Klamath-Pit clade.—The Klamath + Pit clade is composed not only of samples from widely scattered localities in the Klamath and Pit Rivers but also those from south-coastal (i.e., San Benito River) and eastern California (i.e., Eagle Lake). Two general scenarios may explain the close relationship between the Pit River and the south-coastal San Bonito River (Pajaro Basin). *Rhinichthys osculus* may have entered the Pajaro Basin by way of a headwater transfer with the San Joaquin River (Snyder, 1905; Murphy, 1941). Prior to 1.5 mya, the Sacramento River also flowed through the San Francisco Trough to Monterey Bay, whereas the San Benito River flowed north into San Francisco Bay (Taylor, 1985:312, fig. 38). The general extension of the Sacramento River ichthyofauna into south-coastal drainages was clearly demonstrated by these patterns (Snyder, 1905), as represented an extension of the *R. osculus* form in the Snake River (Jordan and Evermann, 1896; Cornelius, 1969).

The Pit River is centrally positioned in this region and was the center of intense orogeny and volcanism during Pliocene and Pleistocene. The Klamath-Cascade region acted as a single, coherent block when its western end was displaced 340 km to the south about 20 mya (Magill and Cox, 1981). Thus, a close relationship between Klamath and Pit Rivers may in part be the result of these drainage realignments (Minckley et al., 1986). Fossils from the early Pliocene connected both Pit and Klamath Basins with the premodern Snake River as the latter drained to the Pacific Ocean (Miller and Smith, 1967; Smith, 1975; Taylor, 1985). The position of this clade in Figure 2 points to its ancient connections, but the timing is clearly uncertain, in part because of a lack of physical evidence coupled with the uncertainty in aging fossil materials (Smith et al., 2000).

Bonneville Basin and the origin of Rhinichthys osculus.—The numerous examples of differentiated fauna in the Bonneville Basin were recognized by Cope and Yarrow (1875) as stemming from long intervals of piecemeal isolation. Their conclusions are strongly supported by the patterns we uncovered in *R. osculus*. For example, a majority of haplotypes from the Northern Bonneville clustered with the Deschutes River (DSC), whereas one (i.e., Box Elder County, UT; BOX1) was consistently sister to the Colorado River. Southern Bonneville haplotypes were also sister to the Upper Colorado, whereas two highly divergent haplotypes were sister to the Lower Snake (Clearwater River; CLR). Taylor (1983; 1985:296, fig. 25) suggested a Late-Miocene drainage connection between southeastern Idaho and the lower Colorado River Basin, a route supported by living and fossil molluscs in western Bonneville Basin. Hubbs and Miller (1948) identified this drainage as a structural trough leading to Pluvial White and Carpenter Lakes. This north-south connection between the Bonneville Basin and the Colorado River is also reflected in the distribution of *Gila* (now *Snyderichthys*) *copei* (Johnson and Jordan, 2000). Haplotypes of this species are separated into northern (e.g., Bear and upper Snake Rivers) and southern (e.g., Utah Lake and Sevier River) clades, with the northern clade more genetically similar to the outgroup taxon (*Lepidomeda mollispinis mollispinis*) from Virgin River. The fragmented history of the Bonneville Basin is clearly evident, and these studies provide compelling evidence of its role as a north-south conduit between southern Idaho and the Colorado River.

Taylor's (1985) western Bonneville route crossed the drainage of Big Spring Creek, at the upper end of Snake Valley (Tooele County, UT), where Smith (1978) noted a distinct, undescribed dace that shared many "spring isolate" characters with the extinct *R. deaconi* (Miller, 1984:table 2). Our two divergent southern Bonneville haplotypes (i.e., Big Springs Creek [BSC2] and Sevier River [SEV4]) differed from conspecifics by greater than eight restriction sites. Finding two highly divergent haplotypes at the same locality represents an uncommon Type-II phylogeographic situation (Avise et al., 1987), generally attributed to secondary contact among allopatric populations. Our study suggests these divergent, southern Bonneville haplotypes may represent a widespread and undescribed form related to *R. osculus* but with an earlier connection to the north. This is supported by the position of these Southern Bonneville haplotypes in our trees, and by the basal location of Northern Bonneville, Los Angeles and Middle Colorado Basins within their respective clades. The close affinity of Colorado River *R. osculus* with those in the Los Angeles Basin, but not with Death Valley, suggests two different invasions in that region. The Northern Bonneville-to-Colorado-to-Los Angeles connection was likely earlier than the Lahontan-to-Owens connection.

It is tempting to infer from these data the origin of *R. osculus* in Western North America. Patterns of haplotype distribution suggest that the premodern Snake River and Lake Idaho had major roles in the distribution and subsequent evolution of *R. osculus* in surrounding basins. The basal position of those basins allied to

the early Snake River (e.g., Upper Snake, Northern Bonneville, Klamath-Pit, and Columbia) could represent the earliest appearance of modern *R. osculus* in the west. Bonneville haplotypes join the tree at separate yet earlier positions, and may represent an early *R. osculus* form in the western paleodrainages of the Mohave and Sonoran desert provinces (sensu Minckley et al., 1986). The long isolation of the Los Angeles Basin, and its sister relationships with the Northern Bonneville and Colorado clades suggest the possibility of an earlier *R. osculus*-like form in this region. The presence of undescribed *Rhinichthys* (Peden and Hughes, 1988) in the Columbia River Basin also indicates that evolution of the group may have been northerly, possibly associated with retreating ice (McPhail and Lindsey, 1986; Bodaly et al., 1992). However, the early Bonneville-to-Colorado distribution, coupled with the accompanying fishhook drainage, suggest that *R. osculus* may, in fact, have originated much earlier, possibly associated with Tertiary Lake Idaho.

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