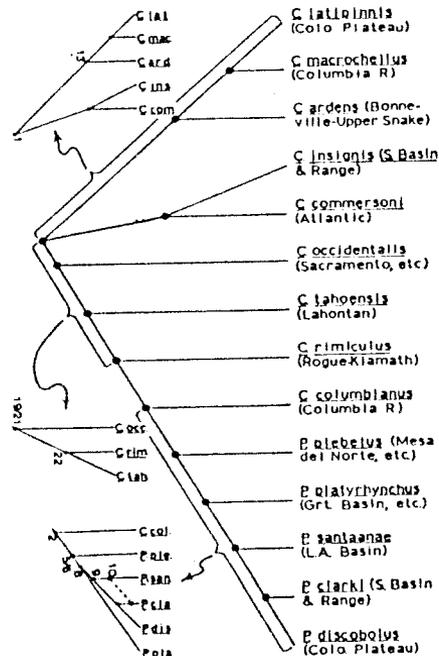


Figure 15.10 Cladistic estimate of phylogenetic relationships of some catostomid fishes of western North America (modified from G. R. Smith and Koehn 1971). Insets below the overall cladogram are reoriented and reinterpreted segments of the original, with nodes numbered to correspond to those on the area cladogram of Figure 15.4 as discussed in text.

commersoni corresponds to node 1 of Figure 15.4 whereas chronologies of divergences of *C. ardens* and *C. macrocheilus* correspond to nodes 13 and 16, respectively. Positions of *C. insignis* and *C. latipinnis* are nevertheless far from congruent with proposed area relationships (see later). Relationships of *C. occidentalis*, *C. tahoensis* and *C. rimiculus* (Fig. 15.10) are, however, congruent with events depicted at nodes 19, 21 and 22 (Fig. 15.4). If such is the case, ancestral distribution of *Pantosteus* is

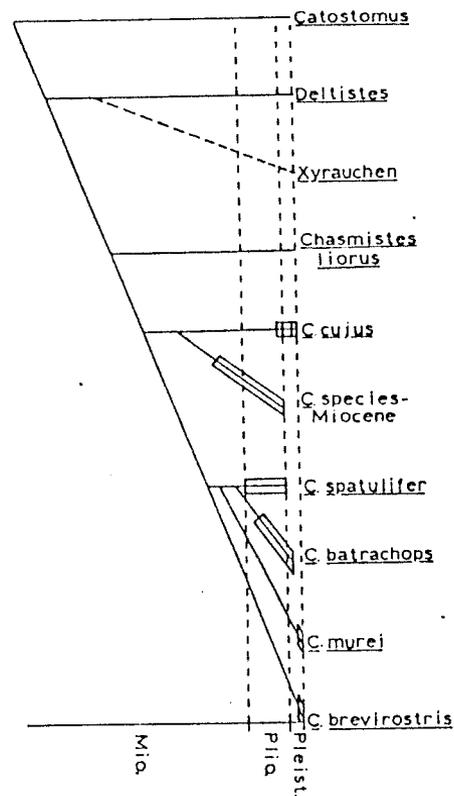


Figure 15.11 Cladistic estimate of phylogenetic relationships of catostomid fishes of the genus *Chasmistes* relative to *Catostomus* and *Dellistes*. *Xyrauchen* was added as implied, but not illustrated, in the original cladogram of R. R. Miller and Smith (1981; Fig. 12-B). Boxed areas represent time ranges for fossils; see text for details and Figure 15.4 for further explanation.

constrained to the small region represented above node 22 (Fig. 15.4), and attainment of its presently wide distribution since 8 mya is implied. Such extensive dispersal seems unlikely and would not have produced the proposed phylogeny (Fig. 15.10).

We note considerable concordance with predictions of area relationships if *Pantosteus* is allowed a much older age of origin. Isolation of *C. columbianus* may have resulted from events at node 2, with subsequent separation of *P. plebeius* in the Rio Grande and Mesa del Norte (nodes 5 and 6). The wide distribution of *P. platyrhynchus* must be attributable in part to dispersal, but corresponds with origin in the Great Basin region by vicariance relating to node 8 (Fig. 15.4), leaving a sister group on the Colorado Plateau/southern Basin and Range/Mohave Block to respond subsequently to events at nodes 9 and 10. Arrangement of these three taxa by G. R. Smith and Koehn (1971) differs from that predicted by area relationships (Fig. 15.4), which indicates that *P. clarki* and *P. santanae* would form the sister group of *P. discobolus* (Fig. 15.10). With minor adjustments we thus find nearly complete congruence of phylogeny with area relationships within *Pantosteus* and basal taxa of the lineage leading to *Pantosteus*.

Considering that the detailed pattern of area relationships may harbor errors, such a phylogeny also is consistent with a different, more generalized scheme of area relations, for which there is a geologic basis. Suppe et al. (1975) discussed data indicating that our region north and west of the Colorado Plateau and north of the Garlock Fault/Las Vegas Valley shear zone behaves as a major "western North American Subplate." Vicariance of this subplate would be depicted in a modified Figure 15.4 as a bifurcation with one limb containing the western North American component (nodes 12-25) and the other limb producing a sister lineage comprising most of the remainder of the region (nodes 5-11). Congruence with the *Pantosteus* group of the phylogeny is improved if such a bifurcation is placed above node 6 to produce one lineage of nodes 8-11 and a sister group of nodes 12-25. This is consistent with geology, since formation of the subplate was likely a result of initiation of transform shear at 29 mya, roughly coincident with opening

of the Rio Grande Rift (27 mya) and rotation of the Colorado Plateau. It is interesting to note that the left limb of the *Catostomus* (s.s.) phylogeny, which presumably would have experienced the same history as the right limb, is discordant in a similar fashion. The two taxa (*C. insignis* and *C. latipinnis*) incongruent with area relationships matched by the other three (*C. commersoni*, *C. ardens* and *C. macrocheilus*) are those not now inhabiting surfaces of the western North American Subplate.

A second set of phylogenetic data was provided by R. R. Miller and Smith (1981) as two hypotheses of relationships within the catostomid genus *Chasmistes*. Their Figure 12-A was "constrained to have character states of the oldest known fossil near the base" and involved many character reversals. Such constraints were not applied in their Figure 12-B, however, which was more parsimonious but involved parallelisms and homoplasy of some characters. We chose to employ the latter (Fig. 15.11) for comparison with area relationships (Fig. 15.4), and found strong congruence.

Early divergence of *Deltistes* from its proposed sister, *Xyrauchen*, is congruent with node 8 (Fig. 15.4); reasons for early divergence of that lineage are not explained by area relationships unless the former was isolated on the western North American Subplate and the latter taxon elsewhere (see above). Subsequent isolation of the Bonneville Basin (node 13) is congruent with divergence of *Chasmistes liorus*. Later divergence of "Miocene *C. cujus* sp." lineage may be most parsimoniously explained by events of node 17, with dispersal derivation of a *C. cujus* ancestor in the Lahontan Basin. Alternatively, an earlier split of this clade might be proposed, which is unexplained by area relationships. Such, however, would predict presence of other derivatives of the *C. cujus* lineage in all areas isolated from the Lahontan, areas where they are presently unknown, by events of nodes 19 to 25. The next divergence, that of *C. brevis* in the

Klamath Basin, corresponds with node 22. Within the final group, separation of *C. muriei* in the upper Snake River relates to node 23 leaving the ancestor of *C. batrachops* in the Oregon Lakes region. The sister of *C. batrachops*, *C. spatulifer*, is thus hypothesized to have arisen by dispersal of a *C. batrachops* ancestor to the middle Snake River area. Fragmentary fossil material from Duck Valley and China Lake referred to *C. batrachops* (R. R. Miller and Smith 1981) might also represent dispersal derivatives, or might be vicariant isolates forming a sister group to *C. muriei* (node 24). Unidentified fragmentary fossils from various localities in the Lahontan Basin also may represent an autochthonous sister of *C. muriei* (Fig. 15.11).

Biological, hydrological and geological realities, as well as methodology employed to construct cladograms, impose limitations on validity of interpretations. Although congruence seems remarkably high in the two available comparisons, we are obligated to provide cautionary comments.

Results of an approach to fish distributions based on tectonism seems useful since hydrography responds predictably to tectonic events. Terminal areas defined mostly by tectonic margins thus correspond well to faunal areas. However, the extent of interconnective events must be kept in mind. It cannot be expected that vicariance biogeography methodology will be as readily applied in inland areas as it has been to less complex, transoceanic intercontinental relations, where barriers are definitive and reticulate events fewer or absent.

Lack of congruence between area and phylogenetic patterns indicate either erroneous depiction of true relationships, complexities resulting from dispersal or speciation through other than allopatry. Inland regions of complex geologic history have ephemeral barriers. Vicariant events may not be permanent because of subsequent direct or indirect tectonic

effects, and dispersal opportunities may be frequent in geologic time. Any attempt to portray all connective events in area relationships results in a reticulum, and necessitates an assumption of unending dispersal of biotic elements to attain cosmopolitan distributions within composite areas prior to subsequent vicariance of any part. Construction of anastomosing cladograms incorporates into the vicariance biogeography methodology the dispersal that it was implicitly designed to detect. We therefore defined areas as geographic units, recognizing that any one may have had multiple and varied hydrographic affinities through geologic time. Each was treated in effect as if it were permanently endorheic, experiencing only subdivision, with no growth or loss of area. All vicariant events were considered to produce allopatry of subdivisions, not as connective events to adjacent regions, although they may in fact be such. We discussed connective events and their chronologies elsewhere in text. Our decision to define vicariant events as those that changed drainage affiliations of areas obviously limits use of resulting diagrams in studies that involve organisms that may not respond to such barriers as do the aquatic biota.

Our rooting of most of the area cladograms on the Oligocene erosion surface, implying pan-regional distributions of ancestral fishes at that time, may obviously be questioned. We deem it likely, however, that drainage integration over the broad, stable, long-lived, low-relief surface was extensive, and that a biota attained a regional distribution far more widespread than any similar monophyletic assemblage displays today. Additionally, potential ancestors of at least some groups in the modern fauna (for example, cyprinids) are known from the limited Oligocene fossil record in the area. Others (for example, catostomids other than the earlier *Amyzon*) have minimal regional ages of Miocene.

Although we attempt no statistical analyses

of goodness of fit, it seems improbable that stochastic processes would have produced observed degrees of concordance of relatively large segments of hypotaxized phylogenies with area relationships indicated by geology. The small sample indicates that regional phylogenetic patterns may result from vicariance processes dating to Oligocene. At least on a regional scale, dispersal and Pleistocene events appear to have had relatively little influence on today's broad patterns. We encourage cladistic analyses of other regional groups, as well as continued scrutiny of area relationships.

EPILOGUE

Our biological interpretations have been based on and often constrained by limited information on relationships developed by a diversity of systematists using equally diverse methodology. Needs for phylogenetic analyses of major fish groups over broad geographic areas are apparent, and until they are available little more can be accomplished than inferences for future research. Not only are such studies of importance within our area, but relationships across the Continental Divide remain little quantified, and we further suspect that indications of sister groups spanning the Pacific Ocean (R. R. Miller 1959a, 1965; Uyeno 1960; Hopkirk 1973; Gosline 1974; Howes 1980, 1984; G. R. Smith 1975; G. R. Smith and Miller 1985) may reflect tectonic phenomena rather than dispersal. G. M. Davis (1979, 1982) documented delivery of components of the freshwater molluscan fauna of Asia via the Indian Plate, and the Pacific Basin is rimmed by allochthonous terranes of uncertain origins (Nur and Ben-Avraham 1982), yet of recent enough accretion to be acceptable vehicles carrying ancestors of some modern faunal elements.

Despite our original intent and timely urgings of Endler (1982a,b), scope of this chapter

allowed only passing consideration of influences of ecology on past and present distributional patterns. Ecology of western fishes has been reviewed by Deacon and Minckley (1974), contributors in Naiman and Soltz (1981), Moyle et al. (1982) and in regional compendia cited earlier. We further have not satisfactorily dealt with especially interesting questions of influences of tectonics and paleoclimatic factors on life histories, community structures or distributional relations, and have dealt only in passing with explanations for the absence of groups from vast regions. Severity of climatic change, however, necessitates some further comments.

Climatic trends toward aridity, the latest of which being the most severe yet recorded (Axelrod 1979), must have resulted in remarkable amounts of species and faunal extirpation. In some of the best studied examples, evolution of lake-adapted taxa in Late Miocene and Pliocene ended with disappearance of large lacustrine habitats in Pleistocene, and such fishes became extinct or exist only as local relicts (R. R. Miller 1946b, 1959a, 1965; Hubbs and Miller 1948a; G. R. Smith 1975, 1978, 1981a,b; M. L. Smith 1981). However accumulated evaporites in lake basins that existed far earlier in Tertiary attest to recurrent droughts over geologic time spans, often on a regional basis, and extinction must have then prevailed as well. Adaptations to environmental variations attending drought conditions in surviving fishes must thus have been necessary in the distant past, and responses to physical, chemical and biological conditions that allowed these obligate aquatic animals to persist, even if by chance in the regional vastness, merit study and definition. That tolerances evolved early is demonstrated indirectly by ecology of deposition of many fossil-bearing strata. For example, the Miocene *Gila traini* lived in highly alkaline waters (Lugaski 1979), as do today many populations of related cyprinids (Williams 1980;

Williams and Bond 1981, 1983). Potentially estuarine forms such as cyprinodontoids were presumably preadapted to inland salinities and other vagaries of western waters (M. L. Smith 1981). By Miocene, extremes intolerable to some groups brought about their regional extinction, while ancestors of the modern fauna persisted. It is, however, important to emphasize that much of western North America is not and has likely never been desert. In fact, gaps in fish distributions generally correspond to desert areas except where geologic waters occur or highland runoff passes into desert terrains, and the most diverse faunas are at intermediate elevations in temperate habitats (Minckley and Brown 1982).

A few forms in special habitats such as thermal springs seem to be narrow niche specialists intolerant to fluctuating environmental features of surface runoff. Taxa that become highly specialized to local conditions may be evolutionarily blocked, with extinction far more probable than survival (R. R. Miller 1950a, 1961a). However, many species restricted to springs and spring-fed habitats show few if any restrictive specializations (Deacon and Minckley 1974; Soltz and Hirshfield 1981), and most widespread or formerly widespread western fishes tend to be generalists.

Some of these less differentiated relict fishes of wetter times must have remained poised in refugia during drought to reoccupy with similarly protected congeners expanded aquatic habitats of the next wet period (Minckley and Brown 1982). Tolerance to extremes viewed as generalist traits thus may have arisen in response to special local conditions, only to be assimilated into hybrid swarms when sympatry was achieved, then sorted out anew in allopatry forced by another cycle of desiccation. Pronounced intraspecific variation in morphology of some western fishes (for example, G. R. Smith 1966; Hubbs et al. 1974; Rinne 1976; Minckley 1980d) also may origi-

nate from historic secondary contacts of allopatric differentiae. Introgression of genes after hybridization of species or semispecies may lead to rapid adaptive evolution (Lewontin and Birch 1966), and severe selective forces are certainly available to act on western fishes. Anderson (1949) speculated that introgression might incorporate new genes into populations that could allow occupation of new habitats and presumably lead to advantageous new adaptive peaks. This scenario differs only in relating to much longer periods of time and far greater space from differentiation of demes or other population units in microisolative pockets (Ehrlich and Raven 1969; Endler 1973, 1977; G. M. Davis 1979, 1982). Mixing of distinct fishes is documented in cyprinodontoids of the Anatolian Basin of Turkey (Villwock 1958, 1963, 1966; Kosswig 1961, 1963) and the Mexican Plateau (Arnold 1972; Minckley 1978, unpublished data); in western North American catostomids (G. R. Smith 1966; Koehn 1969; G. R. Smith and Koehn 1971; G. R. Smith et al. 1983); cyprinids of remnant waters of the Lahontan Basin (Kimsey 1954; Hubbs 1961); and others. Many examples dealing with hybrid swarms have been attributed to failure of isolating mechanisms due to human activities. Natural trends in habitat deterioration must sometimes have similar results (Hubbs 1955). Putative hybrids are indicated in the fossil and archaeological records as well (Hubbs and Miller 1948a; Hubbs 1961; G. R. Smith 1975; R. R. Miller and Smith 1981), and probable or possible hybrid origins of some western taxa are becoming recognized (Echelle and Echelle

1978; G. R. Smith et al. 1979, 1983; R. R. Miller and Smith 1981).

High mountains and fractured lowlands giving rise to springs assure the presence of regional waters, and such appears almost the only thing required for survival by some western fishes, be they of hybrid origin or not. We thus view the western fish fauna as an assemblage sorted out as has been much of the arid-land flora (Axelrod 1958, 1967, 1979) by repetition of drought and tectonism to its present composition. It consists of preadapted cyprinodontoid (M. L. Smith 1981) and evolved cyprinoid generalists capable of persisting by tracking of seismic zones and climatic conditions that provide highly variable but permanent water, plus a smaller contingent of specialists of these and other groups locked in their dependency on scarcer, constant aquatic habitats.

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