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INTERMOUNTAIN FRESHWATER MOLLUSKS, USA (*MARGARITIFERA, ANODONTA, GONIDEA, VALVATA, FERRISSIA*): GEOGRAPHY, CONSERVATION, AND FISH MANAGEMENT IMPLICATIONS

Peter Hovingh[1]

ABSTRACT.—Field collections at more than 2900 sites and the examination of many museum collections and literature allowed me to map the historical and current distribution of several freshwater molluscan faunal groups in the Intermountain region of the United States (Great Basin, Colorado River drainage basin, and upper Snake River subbasin). Historical and current records show that *Margaritifera falcata, Anodonta californiensis,* and *Ferrissia rivularis* have drainage-specific distributions, while *Valvata utahensis* has a specific drainage pattern, and *V. californica* (new combination) has a dispersed pattern. Shell morphometric data of *Valvata* and *Ferrissia* show extensive shell variation between and within populations. Current surveys show that these molluscan populations have been reduced since the colonization by European descendants over the last 150 years. *Margaritifera falcata* was found to be extirpated from eastern California, Nevada, and Utah and was common in only 1 stream. *Anodonta californiensis* populations of 10 or more individuals occurred in only 2 of 13 drainages, as well as in 1 isolated spring. *Valvata californica* was extirpated in 7 of 10 lakes. *Ferrissia rivularis* was very rare in 6 of 12 drainages. Range declines among these fauna are thought to be related to alterations of habitat caused by grazing, irrigation, and urbanization, as well as the intensive management of sport fish in these waters.

Key words: mollusks, Intermountain West, distribution, conservation, fish management, Margaritifera, Anodonta, Gonidea, Valvata, Ferrissia.

The Intermountain region of the western United States includes the endorheic Great Basin and its many subbasins; the Columbia-Snake River basin, largely cutting westward across the Intermountain region; and the Colorado River basin, cutting southward across the high plateau region. The region is bounded by California's Sierra Nevadas on the west, the Cascade Range on the northwest, and the Continental Divide on the east (Fig. 1). Taylor (1970, 1985) documented the living and fossil freshwater molluscan fauna in western North America and proposed drainage affinities for this fauna group. Fish have responded to the complex hydrology with high levels of endemism at both the species and subspecies levels (Hubbs and Miller 1948, Smith 1978). The hydrobiid gastropods include many endemic species, as well as those that have a more general distribution (Hershler 1998). In contrast to the differentiation of fish and hydrobiids, amphibians have responded to this complex system with little or no morphological differentiation (Hovingh 1997), although Green et al. (1996, 1997) and Bos and Sites (2001) suggest that the molecular differentiation indicates more complexity than species distribution maps reveal.

Here I describe the taxonomic and distribution status of mussels (*Margaritifera, Anodonta,* and *Gonidea*) and gastropods (*Valvata* and *Ferrissia*) in the Intermountain West.

METHODS AND MATERIALS

FIELD COLLECTIONS.—Field collections consisted of visually examining lentic and lotic habitats; benthic sampling with a food strainer; and hand collecting from logs, rocks, and debris. More than 2300 sites within the Great Basin were surveyed (Fig. 2A, Table 1). Some 587 sites were surveyed in the Colorado River basin, with the Green River (302 sites) and the Virgin River tributaries (109 sites) most extensively surveyed (Fig. 2B). Over 100 sites were surveyed in the upper Snake River drainages (not shown).

Great Basin springs were selected from 1:100,000 USGS maps. Streams and lakes were sampled at accessible sites from roads and trails.

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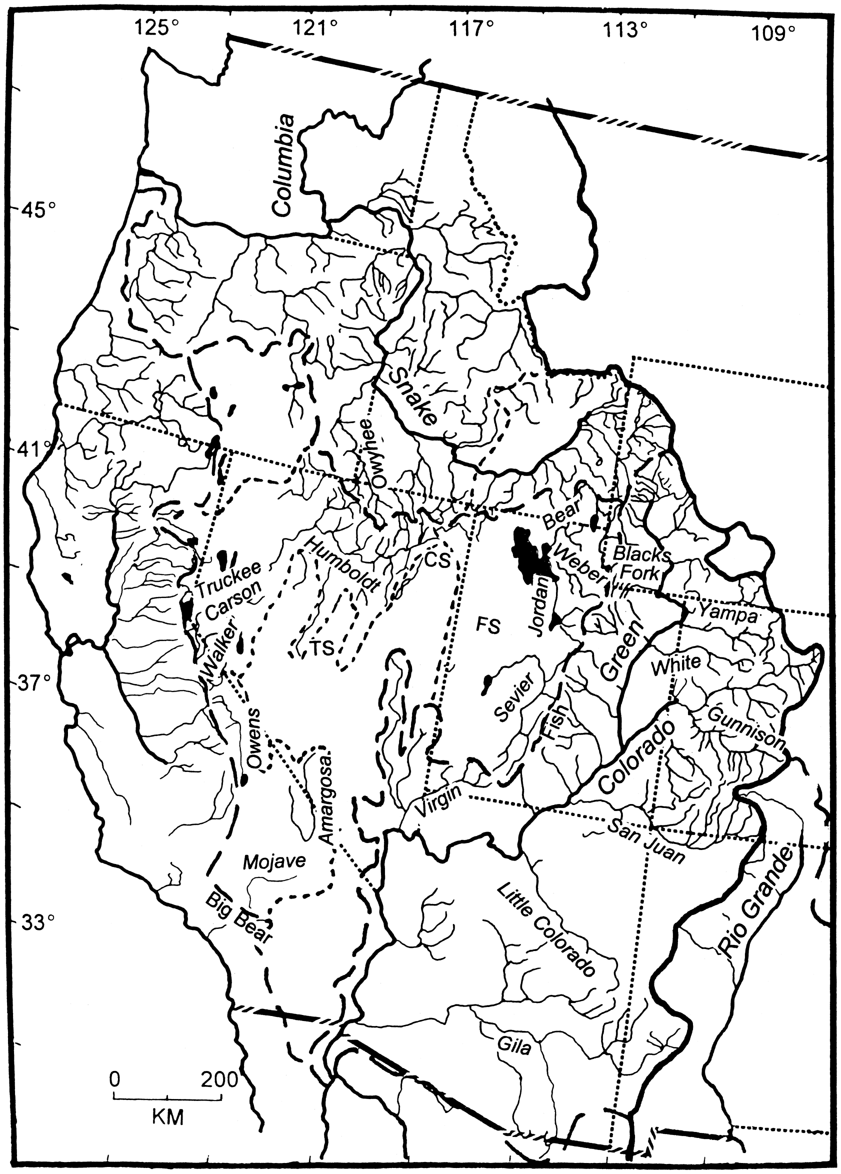

Fig. 1. Locations of aquatic sites named in the text. Springs are abbreviated as follows: Toiyabe Springs (TS), Fish Springs (FS), and Clover Springs (CS). Lakes are not labeled but are shown in solid black: Bear Lake on the Utah-Idaho border; the Great Salt Lake in northwestern Utah; Utah Lake, which is drained by the Jordan River; Sevier Lake, the terminus of the Sevier River; Fish Lake, labeled as *Fish* in southern Utah; Big Bear Lake, labeled as *Big Bear* in southern California; Owens and Walker Lakes as terminals to those drainages; Lake Tahoe on the Nevada-California border and Pyramid Lake (terminal lake) in the Truckee drainage; Eagle Lake, northwest of Pyramid Lake in California; and Malheur Lake and drainages in southeastern Oregon.

Site selection was primarily based on geographical coverage, and attempts were made to examine all aquatic habitats except high-gradient streams. I specifically tried to examine historical molluscan sites in the latter part of the survey. The rarity of mussels indicates the need for a thorough survey of rivers, but this was not attempted.

Initially only live mollusks were collected, but in later stages of the study, the living mussels were only noted, and valves alone were collected. Living *Margaritifera falcata* were

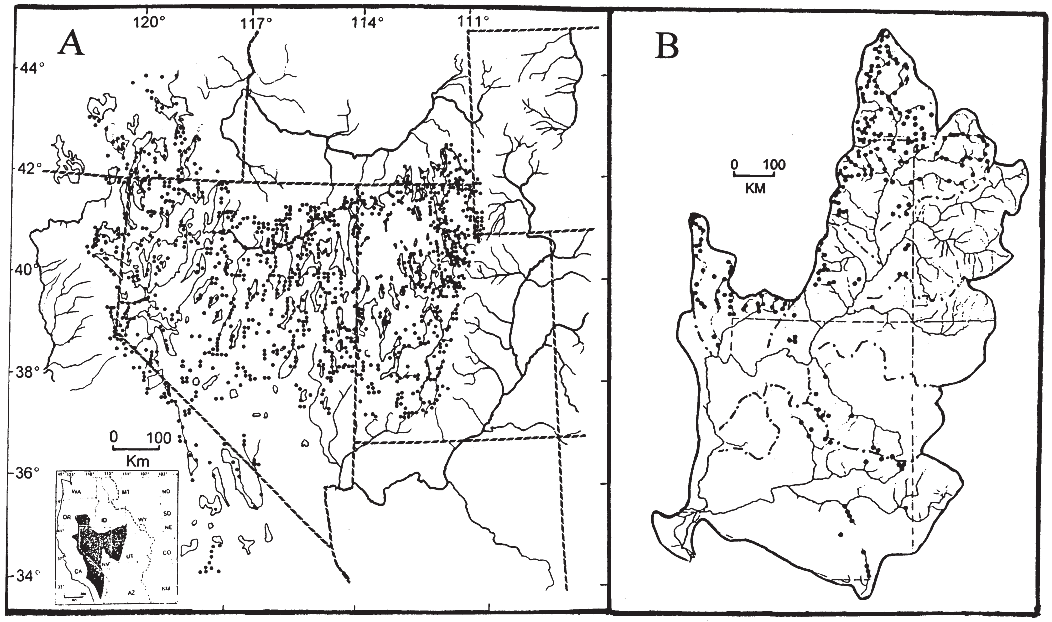

Fig. 2A. Location of surveyed sites within the Great Basin (inset). 2B. Location of surveyed sites within the Colorado River basin (between the Great Basin and the Continental Divide (dashed line) in the inset of **A**. Each dot represents 1 to 10 sites.

TABLE 1. Number of river sites surveyed in the Great Basin drainages.

Drainage	River sites	Total sites
BONNEVILLE BASIN		
Bear River	25	203
Weber River	7	101
Jordan-Provo Rivers	22	207
Sevier River	15	216
LAHONTAN BASIN		
Truckee River	20	52
Carson River	14	36
Walker River	16	45
Humboldt River	17	382
DEATH VALLEY BASIN		
Owens River	10	37
Mohave River	8	10
Amargosa River	1	38

too rare to collect at all. In addition, in the later stages, shells were collected that may represent specimens from Recent to Pliocene deposits. Voucher specimens from this study have been deposited at the Utah Museum of Natural History in Salt Lake City.

MUSEUM COLLECTIONS.—Museum acronyms follow the designations of Leviton et al. (1985): Academy of Natural Science in Philadelphia (ANSP), Barrick Museum in Las Vegas (UNLV), Brigham Young University (BYU), California Academy of Sciences (CAS), Chicago Academy of Sciences (CA), Field Museum of Natural History (FMNH), Los Angeles County Museum (LACM), Museum of Comparative Zoology (MCZ), Ohio State University Museum (OSM), Santa Barbara Museum of Natural History (SBMNH), Smithsonian Institution (USNM), University of Colorado, Boulder (UCM), University of Michigan Museum of Zoology (UMMZ), and Utah Museum of Natural History (UU). These museum collections were examined during a 10-year period beginning in 1990. The lots were examined drawer by drawer for geographical records of the Intermountain region. Selected lots were then examined in detail, and the species were compared. Appendix 1 lists the catalog numbers of all specimens examined and collected for this paper.

MORPHOMETRIC ANALYSES.—Morphometric analyses were performed on *Valvata* (shell width or diameter and height) and *Ferrissia* (length, width, and height) following Burch (1989). The ratio of apex distance from the posterior to the total length was determined with *Ferrissia.* Measurements were taken using an eyepiece with a 64-square grid calibrated at 0.1 mm. Other structural characteristics noted in *Valvata* were the apex (visible or suppressed from a lateral view), the umbilicus (narrow or wide with the umbilicus apex readily visible), whorl sutures (acute to obtuse), and the presence of collabral or axial striae with riblets ranging from close together (≥13 per mm) to well developed (≤9 per mm) on the body whorl (Clarke 1973). Characteristics noted in *Ferrissia* included the vertical slope of the 2 lateral, the anterior, and posterior sides, and the shape of the peritreme.

FOSSIL OR LIVING STATUS.—I attempted to determine if the specimens were alive at the time of collection. Preservation of soft tissue in alcohol was the best evidence of live collection. If all specimens in a given lot were white, they were considered to be semifossils (Call 1884). As noted with the Bear Lake (Utah, Idaho) fauna, fossil radiocarbon-dated shells (8000 BP) can appear fresh (Henderson 1931, Williams et al. 1962), and Oviatt (1987) found "fresh-appearing, articulated *Sphaerium* shells" dated 23,000 BP in the Old River Bed of the Sevier River drainage. Opercula in *Valvata* suggested a recent living specimen. *Ferrissia* were noted as fossils if their shells were greatly thickened and were of diminutive size (representing the uneroded apex). Literature references are noted for studies relating to paleogeography, although the specimens were often consumed for radiocarbon dating.

RESULTS

Margaritifera falcata Gould 1850
Western Pearl Shell

TAXONOMIC CONSIDERATIONS.—There are references of *Margaritifera margaritifera* occurring in the western United States (Call 1884, Walker 1910, Chamberlin and Jones 1929, Henderson 1936a), but Taylor (1988) found only *M. falcata* in the western United States and Canada, based on the cardinal teeth structure, and found an undescribed species in central Idaho (drainage distribution unknown). I adopted Taylor's (1988) taxonomic analysis, which provides geographical continuity by drainage history.

HISTORICAL DISTRIBUTION.—The distribution of *M. falcata* is included within the range of the native western salmonid fish (Scott and Crossman 1973, Minckley et al. 1986), based on the necessity of salmonid fish for glochidia survival. *Margaritifera falcata* distribution is more geographically limited than the distribution of salmonid fish; it is found in drainages from the Kern River in southern California to the coastal drainages of southeastern Alaska and east from the northern Great Basin to the Columbia-Snake River basin and the upper Missouri River (Burch 1975, Taylor 1981, 1988). There are no specimens from the Colorado River basin, although this species was thought to exist in Arizona (Walker 1910).

Within the Intermountain area, *M. falcata* has been found in the Jordan, Weber, and Bear River drainages of the eastern Bonneville Basin; in the Walker (fossil only; Call 1884), Carson, and Truckee Rivers in the western Lahontan Basin; in the Humboldt River of the northern Lahontan Basin; in the Alvord Basin of Nevada (fossil dated 7000 to 9000 BP in an early American midden; Parmalee 1988); and in the Malheur Lake drainage of Oregon (Fig. 3). Although Call (1884) mentioned semifossil or post-Bonneville presence at numerous locations in the Sevier Desert, neither his Table III ("Fossil Bonneville Mollusca") nor his Table V ("Distribution of Freshwater Shells") lists any fossil or semifossil specimens from the Bonneville Basin. There are no specimens of *Margaritifera* from the Sevier River drainage, the Sevier Desert, or the western Bonneville Basin, contradicting Call's (1884) statement that they are "common throughout the Basin" (see also Roscoe 1963, 1964, Hunt 1981).

There is a possibility that *M. falcata* was translocated by the movement of sport fish, such as rainbow trout from the Pacific Coast, beginning in 1874 (Scott and Crossman 1973). Rainbow trout arrived in Utah in 1883 (Sigler 1953) and were found in Utah Lake and the Provo River by 1894 (Heckmann et al. 1981). The first trout hatchery in Utah was built in 1910, and by 1930 the Midway (Provo River drainage) and Kamas (Weber River drainage) hatcheries were built. To assess the possibility of *M. falcata* introductions, 2 criteria were used: (1) museum specimens were collected before 1890 and (2) individual specimens >55 mm were assumed to be at least 15 years old. Based on these 2 criteria, specimens collected between 1880 and 1890 near Salt Lake City, the Humboldt River, and the Truckee River are considered to be native. However, there is some uncertainty whether the specimens found in the Weber and Provo River drainages are native; all are dated largely after fish hatchery construction. Specimens collected after construction of the Kamas fish hatchery include those from Beaver Creek (the Weber River tributary that passes the hatchery) in 1947 (FMNH 111628, 179817), those from Kamas in 1939 (Woolstenhulme 1942), and those from the Kamas fish hatchery itself in 1981 (OSM 52426). With the exception of the specimen from East Canyon (UCM 10311) and the Beaver Creek drainages, there is no record of *M. falcata* in the Weber River. The historical distribution may have been confined to streams west of the northern Wasatch Mountains and the Bear River in the Bonneville Basin and not in the Provo and Weber Rivers. *Margaritifera* archeological artifacts were identified from the Bear River and from Blacks Fork in the Green River drainage (Warren 2000), suggesting, at least in the case of Blacks Fork, that early Americans may have been responsible for transporting some shells.

PRESENT DISTRIBUTION.—I found *M. falcata* in the upper Snake River in Wyoming and Idaho, the upper Bear River in Wyoming, and the Malheur Basin in Oregon. I did not find specimens at 155 sites in Utah, Nevada, and eastern California (Fig. 3).

NATURAL HISTORY.—Known fish hosts for the parasitic mussel glochidia were cutthroat trout fingerlings in Pole Creek (upper Snake River, Wyoming) and introduced brown and rainbow trout in the Truckee River, but not 8 other fish species in those 2 drainages (Murphy 1942, Bangham 1951). In the Truckee River, glochidia were released from mid-June to early July, when water temperatures increased from 10° to 15°C (Murphy 1942). Of note, both cutthroat and rainbow trout spring migrations and spawning occur at similar water temperatures (Scott and Crossman 1973, Sigler et al. 1983). Historically, young adult cutthroat trout migrated up the Truckee River to Lake Tahoe in May, June (mostly, corresponding to glochidia release), and July, whereas the old adults had a fall migration that ended near Reno (Snyder 1917, La Rivers 1994). Glochidia remained on their host for 36 days (Murphy 1942). The Pole Creek population is unique in that after death the calciferous shell disappears before the proteinaceous material.

Mussel valves reached a length of 92 mm in the Truckee River (Murphy 1942) and 84 mm in the Bear River (USNM 635195); both are much smaller than the 150 mm size in the Columbia River drainage (Roscoe and Redelings 1964, Vannote and Minshall 1982). The Bear River population profile (USNM 635195: $N = 89$; range, 40–84 mm; mode, 73 mm) suggests a younger mobile population (20 to 40 years) that could survive limited sediment deposition, in contrast to the more stable and immobile populations in large block boulder reaches of the river, which contain individuals as old as 100 years (Vannote and Minshall 1982).

CONSERVATION CONSIDERATIONS.—In the early 1940s the Truckee River contained an estimated 20,000 *M. falcata* more than 40 mm in length in one 0.8-km stretch of river, and another population occurred 16 km upstream (Murphy 1942). Six specimens were collected in 1965 (CAS). I found only 1 shell fragment in this river. *Margaritifera falcata* was once common in the Salt Lake City region of the Bonneville Basin (Call 1884) but was rare in the Humboldt River in Nevada (Call 1884, Walker 1916). In 1956 one hundred *M. falcata* were collected in the Bear River in Wyoming, while in 1998 only 5 live specimens (lengths: 43, 60, 65, 70, 83 mm) and 8 empty bivalve shells were found at this same site. A few thousand individuals per 140 m^2 were observed in Washington State (Roscoe and Redelings 1964), suggesting that the current numbers represent depleted populations.

Many factors may have contributed to *M. falcata* decline. The spawning migrations of Pyramid Lake's cutthroat trout were destroyed in 1905 when the Derby Dam was completed on the Truckee River. In Utah's Jordan River drainage, populations could have been extirpated in 1948 by the destruction of Hot Springs Lake, a 3.5-km^2 lake that may once have contained populations of cutthroat trout that bred in the streams around Salt Lake City. Cutthroat trout native to Utah Lake were extirpated by 1936 (Radant and Sakaguchi 1980) by overfishing and spawning habitat destruction, which terminated spawning migrations up the Provo River (Heckmann et al. 1981).

Other factors contributing to the decline of *M. falcata* include human alterations of Intermountain rivers (Vannote and Minshall 1982), such as dredging and channeling rivers for

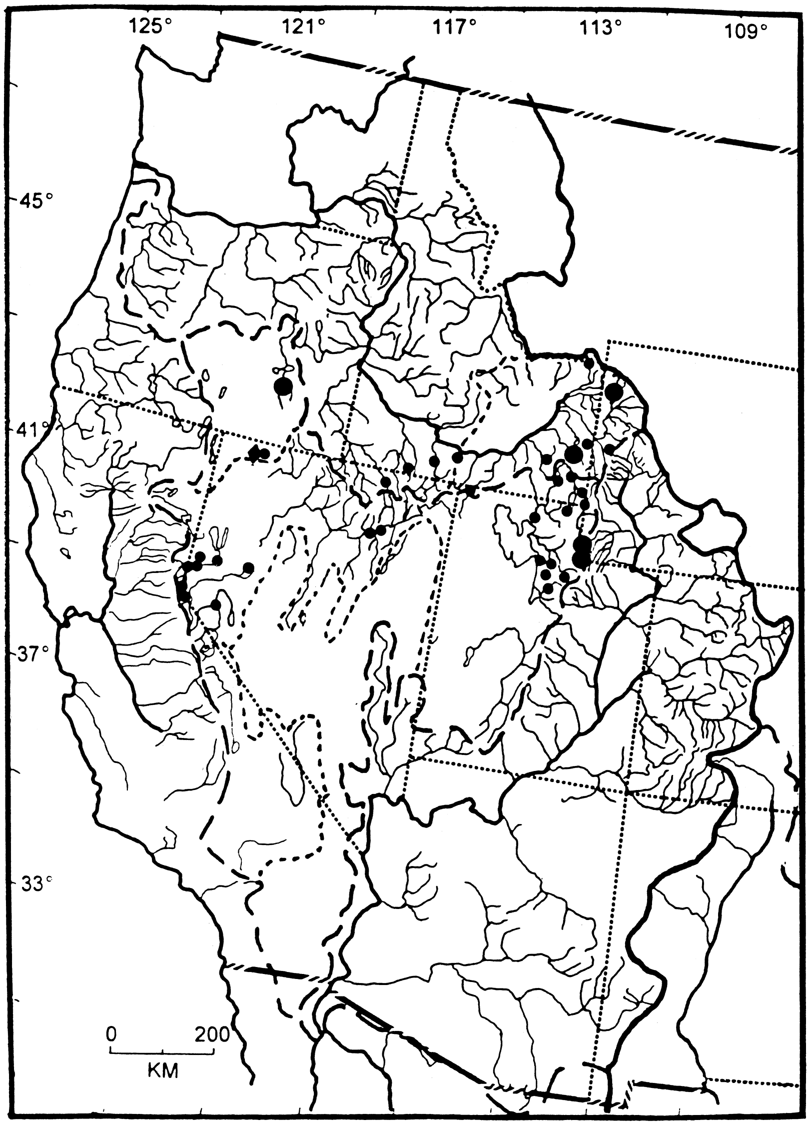

Fig. 3. *Margaritifera falcata* distribution in the Intermountain region. Large dots represent the current distribution, small dots the historical distribution, diamonds the fossil or semifossil distribution (1 site in northwestern Nevada). The historical locations in southwestern Idaho (4 sites) and the uppermost location on the Snake River (1 site) in Idaho were not examined in this study.

water diversion and flood control; dam construction (16 hydroelectric power plants and 22 dams and reservoirs exist in the Bear River drainage basin); the use of river corridors as highway corridors; and declining water quality associated with reservoirs, urban areas, and agricultural practices (cattle grazing, irrigation return flows). On this last point, it may be significant that the mortality of *M. margaritifera* in Europe was correlated with an increased nitrate concentration (Bauer 1988).

Anodonta californiensis Lea 1852
California Floater

TAXONOMIC CONSIDERATIONS.—Lea (1839) described 3 western *Anodonta*: *A. nuttalliana* (p. 77), *A. wahlamatensis* (p. 78), and *A. oregonensis*

(p. 80) from "Wahlamat, near the junction with the Columbia river." This location is most likely the Willamette River. In describing *A. californiensis* from Rio Colorado, California, Lea (1852) stated: "This species is more nearly allied, indeed it is closely allied to *An. Nuttalliana,* which I described many years since, and which was brought by Mr. Nuttall from Wahlamat river, in Oregon." Henderson (1924, 1936a), Chamberlin and Jones (1929), and Taylor (1981, 1985) recognized these 4 species, whereas others have consolidated these species to as few as 1 (Call 1884, Burch 1975, Clarke 1981). *Anodonta dejecta* Lewis 1875 in Arizona was synonymized with *A. californiensis* (Bequaert and Miller 1973).

For this paper I kept with the recent literature of the Intermountain region, which may involve considerable conjecture, and identified *A. californiensis* by its moderate fin. I found no high-fin *Anodonta* (*A. nuttalliana or A. wahlamatensis*) in this study. *Anodonta oregonensis* was identified in literature and museum collections in the early 1900s as existing in the Sevier and Humboldt Rivers. Now *A. californiensis* is identified in other literature and newer museum collections, with some museums leaving the western *Anodonta* identified only to the genus. If a synonymy in this group occurs, nomenclature priority will require revising all collections, possibly following Call's (1884) view that these are *A. nuttalliana*.

HISTORICAL DISTRIBUTION.—Western *Anodonta* extend from Alaska (*A. beringiana* Middendorff 1851 and *A. oregonensis*) south to Mexico (*A. californiensis* and *A. dejecta*) and as far east as Utah (*A. nuttalliana, A. oregonensis,* and *A. californiensis*), with *A. wahlametensis* found in 2 separate populations in Washington and California (Taylor 1966, 1981, 1985, Burch 1975, Clarke 1981, Warren and Harington 2000).

Pleistocene *A. californiensis* occurred in Arizona and southern Nevada tributaries in the lower Colorado River drainage (Bequaert and Miller 1973, Quade et al. 1995) and in the Salton Trough, the latter basin representing an altered flow of the Colorado River. The Pleistocene uplift of the San Bernardino Mountains and drainage transfer could have affected the distribution of this species in southern California (Taylor 1985). A paleodrainage outflow of the Colorado River during the late Miocene has been located in the Los Angeles basin (Howard 1996), but the Colorado River basin and the Death Valley basin have been hydrologically separated for at least 4 million years (Brown and Rosen 1995).

Anodonta californiensis was found in 1934 living in the Death Valley basin in the Mojave River (LACM 104571, 104581). Pleistocene and Holocene fossils exist from the Owens Lake drainage (SBMNH 10540; Firby et al. 1997) and the Mojave River drainage (Wells et al. 1987) but not the Amargosa River drainage.

In addition, *A. californiensis* has not penetrated the interior basins of Nevada, although many of these hydrologically isolated basins contain native cyprinid fishes. *Anodonta californiensis* has not been noted in the upper Snake River of Wyoming (Beetle 1989) but is known downstream in Idaho. Pleistocene records occur in the Bonneville Basin (Eardley and Gvosdetsky 1960, Currey et al. 1983, Oviatt et al. 1999) and in the Lahontan Basin (Call 1884, Benson et al. 1992).

The populations in the Little Colorado River drainage may have been transported by humans, by stream capture, or, most unlikely, by glochid-parasitized fish migrating through the Grand Canyon. The Colorado River drainage population (Huntington Creek) in Utah suggests human transport (Figs. 4–5). This location consists of a 20-m-long fishing hole downstream from a high-gradient stream and upstream from the San Rafael River, a river of high sediment, high alkalinity, and frequent flooding. This population is totally isolated, except for human intervention. These 2 examples are the only *Anodonta* populations in the entire Colorado River drainage upstream from Las Vegas, Nevada.

CURRENT DISTRIBUTION.—I found *A. californiensis* widely distributed as living specimens and as shells in the Humboldt River drainage (Lahontan Basin) in northern Nevada; in the Bonneville Basin in Utah, Nevada, and Wyoming; and in the Malheur and Warner Basins in Oregon (Fig. 4).

NATURAL HISTORY.—The fish host for this species is listed as an introduced mosquito fish (Hoggarth 1992). Utah chub is the only fish in Redden Spring in western Utah (Workman et al. 1979), making this fish a native host. The list of hosts for *A. californiensis* glochids certainly will be expanded by further studies. Adults were mature with 4 shell annuli age in

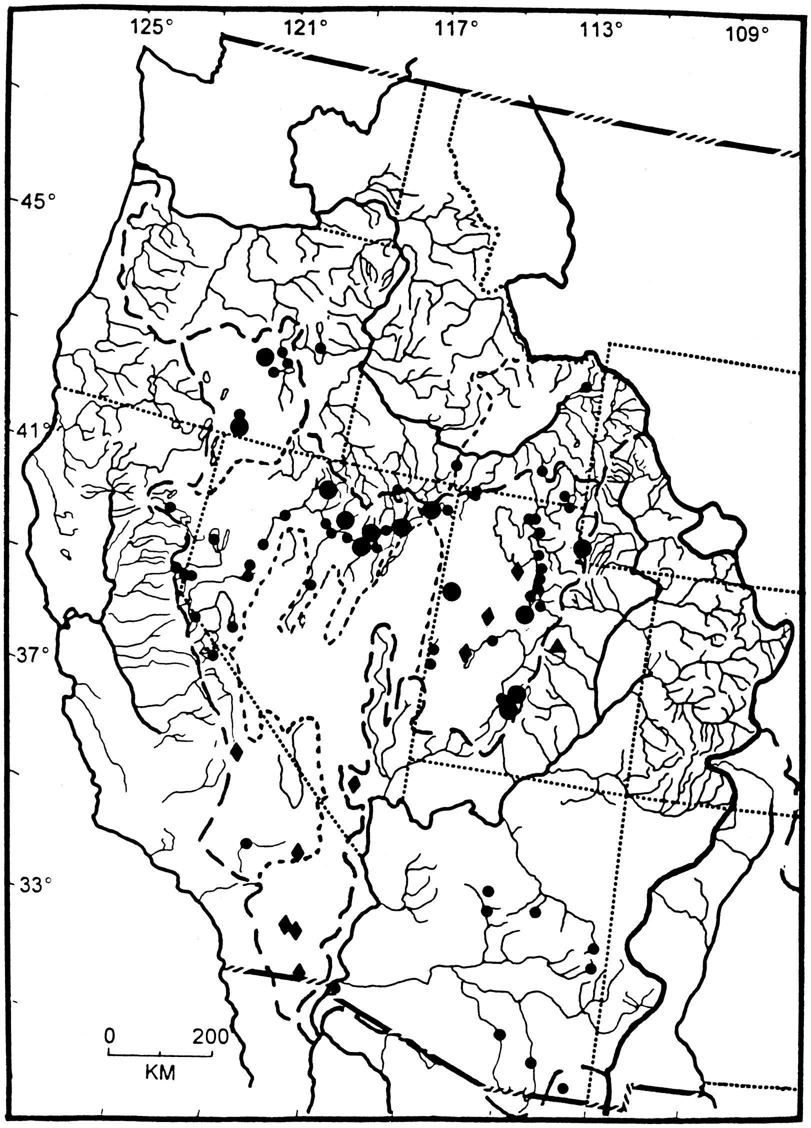

Fig. 4. *Anodonta californiensis* distribution in the Intermountain region. Large dots, small dots, and diamonds are marked as described in Figure 3. A triangle (1 site) indicates specimens resulting from human transport. The 5 historical sites in the Snake River drainage of Idaho, Nevada, and Oregon and the 9 historical sites in Arizona were incompletely surveyed.

A. californiensis or with 8 shell annuli in *A. wahlamatensis* (Heard 1975).

CONSERVATION CONSIDERATIONS.—It is difficult to assess the status of *A. californiensis* in the Intermountain region largely because it is still widely distributed, but it is very scarce. It has most likely been extirpated from the Colorado River basin in Arizona and from the Death Valley basin (Mojave River), Los Angeles Basin, and Central Valley in California (Bequaert and Miller 1973, Taylor 1981), areas in which intensive agricultural and urban development have occurred. A midden associated with a Chinese community in Tucson, Arizona, showed *Anodonta* was common from 1880 to 1885 but had died out by 1915 (Bequaert and Miller

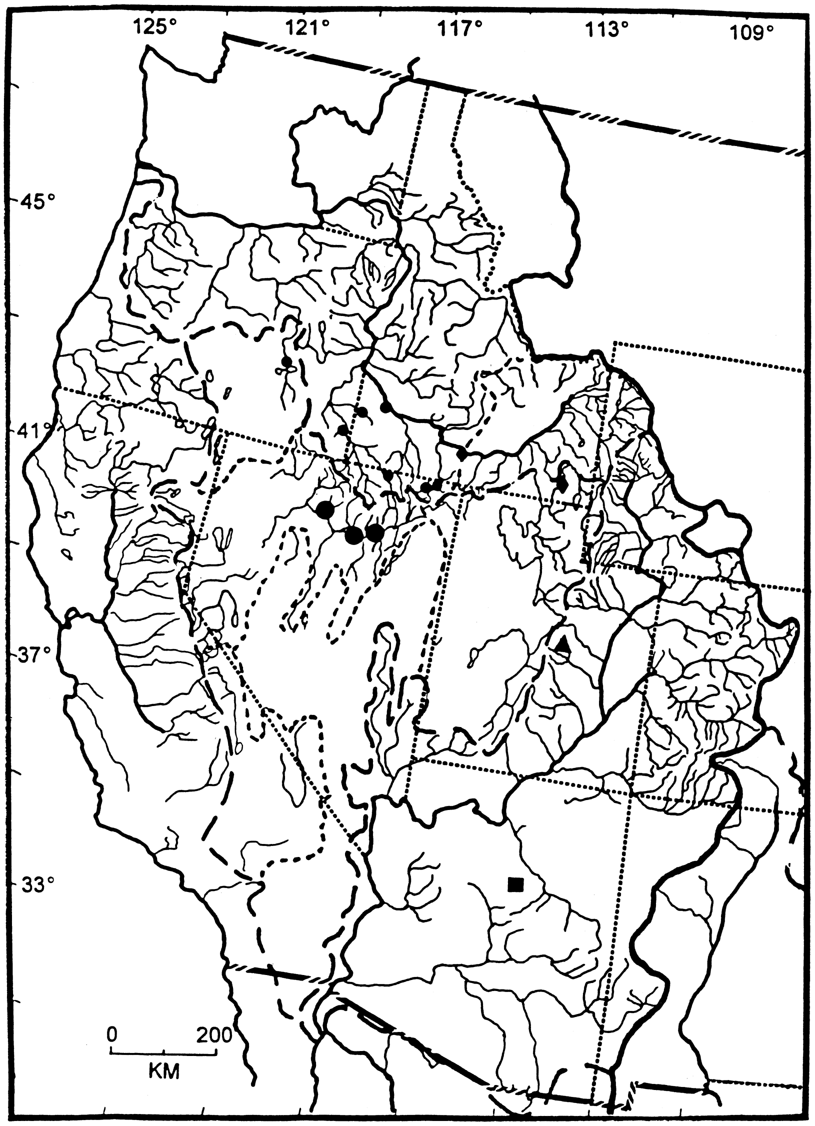

Fig. 5. Distribution of *Gonidea angulata* (marked as in Fig. 3). The fossil record in southeastern Idaho and the historical sites in the Snake River drainages were not examined. *Pyganodon grandis* (square), *Anodonta californiensis* (triangle), and the current distribution of *G. angulata* (large dots on the Humboldt River in Nevada) resulted from human transport.

1973). Henderson (1931), citing Tanner's dredging efforts, noted that *A. californiensis* was the only living mollusk in Utah Lake. Utah Lake was greatly reduced by drought in 1933, and by 1977 most fish in the lake were introduced species.

Anodonta californiensis was abundant in the Humboldt River near Carlin in 1912 and still occurred in 1939 (Walker 1916, Jones 1940), but it was not found in this same region in recent surveys (D. McGuire, report prepared for Barrick Gold Corporation, Elko, Nevada, 1995). McGuire (1995 report) found 3 live mussels and 25 empty shells in a 10-hour search of Rock Creek (Humboldt River drainage) in a 5-km stream survey. Three locations in the current survey contained at least 6 *A. californiensis,* whereas the 12 other locations contained 1 or, rarely, 2 specimens.

Anodonta californiensis can live in reservoirs if the reservoirs are maintained at stable levels during a series of high-water years and can reach high numbers in these situations. However, most reservoirs are actively managed with extensive drawdowns, and the mussels are extirpated during these low levels. Purges from reservoirs have dislocated and destroyed *A. californiensis* in the Bear River. The habitats which *A. californiensis* now occupy are streams and springs that (1) are not actively managed for sport fish, (2) are in the higher reaches of drainage basins where better water quality occurs, and (3) are in regions with low human population densities.

Pyganodon grandis Say 1829
Giant Floater

This eastern species, also known as *Anodonta grandis* and *Anodonta corpulenta* (see Hoeh 1990), was found in Arizona between 1951 and 1969 (Fig. 5) as a result of human transport via fish (Bequaert and Miller 1973, Heard 1975). The species was still present in upper Lake Mary in 2002 (this study).

Gonidea angulata Lea 1839
Western Ridge Mussel

DISTRIBUTION.—*Gonidea angulata* is found from southern British Columbia to the Los Angeles Basin in southern California, east to Idaho and northern Nevada (Henderson 1936a, Taylor 1981). A fossil found in Lake Thatcher (Taylor 1985) is the only record in the Snake River drainage above Shoshone Falls. Taylor (1981) noted that *G. angulata* has probably been extirpated from the Central Valley to southern California by agricultural and urban developments.

I found *G. angulata* in abundance in the Humboldt River in the same area that contained only *Anodonta californiensis* in 1912 and 1939 (Walker 1916, Jones 1940; Fig. 5), suggesting recent transport by humans. The mobile *G. angulata* is well adapted to survive in streams with high sediment deposits and can reach high densities on gravel and stabilized sandbars (Vannote and Minshall 1982). Small mussels are found downstream from the large adult population upstream of Carlin, suggesting that the *G. angulata* population is expanding. It is not known what effect this introduction will have on the rare native *A. californiensis.*

Western Valvata

TAXONOMIC CONSIDERATIONS.—The following prosobranch gastropods have been found in western North America: *Valvata humeralis* Say 1829 (see Say 1840), *V. lewisi* Currier 1868, *V. mergella* Westerlund 1883, *V. sincera* Say 1824, *V. utahensis* Call 1884, and *V. virens* Tryon 1863. Only *V. utahensis* has spiral angulations (Walker 1902, Heard *in* Burch 1989). *Valvata lewisi* has been suggested to be a synonym of *V. sincera* (Clarke 1973, Beetle 1989), and Hannibal (1910) suggested that *V. lewisi* and *V. sincera* west of the Rocky Mountains would possibly be *V. humeralis.*

Valvata were compared with the following additional lots: *V. tricarinata* Say 1817 from Wisconsin (UU 4108) and New York (UU 3670); *V. piscinalis* Müller 1774 from the Netherlands (UU 3869); *V. humeralis* holotype from Mexico (ANSP 58064); *V. virens* from Clear Lake, California (UMMZ 143591; ANSP 371413 paralectotype, 365358); *V. mergella* from Alaska (UU 13037); and *V. sincera* from Michigan (MCZ 30759; FMNH 114683, 104897, 105173; UMMZ 31651), Illinois (FMNH 76430 listed as *V. humeralis*), and Great Slave Lake, Northwest Territory (UU 14237).

Valvata virens Tryon 1863
Emerald Valvata

Valvata virens is a distinctively globose species, with a pyramid shape and an acute apex that is clearly visible from all lateral views. Some specimens have a worn apex, but the apex is still very conspicuous. It was found only near Watsonville and Clear Lake in California (Taylor 1981; Fig. 7).

Valvata utahensis Call 1884
Desert Valvata

Valvata utahensis is a polymorphic species exhibiting a wide range of forms: (1) conspicuously bicarinate (dorsal and ventral; *V. utahensis* morph *horatii* Baily and Baily 1951, see Heard *in* Burch 1989) in Bear Lake; (2) conspicuously dorsal carinated with ventral angulations, (3) whorls with a flat, angular appearance, and (4) dorsal carina and angulation absent, whorls rounded but with ventral angulation. Specimens that lack such ventral angulation would be considered globose *V. californica* (see below).

Valvata humeralis Say 1829
Glossy Valvata

Only 1 specimen, representing the holotype of *V. humeralis,* occurred in the collections. This shell was described as "subglobose, depressed: *spire* convex, not prominent: *whirls* three and a half, with the shoulder depressed, plane; wrinkled across, or rather with slightly raised lines: *aperture* appressed to the penultimate whirl, but not interrupted by it: *umbilicus* rather large" (Say 1840). It was distinguished from *V. sincera* by a planar surface near the suture. No specimens from the western United States matched this holotype, suggesting that *V. humeralis* may be confined to Mexico.

Valvata californica Pilsbry 1908,
new combination

"The shell is much more depressed than *Valvata humeralis*, the last whorl descending less; whorls convex below the suture, not flattened there as *V. humeralis* is" (Pilsbry 1908). Appendix 2 shows a continuum between globose (width/height = 1.1) and depressed shells (width/height = 1.9) of some lots of western *Valvata.* Shell shape is site specific and does not have any predictable geographic distribution. Furthermore, the Big Bear Lake, California, population is average (width/height = 1.5). I suggest that the basis for the subspecific description is not valid. Since the western form does not display the flattened whorls of the *V. humeralis* holotype, I recommend the following changes in the name: *Valvata californica* Pilsbry 1908, new combination (glossy valvata); type locality, Big Bear Lake, California; synonyms (only in the United States and Canada), *V. humeralis, V. humeralis californica.* To prevent confusion hereafter, I will refer to this western United States *Valvata* as *V. californica* since there is no basis for the subspecies taxonomy and its shell is structurally different from *V. humeralis.*

The globose form of *V. californica* (width/height = 1.1–1.2) occurs with *V. utahensis,* and it may be conspecific with *V. utahensis. Valvata californica* shell sculptures were smooth (striae obsolete) or with fine collabral striae or depressed riblets close together (≥13 mm on the body whorl; Clarke 1973). The Gerlach population (UMMZ 237249) was exceptional, containing 10–12 collabral striae · mm^{-1}. This specimen contained a depressed apical whorl, distinguishing it from *V. virens.*

Hannibal (1910) suggested that *V. lewisi* and *V. sincera* west of the Rocky Mountains might be *V. californica.* The distinguishing feature of *V. californica* in this case is the lack of, or very depressed, collabral striae. The Great Slave Lake population had the same shape (Appendix 2) and similar body pigment as the Bluff Lake population, but the former had lamellate "blade-like" striae, clearly visible at 13X (see *V. sincera helicoidea* Dall 1905 and *V. s. sincera* Say 1824 *in* Clarke 1973). The type specimen of *V. sincera* is lost (Walker 1906), but the populations of *V. sincera* that were examined generally had prominent and thickened ribs and lamellate striae. A few individuals from these lots had more depressed riblets, approaching the shell of *V. californica*. The general shapes (globose to planar) of *V. sincera* and *V. californica* were similar when populations with the same width-height ratio were compared. The aperture of both *V. sincera* and *V. californica* could be round, or the internal side could be oval. *Valvata sincera* in Colorado (Wu 1989) is considered by these analyses to be *V. californica.* One lot (FMNH 105173) consisted of specimens with depressed riblets, with apex totally depressed below the first whorl (different from *V. californica*), and with a dorsally flat body whorl (2 individuals). The holotype *V. humeralis* has the body whorl rounded, with dorsally flattened interior whorls.

One population (Taylor Canyon, Owyhee-Snake River drainage, Nevada) differed from *V. californica* by its small size (2.6 mm width), its totally black body, and its having fewer than 3 whorls. Its planar shape (width/heigth = 1.6) and lack of collabral striae were similar to *V. californica.*

DISTRIBUTION.—*Valvata californica* is a western species (Fig. 6) with unknown northern or eastern boundaries (Taylor 1981) or southern boundaries in Mexico. This species occupies the Colorado River, the upper Rio Grande, the Columbia-Snake River, the California Pacific Coast drainages, and the Great Basin (Fig. 6). Living *V. utahensis* are known only from the Snake River drainage (Fig. 7), and the species is listed as endangered in the United States. *Valvata utahensis* have been found in Idaho and Utah (Taylor 1985). *Valvata virens* have been reported from 2 locations in California (Taylor 1981; Fig. 7).

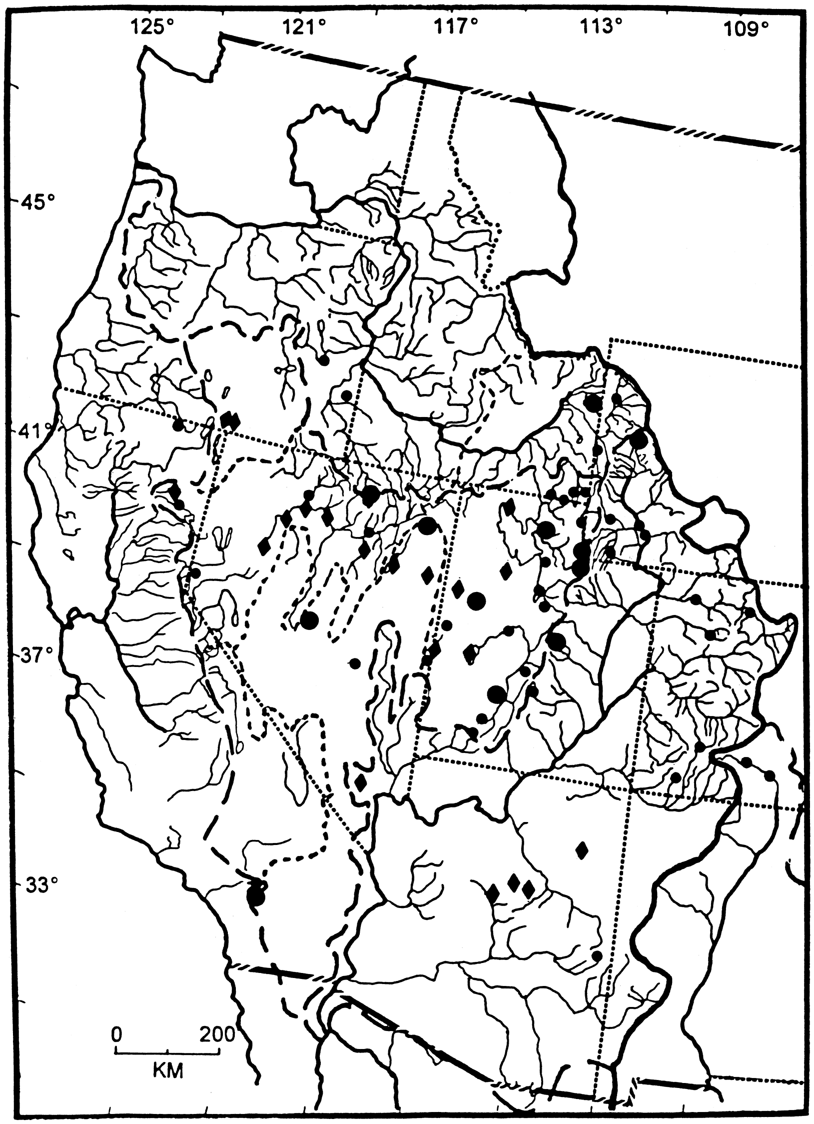

Fig. 6. *Valvata californica* distribution (marked as in Fig. 3). Historical locations in southern Colorado, Arizona, and eastern Oregon were not examined.

Fossil *V. californica* are widely distributed in western North America from the Miocene and Pliocene, with Pleistocene records often indistinguishable from shells of very recent and living specimens (Eardley and Gvosdetsky 1960, Trimble and Carr 1961, Williams et al. 1962, Roscoe 1963, Taylor 1985, Quade 1986, Oviatt et al. 1987, Taylor and Bright 1987, Quade and Pratt 1989, Quade et al. 1995, Bourchard et al. 1998). These studies show that *V. californica* preceded *V. utahensis* in the Bonneville Basin (Eardley and Gvosdetsky 1960), and the ranges of *V. utahensis* and *V. californica* contracted during the Holocene. The fossil shells of *V. utahensis* (UU 14037) are the first records from the Humboldt River, altering the distribution pattern shown by Taylor (1985). Fossil shells of *V. utahensis* and *V. californica* (dated 7000 BP) were found at an archeological site in northern Mills Valley in the Sevier River drainage (T. Sharp and SWCA Environmental Consultants, personal communication, 2003),

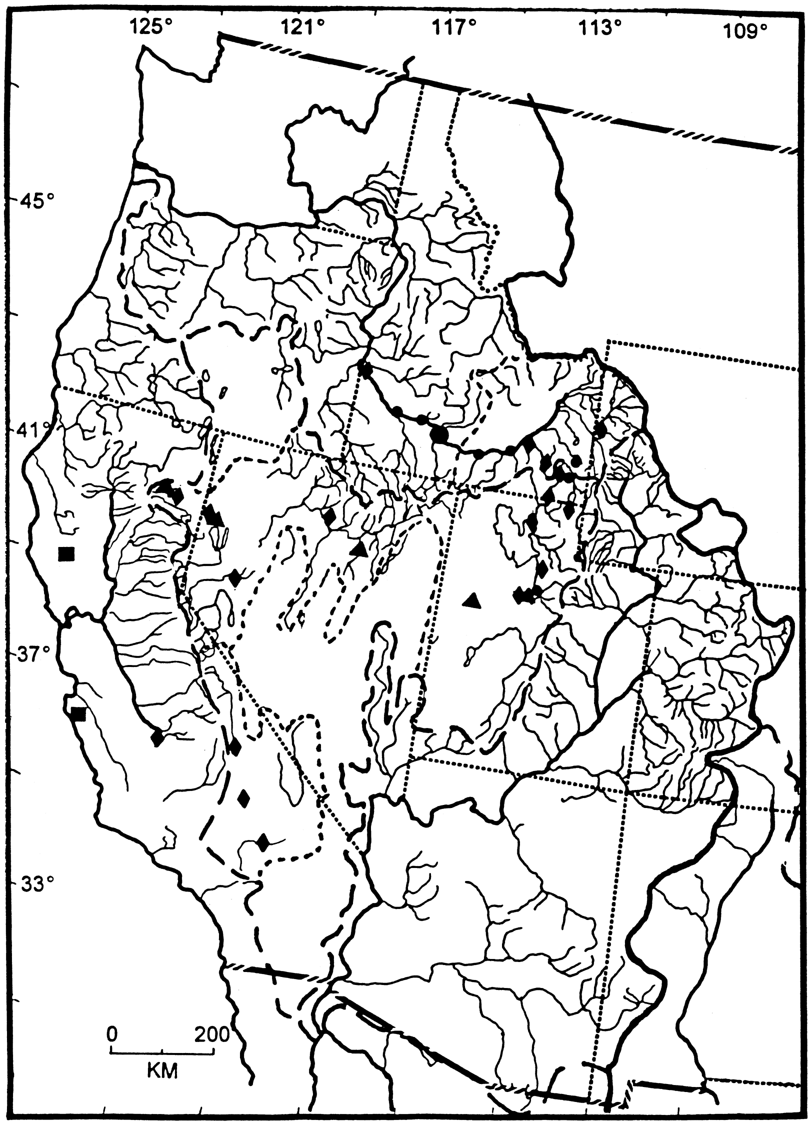

Fig. 7. Distribution of *Valvata utahensis* (marked as in Fig. 3) with the globose forms of *V. californica* shown as triangles. Historical locations of *V. virens* in California are shown as squares.

expanding the range of *V. utahensis* in the Bonneville Basin (not shown in Figs. 6–7). Other fossil *Valvata* species were found in western North America (Yen 1946, Taylor 1966, 1985, Bequaert and Miller 1973, Good 1987).

NATURAL HISTORY.—*Valvata* occupy habitats ranging from large lakes to small ponds, marshes, streams, and springs. The limited distribution of *V. virens* (1 lake and 1 pond; Taylor 1981) and *V. utahensis,* along with the dispersed distribution of *V. californica,* would suggest that dispersal of these species has not occurred during the Quaternary (Taylor and Bright 1987, Hovingh 1993). *Valvata californica* is found in glacier-associated drumlin ponds in the Wasatch Plateau (central Utah) and northwest of Pinedale, Wyoming. These habitats freeze solid in winter, are isolated from each other, and have no drainage.

Four isolated spring complexes in the study area (Fish Springs in Utah and Clover, Tonapah, and Taylor Canyon in Nevada) contained *V.*

californica, whereas the hydrobiid gastropods *Pyrgulopsis gibba* Hershler 1995 and *P. kolobensis* Taylor 1987 are widely distributed in many springs and basins (Hershler 1998). Both *Valvata* and *Pyrgulopsis* occupy similar habitats and were captured at the same time in Fish Springs, whereas *Valvata* in the Tonapah Basin occupied the spring head while *Pyrgulopsis* occupied the outflows. *Valvata californica* and *V. utahensis* coexisted in Utah and Bear Lakes and in Mills Valley. *Valvata californica* and *V. virens* coexisted in Clear Lake, but the extent of habitat overlap is unknown.

CONSERVATION CONSIDERATIONS.—Assessment of the status of *Valvata* in the Intermountain region requires separation of shells from palaeo-populations and recent living populations. *Valvata utahensis* was extirpated from Utah Lake; Call (1884) was the only person to collect shells of this species with opercula (Chamberlin and Jones 1929). From 1903 to 1956 *Valvata californica* from Big Bear Lake in California was collected in abundance as shells with opercula, but in 1995 no shells were found. In 1929 Fish Lake in Utah contained *V. californica* (Chamberlin and Berry 1930), but it is absent there today. *Valvata virens* was extirpated in California (Taylor 1981). Both Big Bear Lake, California (Automobile Club of Southern California 1928), and Fish Lake, Utah, have the same physical appearance today as in the early 1930s, but both are currently managed for revenue-enhancing, nonnative sport fish and water supplies. Fish in Big Bear Lake were chemically extirpated in the 1960s, and pumpkinseed sunfish were introduced (M. Giusti, California Fish and Game communications, 1999). Sunfish are predators of mollusks (Scott and Crossman 1973, Carlander 1977, Stein et al. 1984). Two Colorado lakes formerly containing *Valvata* are now managed for sport fish, including introduced crayfish. *Valvata californica* co-occur with native fish in the Fish Springs, Clover, and Tonapah Basins. They have disappeared in waters that are managed for nonnative sport fish, although they occurred in lakes (Utah, Fish, and Clear Lakes) with native fish communities.

Ferrissia rivularis Say 1817
Creeping Ancylid

TAXONOMIC CONSIDERATIONS.—*Ferrissia* is a complex of freshwater limpets consisting of *F. fragilis* Tryon 1863 (with forms *hendersoni*, *shimekii*, and *isabellae*), *F. parallelus* Haldeman 1841, *F. rivularis* Say 1817, *F. walkeri* Pilsbry and Ferriss 1906, and *F. mcneilli* Walker 1925 (Basch 1963). In the eastern United States and Canada, *F. parallelus*, *F. fragilis*, and *F. walkeri* are identified as living in standing or slow-moving waters, while *F. rivularis* and *F. mcneilli* (the latter found only in Alabama) are living in flowing water (Basch 1963, Clarke 1973).

Basch (1963) noted much confusion in *Ferrissia* taxonomy, and museum collections reflect this confusion when *F. fragilis* and *F. rivularis* have been cataloged from the same locations: Lily Lake, Nevada County, California (CAS 28161, 52108; SBMNH 117947); Utah Lake, Utah (MCZ 4578, 243275; UCM 7410; ANSP 144620; UMMZ 219474); Chiricahua Mountains, Arizona (CAS 21093, 52105); and Sabino Canyon, Arizona (ANSP 115256–59, 328339; FMNH 58051, 64331). Wu (1989) recorded *F. rivularis* and *F. walkeri* in the same Yampa River sites in Colorado. Species diversity of the western *Ferrissia* may account for the above taxonomic confusion.

Intermountain collections were compared with type specimens of *F. rivularis* ANSP 21982, *F. fragilis* ANSP 22011, *F. parallelus* ANSP 21996, and *F. walkeri* ANSP 87479. In addition, comparisons were made with FMNH 64331 (Arizona), UU 11697 (Ohio), UCM 27178, 29943, 29952 (Colorado), UU 14239 (Queen Charlotte Islands, B.C.), UU 10114 (Australia), and *Ancylus fluviatilus* Müller 1774 from Belgium (UU 12218) and England (UU 3861).

There were many variations in shape of the individual shells examined in this study. The peritreme varied from near parallel to straight on the right side and oval on the left side, to oval on both sides, to greatly expanded in the anterior, and from narrow to wide. The lateral sides varied from acute concave on both sides (3 Bear River specimens, UMMZ) to straight on both sides, to straight on the left side and concave on the right side, to convex on the left side and concave on the right side. The morphometric range did not change much, and the sample means were within the standard deviation of most lots (Appendix 3). Shells were depressed (height/length = 0.32) in samples from Utah Lake (UU 13986), the San Pedro River (UU 14230), and Queen Charlotte Islands (UU 14239); these samples were collected from plants. Populations from Sabina

Canyon (FMNH 64331) and the San Pedro River (UU 14230) had an apex-length ratio < 0.3 and distinctly to the far right of center, characteristics suggesting *F. walkeri* except for their lotic habitat. No populations contained the apex in midline, and only the San Pedro population had a width-length ratio < 0.55, thus excluding *F. parallelus.* All populations had a length > 3.5 mm except the Gila River populations, thus excluding *F. fragilis.*

I consider all Intermountain ancylids to be *F. rivularis,* with shells having diverse structural features, as noted by Basch (1963; Appendix 3). The exception may be the Gila River populations that meet the criteria of *F. walkeri.* Further studies of the Gila River may determine if 2 populations there are site specific or drainage specific. All Intermountain *Ferrissia* were found in lotic habitats except the Utah Lake population. However, habitat criteria for ancylid identification may be taxonomically perilous, as aquatic habitats are more diverse than just streams and lakes. Lakes may have high turnover of volume related to stream input, and these habitats may be comparable to a pool in a stream drainage. Also, anyclids occurring at the interface of substrate could have similar habitats in flowing water and the wave zone in lakes.

DISTRIBUTION.—*Ferrissia fragilis* and *F. parallelus* are found in western North America (Basch 1963, Clarke 1981, Taylor 1981, Burch 1989, Wu 1989). *Ferrissia walkeri* is listed for 3 widely disjunct populations: Michigan, Arkansas, and the southern tip of Baja California, Mexico (Basch 1963). *Ferrissia rivularis* is found throughout most of the United States and in Canada (Clarke 1981, Burch 1989). *Ferrissia* is transported by humans via ornamental water lilies and other aquatic plants (Henderson 1935b, Bequaert and Miller 1973).

Figure 8 shows the historical and current locations for *F. rivularis.* I found *F. rivularis* in Silver Lake and Klamath basins (Oregon); the Lahontan Basin (California and Nevada) in the Truckee and Humboldt Rivers (except the Reese River); the Bonneville Basin (Utah, Idaho, Wyoming, Nevada) in the Snake Valley, the Provo River, Utah Lake, and Bear River; the Snake River drainage (Idaho) in Salmon Falls Creek and in the Raft River (draining into the Snake River respectively below and above the barrier Shoshone Falls); the Green River drainage (Wyoming, Utah, Colorado) in the Blacks Fork, New Fork River, and Yampa River; the Colorado River drainage in the Gunnison River (Colorado) and in the Gila River (Arizona). I did not find *F. rivularis* in the Walker, Carson, or Quinn Rivers (Lahontan Basin); the Mono Basin; the hydrologically isolated interior basins of Nevada; the Death Valley drainage; Deep Creek, Thousand Springs Creek, the Weber River, or the Sevier River (Bonneville Basin); or in the Henrys Fork, White River, or Duchesne River (Green River drainage).

NATURAL HISTORY.—*Ferrissia* are hermaphroditic and may be aphallate with self-fertilization or parthenogenesis (Basch 1963). Eight eggs are typically produced per adult per year (Burky 1971), and in *F. parallelus,* 12 egg capsules with 1 to 3 eggs each are typical (Clarke 1973). Life expectancy is 2 summers at the most (Russell-Hunter 1978). There is much interpopulation variation with both genetic components (shell chemistry and peritreme shape) and environmental components (shell steepness; Russell-Hunter 1978, Russell-Hunter et al. 1981). The interpopulation variation may be attributed to hermaphroditic or self-fertilization life histories and to passive dispersal (Russell-Hunter 1978, Russell-Hunter et al. 1981).

Ferrissia rivularis is found in habitats ranging from eutrophic to oligotrophic, low to high calcium concentration, and low to high mineral content (Russell-Hunter et al. 1981, Keating and Prezant 1998). The occasional presence of *F. rivularis* in lakes and ponds may be explained by the nature of the pond (a slow, inflowing stream), by a chance invasion from a riverine Pleistocene refugium (Utah Lake), or by adaptation to a new environment (such as a reservoir). In general, museum records of *Ferrissia* are sparse, most likely because plant stems or the undersides of rocks were not examined in historical surveys.

CONSERVATION CONSIDERATIONS.—Dams have caused a "precipitous decline" in river mollusk species (Basch 1963), including limpets. Management of streams for known limpet predators, such as brown trout (Basch 1963), may explain the current spotty distribution of *Ferrissia*. Streams in the Intermountain region have also been dredged to constrain flood flows, and many have been diverted for irrigation. *Ferrissia* were historically more abundant, according to records from the Weber and Bear Rivers in the Bonneville Basin and

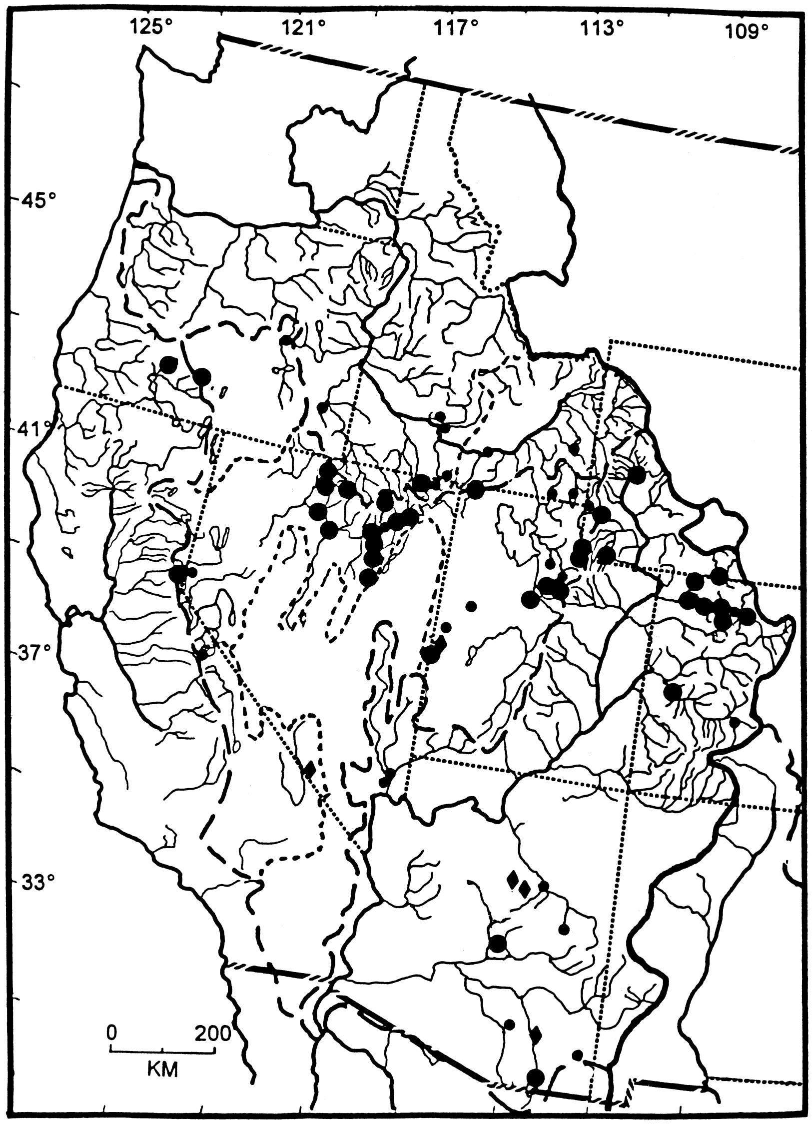

Fig. 8. *Ferrissia rivularis* distribution (marked as in Fig. 3). Fossil locations in southern Nevada, western Utah, and Arizona. Snake River historical sites were not surveyed in this study.

from Bloody Canyon in the Mono Lake basin, California. Trout streams (all containing introduced trout) include the Provo, Weber, Bear, Blacks Fork, Truckee, and Bloody Canyon streams and are now largely unoccupied by limpets. An exception is the New Fork River (upper Green River drainage, Wyoming), where the gravel-cobble substrates contain up to a dozen specimens on a 10-cm rock. Two streams with few trout (the middle Yampa and Humboldt River drainages) were the only streams that contained limpets at many locations and in the tributaries.

Discussion

If aquatic ecosystems and their native species are to be preserved and managed, it is important to have well-corroborated species boundary, distribution, and population trends. Unfortunately, such information is not readily available for invertebrates in the western United

States. The following discussion is divided into the general problems of taxonomy, distribution, and natural history as they relate to declining mollusk species and their conservation.

Taxonomy and Distribution

Species distributions may often define the species itself. With modern tools such as molecular genetic analysis, new concepts of the species and species redefinitions are occurring. The populations of gastropod *Lymnaea stagnalis* Linnaeus 1758, separated by the Alps in Europe, were differentiated at the molecular level without morphological variation, suggesting geographical isolation (Remigio and Blair 1997a, 1997b). Three *Stagnicola* species with distinctive shell shapes in the post-glacial Great Lakes region were genetically indistinguishable (Remigio and Blair 1997a, 1997b), suggesting a recent post-glacial occupation of a new habitat with local adaptations. These evolutionary processes may be occurring in the Intermountain region.

The interbasin distribution of aquatic mollusks may have been very selective through differences in fish distribution, drainage history, and species-specific geographical barriers. The Continental Divide is a major aquatic barrier. The distribution of *Margaritifera falcata* and cutthroat trout in the upper Missouri Rivers was a natural breach in the barrier across the divide. Major river drainage boundaries are also selective barriers. Neither *M. falcata* nor *Anodonta californiensis* moved between the upper Snake River and the upper Green River, although cutthroat trout have migrated between these drainages (Hansen 1985, Taylor 1985). However, the gastropods *Valvata californica, Fluminicola coloradoensis, Ferrissia rivularis,* and *Stagnicola hinckleyi* occur both in the upper Green River and upper Snake River drainages, indicating a past breach in this barrier.

Large Pleistocene lakes were as much a barrier as drainage divides. *Fluminicola coloradoensis, Ferrissia rivularis,* and *M. falcata* occur in the Great Salt Lake drainages but not in the Sevier River drainage. These drainages were tributaries of Pleistocene Lake Bonneville. Similar large lake barriers isolated amphibians (Hovingh 1997) and crayfish (Johnson 1986). Large lakes may serve as barriers by creating highly variable shorelines with high-energy wave action or through limited migration after the lake desiccated.

Within rivers, major waterfalls act as barriers. The Shoshone Falls separate the upper Snake River with its fish affinities to the Bonneville Basin from the lower Snake River with its affinities to the Columbia River. This waterfall barrier separates 21 species of fish (Smith 1978) and 2 species of amphibians (Hovingh 1997). Species that occur above and below this barrier, such as *M. falcata, A. californiensis,* and *F. rivularis,* may be candidates for cryptic evolution. Another barrier type in rivers is represented by the Grand Canyon in Arizona. The lower Colorado, including the Gila and Virgin Rivers, appears to be isolated from the upper Colorado River, as demonstrated by disjunct populations of *Ferrissia* and *Anodonta.* Lower Colorado River aquatic fauna may be more closely associated with the Salton Sea, Death Valley, and the Los Angeles Basins.

The widespread distribution of a species may indicate evolutionary stasis. *Valvata californica* has a wide distribution in the Intermountain region in space and time, preceding the formation of the Great Basin in the Miocene, the Wasatch and Sierra Nevada ranges in the Pliocene, and the current Colorado River. This species may represent an evolutionary stasis over 5 to 7 million years (Brett and Baird 1995). Until more is known about such widespread species, conservation efforts should maintain populations at the subbasin drainage level to preserve the full taxonomic variation.

Natural History and Conservation

Mollusk fecundity is extremely variable as a life history strategy. Some species live for 10 to 100 years and produce thousands of glochids annually that attach to fish, whereas *Ferrissia* lifetime reproductive output may be only a dozen offspring. However, glochid attachment to fish does not necessarily ensure survival if few fish are present and only a few glochids metamorphose. Hermaphroditic reproduction and self-fertilization can enhance reproductive output, and this mode occurs in *Valvata,* in *Ferrissia,* in a small percentage of *Margaritifera falcata*, in *Anodonta californiensis,* and in *Gonidea angulata* (Basch 1963, van der Schalie 1970, Heard 1970, 1975 *in* Burch 1989). Low reproductive rates with self-fertilization may explain the persistence of some small populations in the Intermountain region.

Grazing, irrigation, and urbanization through water diversion, channelization, and dams (Rawlings and Neel 1989, Ward 1998), all leading to deterioration of aquatic habitat, are usually the reasons listed for the decline of bivalve mollusks (Bogan 1993, Williams et al. 1993, Watters 1996, Vaughn and Taylor 1999). The current locations of molluscan fauna in the Intermountain region are in springs, streams, and ponds near headwaters in primarily rural landscapes, suggesting that water quality is a major constraint today.

Largely overlooked in the decline of aquatic fauna are manipulations of fish communities. Fish are hosts for mussel glochidia, introduced fish may prey on mollusks (Bogan 1993, Strayer 1999), and dams can limit fish distribution (Watters 1996, Vaughn and Taylor 1999). Intermountain streams have been extensively managed for nonnative trout fisheries for more than 50 years and are no longer a suitable habitat for *Margaritifera falcata,* even if the introduced rainbow trout supports the glochidia stage of mussel development. Sport fish management has not substituted for the loss of trout migration or the native trout.

Sport fish management is a "top-down" strategy that disrupts natural fish communities, food webs (Moyle 1976, Bisson 1978, McGinnis 1984, Northcote 1988, Power 1990, Dunham et al. 1999, Walser et al. 1999), and mollusks (Basch 1963, Carlander 1969, Scott and Crossman 1973). More than 9 species of fish have been stocked in Fish Lake (Utah) since 1906 (Sigler 1953). Since the 1960s the annual stocking rate there has been more than 20,000 kg of catchable rainbow trout and 120,000 fingerling trout (Utah Division of Wildlife Resources, personnal communication, 1999). Studies on the diet of the trout showed that gastropods were "an appreciable item" (Hildebrand and Towers 1927, Sigler 1953). A study by Chamberlin and Berry (1930) noted the abundance of gastropods in Fish Lake: Lymnaeidae (2 species), Planorbidae (3 species), the endemic Physidae *Physella microstriata,* and *Valvata californica* (Chamberlin and Berry 1930). By 1989 there were Lymnaeidae (2 species, 1 of which was introduced) and Physidae (1 species was introduced). Deep lake dredging did not reveal any living mollusks (A.H. Clarke, report prepared for U.S. Fish and Wildlife Service, 1991). The extirpation of mollusks also occurred in Navajo and Utah Lakes in Utah and in Clear, Big Bear, and Tahoe Lakes in California (Murphy 1951, Heckmann et al. 1981, La Rivers 1994, Frantz and Cordone 1996, this study). Introduced fish have affected other fish (La Rivers 1994, Walser et al. 1999), amphibians (Bradford et al. 1993, 1998), and macroinvertebrates (Lamontagne and Schindler 1994, Frantz and Cordone 1996, Parker et al. 1996, Bradford et al. 1998, Carlisle and Hawkins 1998), in contrast to aquatic systems in which macroinvertebrates coevolved with fish (Hershey 1990, Merrick et al. 1992, Strayer 1999). In addition to introductions of fish, fish food (nonnative shrimp and crayfish) is also introduced. Such introductions affect the aquatic system in different ways (Johnson 1986, Frantz and Cardone 1996).

The "top-down" habitat management is rather far reaching when one examines the potential effects on aquatic fauna by introduced fish. Most stocking programs (1) had inadequate habitat studies, including invertebrate monitoring and surveying, (2) did not consider whether the lake habitats are managed by the Wilderness Act and national park designation for biodiversity and ecosystem criteria (most lakes in wilderness areas and national parks were stocked with fish, and the stocking continues), (3) failed to distinguish introduced species from native species, and (4) failed to determine whether the habitats stocked have self-sustaining native populations (Bahls 1992). Long-term sustained yield, ecosystem management, and native invertebrate biodiversity typically are not goals of fish-stocking programs.

CONCLUSIONS

1. The bivalve mussels *Margaritifera falcata* and *Anodonta californiensis* have greatly diminished numbers compared to historical reports. *Margaritifera* has been extirpated from eastern California, Nevada, and Utah and was common (≥10 specimens) in only 2 of 9 streams. *Anodonta* was common (≥10 specimens) in only 2 of 13 streams. These reduced numbers can be attributed to sport fish management, as well as impacts from agricultural and urban development.

2. *Valvata californica* populations were exterminated in lakes dedicated to sport fish introductions. *Valvata californica* survived in habitats with native fish or in fishless habitats

and was found to be common in 3 lakes but extirpated in 7 lakes.

3. *Ferrissia rivularis* was confined to specific drainages, being most abundant in the Humboldt River in Nevada and the Yampa River in Colorado. Both systems had lower sport fishery use. Half of the historically recorded streams contained a rare specimen (1 or 2) or no specimens at all.

4. Taxonomic issues include species definition. *Anodonta californiensis* is the only *Anodonta* living in the Intermountain region, where 4 species or morphs had formerly been listed. *Valvata californica* has a highly variable shell shape, from globose to planar across its distributional range, suggesting no support for the subspecies *V. humeralis californica* classification, and does not have planar upper whorls different from *V. humeralis.* The taxonomy of *Ferrissia rivularis* and *F. fragilis* in museum records is confused, but only 1 species occurs through most of the Intermountain region, with a possible 2nd species *(F. walkeri)* in Arizona.

5. The distribution of these molluscan fauna is unpredictable but may be tied to events during and since the Miocene. Each taxon has its own aquatic intra- and interbasin barriers, and large Pleistocene lakes were, in part, a barrier to species dispersal.

6. The "top-down" manipulations of fish communities by fish stocking may have had a greater effect on molluscan distribution than urbanization and agricultural development.

7. The negative impacts of sport fish manipulations on biodiversity and ecosystem cannot be measured because of the frequency of these manipulations on most aquatic systems for more than 50 years.

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APPENDIX 1. Literature and museum collections used in the distribution studies. Parentheses denote specimens without catalog numbers.

Margaritifera

BONNEVILLE BASIN.—Literature: Call 1884; Henderson and Daniels 1917; Chamberlin and Jones 1929; Henderson 1935a, 1936a (collected at Evanston in 1895); Woolstenhulme 1942; Beetle 1989; Hovingh 1994 observation. **Wyoming:** CAS 154; UMMZ 172947; USNM 477114, 635194–96; UU 13999–14000, 14008. **Idaho:** ANSP 365568, OSM 52427, USNM 652862, UU 14007. **Utah:** BYU ( ); CAS 5622; FMNH 111628, 179817; MCZ 6356, 199708; OSM 14389, 52426; UCM 10311; UMMZ 88498; UU 3786, 14004, 14120.

LAHONTAN BASIN.—Literature: Call 1884, Walker 1916, Murphy 1942, Frantz and Cordone 1996. **Nevada:** CAS 154; MCZ 6358; OSM 14343, 14348; UMMZ 5560–62; USNM 86298, 102561, 120349. **California:** CAS ( ), 42268; LACM 103889; SBMNH 105586; UCM 20098; UMMZ 195564; UU 14011.

OREGON BASINS.—Literature: Parmalee 1988. **Oregon:** FMNH 198170, UU 13736.

SNAKE RIVER DRAINAGE (UPPER SNAKE RIVER).—Literature: Henderson and Rodeck 1934, Henderson 1935a, Bangham 1951, Heard 1970, Beetle 1989. **Wyoming:** ANSP 390191; OSM 45703, 45713, 50516; UMMZ 104097, 183402, 229595; USNM 635192; UCM 29582; UU 14071, 14168–69. **Idaho:** CAS ( ), MCZ 6357, OSUM 36275, SBMNH 107845, USNM 652860, UU 14166–67. **Utah:** OSM 52423. **Middle Snake River and Owyhee River, Idaho:** OSM 30116, 30587, 30589; USNM 128830, 783066. **Nevada:** UCM 3757.

Anodonta

BONNEVILLE BASIN.—Literature: Call 1884; Henderson and Daniels 1917; Henderson 1924, 1931, 1936a, b; Chamberlin and Jones 1929; Jones 1940; Eardley and Gvosdetsky 1960; Roscoe 1964; Oviatt 1988; Beetle 1989; Hovingh 1989, 1992, 1993 observations. **Wyoming:** OSM 52428, 52511; UU 12902, 13998, 14000, 14009, 14012. **Idaho:** FMNH 179808–9, MCZ 118477, OSM 25794, USNM 652863. **Utah:** ANSP 25068–69, 129920, 144309; BYU ( ), ( ); CAS 157, 159; FMNH 99372, 179803, 179807, 179827, 190806; LACM 114091; MCZ 6543, 6844, 16701, 16758, 16771, 37471, 40371, 103535–36, 298964–65; OSM 24965, 26011, 26014, 26089, 26092, 40550, 52429; SBMNH 109475; UCM 7418, 10580, 13753, 17346, 17364–65, 17367, 17379, 32028, 33280; UMMZ 35093, 52261, 57599–600, 103227, 103232, 103240, 159995–96, 169777; UNLV ( ); USNM 86367–68, 104151–52, 308922, 339741, 512227, 524299, 591393, 652821; UU 7854, 8972, 9851, 12160, 12549, 12552, 12643, 13991, 13993, 13997, 14006, 14013, 14065, 14119. **Nevada:** CAS 23906, 25725; UMMZ 132574; UU 11883, 14003 (1998).

LAHONTAN BASIN.—Literature: Call 1884; Walker 1916; Murphy 1942; Baily 1950; Jacobson 1952; Benson et al. 1992; McGuire communication 1995; Hovingh 1992, 1997 observations. **Nevada:** ANSP 48272; CAS 5680, 33134, 42317; MCZ 6541–42, 37472, 298974–75; OSM 14372, 17174, 30848; SBMNH 10363; UCM 20562, 37090; UMMZ 5555–59, 103192, 103199, 103213, 103234, 132572–73, 159998, 195493, 195563, 229555; USNM 86371, 86395, 86399, 120905–6, 322254, 472821, 504497, 519299, 652802, 652811; UU 11224, 13690, 13735, 14001, 14005, 14010, 14036. **California:** CAS 42308, 42313, 42315; MCZ 298973; UMMZ 160000.

DEATH VALLEY DRAINAGE BASIN.—**California:** ANSP 25066; LACM 104571, 104581; SBMNH 10540; USNM 652801.

SALTON TROUGH.—**California:** CAS 907, 22626, 22672, 22689, 42316, 42320; FMNH 198152; SBMNH 105195, 113267; UCM 14305, 17798; UMMZ 50038, 64018, 205563; USNM 7072.

OREGON BASINS.—Literature: Hovingh 1996 observations. **Oregon:** ANSP 25065; LACM 104699, 140692; UMMZ 61863, 103211, 103216, 103224, 132278; UU 13465.

SNAKE RIVER DRAINAGE.—Literature: Hovingh 1991, 1992 observations. **Idaho:** OSM 30117; SBMNH 109037, 110680; UCM 15170. **Utah:** BYU ( ).

COLORADO RIVER DRAINAGE.—Literature: Bequaert and Miller 1973. **Arizona:** OSM 54268; UMMZ 103246; USNM 6394, 25466, 86096, 86393, 86398, 128801, 130172, 130180, 150097, 271268–69, 272304. **California:** LACM 126304. **Utah:** FMNH 179804; UU 12159.

Gonidea

LAHONTAN BASIN.—**Nevada:** USNM 854812, 883542; UU 11822, 12474–75.

OREGON BASINS.—**Oregon:** UMMZ 61864 (1934).

SNAKE RIVER DRAINAGE.—**Idaho:** Literature: Taylor and Bright 1987. ANSP 41033, 118401; OSM 30118; UMMZ 227593. **Oregon:** OSM 48220. **Nevada:** UCM 3758; USNM 635211–13.

Valvata californica (synonyms in the United States: *Valvata humeralis* and *Valvata humeralis californica*)

BONNEVILLE BASIN.—Literature: Call 1884, Chamberlin and Jones 1929, Jones 1940, Woolstenhulme 1942, Roscoe 1964, Russell 1971, Taylor 1986 communications. **Wyoming:** UU 10341, 12901, 14186. **Idaho:** ANSP 57016, 144606, 187744, 187583; FMNH 58311, 59943, 76432, 179224; MCZ 36580; UCM 7252, 7263, 7289, 17419; UMMZ 35908, 97943, 97945; UU 13418, 14064. **Utah:** ANSP 12022, 46687, 63152, 76994, 91898, 144628, 145549, 187745; CAS 25725, 48976; FMNH 28909, 111911, 224305, 224315, 224518; MCZ 2520, 2525, 36579, 85009; OSM ( ); UCM 7397, 7407, 9615; UMMZ 42473, 143563, 197776–77; USNM 47823, 73959, 308926, 742005, 742018; UU 3672, 9817, 9823, 9829, 9833, 10198, 10202, 10206, 10210–11, 10301, 11914, 12149, 12784, 12854, 12863, 12891, 13666, 13678, 13684, 13835, 13922, 14057, 14069, 14128, 14140, 14184, 14186, 14188–89, 14191–92, 14194, 14197.

LAHONTAN BASIN.—**Nevada:** ANSP 187746; CAS 55811; UMMZ 42789, 229359; USNM 272320, 322255, 477670; UU 14002, 14043, 14097. **California:** ANSP 73649; CAS ( ), ( ), 2748, 23666, 27785–86, 51254, 55811; USNM 361551; UU 14019, 14030.

INTERIOR BASINS.—Literature: Quade and Pratt 1989. **Nevada:** UNLV 2089, 3191; USNM 873176, 874406; UU 9760, 10845, 12908–9, 12941, 13677, 14021, 14196.

OREGON BASINS.—**Oregon:** ANSP 12025; CAS 32763; USNM 308990.

GREAT PLAINS DRAINAGE.—**Colorado:** UCM 12266, 27411, 28036, 30435, 34498.

COLORADO RIVER BASIN.—Literature: Chamberlin and Jones 1929, Chamberlin and Berry 1930, Bequaert and Miller 1973, Beetle 1989, Wu 1989. **Arizona:** ANSP 82994, 146997, 163962; UNLV 3013, 3022, 3215, 3274.

Utah: FMNH 111819; UMMZ 197769–70; UU 14152, 14157, 14160. **Wyoming:** UMMZ 150759, 219534, 219558; UMMZ-SSNM (T61-200S); UU 14175, 14178. **Colorado:** UCM 1035, 9332, 27398, 28054, 28091, 28095.

LOS ANGELES BASIN.—ANSP 12023, 105046, 141363, 143080, 221687, 371408; CAS 23457, 51235, 51256; FMNH 121510; LACM 70047, 70370, 70383, 96142, 97657, 106418, 106783, 106798, 85-54, 85-65, 85-70, 85-71; MCZ 56708, 71021, 176708; OSM ( ); UCM 7677–78, 17846; USNM 175095, 518311; UU 14148.

WEST COAST DRAINAGES.—**California:** USNM 23411, 251923.

SNAKE RIVER DRAINAGE.—Literature: Henderson 1933, Beetle 1989. **Wyoming:** UMMZ 229409, 229425; USNM 536413, UU 14072. **Idaho:** UU 12963, 14193. **Nevada:** UU 12987, 13676, 14185. **Oregon:** USNM 308994.

Valvata utahensis

Literature: Call 1884, Chamberlin and Jones 1929, Taylor 1985, Taylor and Bright 1987, Sharp and SWCA Environmental Consultants communications 2003.

BONNEVILLE BASIN.—**Wyoming:** UMMZ 229544. **Idaho:** ANSP 63153, 144604, 187689, 187747; FMNH 10543, 58298, 59927, 76423; UCM 7264, 7290; UMMZ 35909, 99653–54, 219293, 229544; USNM 525096. **Utah:** ANSP 12026, 72059, 322807, 322810; FMNH 28898, 104903, 120949, 224329; MCZ 2522–23, 177423; OSM ( ); UCM 7408; UMMZ 99651, 99655, 167025, 219478, 231776; USNM 31277, 173384, 510623, 742016, 742937; UU 1151, 3611, 14038, 14056, 14127.

LAHONTAN BASIN.—**Nevada:** UU 14037.

WEST COAST DRAINAGES.—**California:** UMMZ 220007.

SNAKE RIVER DRAINAGES.—**Idaho:** UU 13059, 14187.

Valvata virens

WEST COAST DRAINAGES.—Literature: Taylor 1981. **California:** CA 24126; ANSP 12024, 44217, 121828, 121908, 124773, 365358, 371413; LACM 61412, 97393, 124595, 124703, 124705, A.8862; MCZ 175922, 175992; OSM ( ); UCM 1685, 21505; UMMZ 143591; USNM 11812, 25012, 28461–62, 30560, 47818–20, 56394, 63991, 121094, 225012, 516352, 742023–24, 742026; UU 3716. **Nevada:** UMMZ 237249 *(humeralis)*.

Ferrissia rivularis

BONNEVILLE BASIN.—Literature: Eardley and Gvosdetsky 1960, Russell 1971, Winger et al. 1972, Winget et al. 1982, Taylor 1986 communications, Hovingh 1998 observations. **Wyoming:** UMMZ 229494, 229503, 229527–29, 229543; UU 12893, 13960. **Idaho:** UCM 7294, UMMZ 229502. **Utah:** ANSP 144620; FMNH 111820, 178377; MCZ 4578, 243275; OSM ( ), ( ); SBMNH UAZ 4802; UCM 7410; UMMZ 219474; UU 3756, 9650, 13390, 13986–88.

LAHONTAN BASIN.—Literature: Jones 1940, Taylor 1981, McGuire 1992 communications. **Nevada:** CAS 55811; UMMZ 229362; UU 10373, 10375, 10392, 10426, 10431, 10917, 11891, 12473, 12476, 12990, 12995, 12999, 13010, 13014, 13030, 13466. **California:** UU 13427.

DEATH VALLEY DRAINAGE.—**California:** SBMNH: UAZ 4920.

SNAKE RIVER DRAINAGE.—**Idaho:** CAS ( ), 34168; UMMZ 219431, 229053, 229058, 229137, 229196, 229214, 229278, 229317, 229374. **Utah:** UU 11901. **Nevada:** UMMZ 229318, UU 9593.

OREGON BASIN.—Literature: Hovingh 1995 observations. **Oregon:** UCM 16002; UMMZ 229138; UU 13458, 13468.

COLORADO RIVER BASIN.—Literature: Bequaert and Miller 1973, Wu 1989. **Arizona:** P. Spindler collection; ANSP 115256–59, 328339; CAS 21093, 52105; FMNH 58051, 64331; SBMNH UAZ 3450, 48802; UU 14230–31. **Wyoming:** UU 13961–62, 13969, 13981, 13989, 14183. **Colorado:** UCM 27274, 27278, 27336, 27343, 27349, 27351, 27356, 28065, 28500, 34665–67; UU 13370, 13406, 13979–81, 13983–85, 13990. **Nevada:** UNLV 3432, 3437, 3444.

APPENDIX 2. Shell morphometrics of *Valvata* from the western United States with width (W) in mm, ratio of width and height (W/H), sample standard deviation (±*s*), and population number (*N*). Initial letters denote the geographical region, the first letter indicating the basin (B, Bonneville; L, Lahontan; G, other basin in the Great Basin; C, Colorado River drainage; R, Rio Grande drainage; S, Columbia-Snake River drainage; L, Los Angeles Basin) and the second letter indicating the state (U, Utah; N, Nevada; C, Colorado; Ca, California; W, Wyoming; Wa, Washington).

Sample (*N*)	Width ± *s*	W/H ± *s*
V. virens ANSP 365358 (10)	5.4 ± 0.2	1.0 ± 0.0
V. utahensis UU 14056 (11)	5.3 ± 0.4	1.1 ± 0.1
LN, Gerlach UMMZ 237249 (12)	4.4 ± 0.3	1.1 ± 0.1
LN, Pine Creek UU 14002 (6)	4.5 ± 0.2	1.1 ± 0.1
BU, Fish Springs: south UU 14197 (10)	3.6 ± 0.2	1.1 ± 0.1
BU, Fish Springs: north UU 14195 (10)	4.3 ± 0.2	1.2 ± 0.1
LN, Humboldt UU 14037 (10)	4.6 ± 0.2	1.2 ± 0.1
GN, Toiyabe UU 14196 (10)	5.0 ± 0.3	1.3 ± 0.1
GN, Clover UU 12941 (10)	4.1 ± 0.3	1.3 ± 0.1
CU, Navajo Lake FMNH 28909 (10)	4.5 ± 0.4	1.3 ± 0.1
CC, Gilley UCM 28091 (10)	4.9 ± 0.3	1.3 ± 0.1
RC, UCM 12266 (10)	3.5 ± 0.2	1.4 ± 0.1
BU, Utah Lake UU 14057 (10)	3.9 ± 0.4	1.4 ± 0.1
BU, Yankee Meadow UU 11914	4.3 ± 0.4	1.4 ± 0.1
CU, Emery UU 14157 (10)	4.8 ± 0.2	1.4 ± 0.1
CW, Teton UU 14193 (8)	3.8 ± 0.7	1.4 ± 0.1
BW, Bear River UU 12901 (10)	5.0 ± 0.4	1.4 ± 0.1
BU, Hot Springs Lake MCZ 2520 (10)	3.4 ± 0.2	1.4 ± 0.1
BU, Weber UU 14194 (10)	3.6 ± 0.7	1.5 ± 0.1
SWa, Yakima MCZ 200699 (8)	3.7 ± 0.3	1.5 ± 0.1
CU, Fish Lake FMNH 111819 (8)	4.1 ± 0.6	1.5 ± 0.1
LCa, Big Bear Lake ANSP 105046 (10)	4.7 ± 0.4	1.5 ± 0.1
CC, Cabin UCM 28095 (10)	3.8 ± 0.3	1.6 ± 0.1
BU, Tushar UU 9823, 9829, 9833, 9817 (11)	3.5 ± 0.8	1.6 ± 0.1
SWa, Stevens Co. MCZ 176707 (8)	3.8 ± 0.4	1.6 ± 0.1
SN, Taylor UU14185 (10)	2.6 ± 0.1	1.6 ± 0.1
LCa, Bluff Lake UU 14148 (15)	4.8 ± 0.3	1.8 ± 0.2
V. sincera Great Slave Lake UU 14237 (13)	4.1 ± 0.5	1.9 ± 0.1

APPENDIX 3. Shell measurements of *Ferrissia* in Intermountain locations and of type specimens. The following abbreviations are used: number of specimens (*N*), often combining several lots within a drainage; length (L), width (W), and height or elevation (H), as defined by Burch (1989); the ratio of the distance of the apex from the posterior end and the total length (A/L). Upper line, mean ± *s* (sample standard deviation, applied to samples with 5 or more specimens). Lower line, range of measurements. Specimens with bodies preserved in alcohol (E); shells only (S).

Basin Subbasin	*N*	Length (mm) (Range)	W/L (Range)	H/L (Range)	A/L (Range)
BONNEVILLE BASIN (E)	29	4.03 ± 0.66	0.63 ± 0.04	0.34 ± 0.04	0.34 ± 0.03
		(2.9–5.6)	(0.47–0.69)	(0.25–0.44)	(0.28–0.44)
West Bonneville (E)	8	4.05 ± 0.52	0.61 ± 0.06	0.37 ± 0.04	0.32 ± 0.02
		(3.3–4.7)	(0.47–0.69)	(0.31–0.44)	(0.28–0.36)
Utah Lake (E)	14	3.92 ± 0.75	0.63 ± 0.04	0.32 ± 0.03	0.36 ± 0.04
		(2.9–5.6)	(0.56–0.67)	(0.25–0.38)	(0.31–0.44)
East Bonneville (E)	7	4.21 ± 0.65	0.64 ± 0.02	0.37 ± 0.03	0.33 ± 0.02
		(3.8–5.0)	(0.63–0.68)	(0.32–0.40)	(0.31–0.37)
East Bonneville (S)	43	4.15 ± 0.53	0.63 ± 0.04	0.36 ± 0.04	0.36 ± 0.04
		(2.9–5.5)	(0.50–0.72)	(0.29–0.44)	(0.29–0.48)
SNAKE RIVER (E)	10	4.02 ± 1.08	0.59 ± 0.04	0.34 ± 0.04	0.32 ± 0.04
		(2.5–5.9)	(0.51–0.65)	(0.30–0.41)	(0.27–0.40)
SNAKE RIVER (S)	10	3.68 ± 0.74	0.56 ± 0.06	0.35 ± 0.04	0.37 ± 0.03
		(2.9–5.1)	(0.48–0.66)	(0.29–0.41)	(0.32–0.41)
LAHONTAN BASIN					
Humboldt River dr. (E)	77	3.96 ± 0.79	0.63 ± 0.04	0.38 ± 0.05	0.34 ± 0.04
		(2.3–7.0)	(0.49–0.69)	(0.29–0.48)	(0.24–0.42)
Humboldt River dr. (S)	8	3.6 ± 0.29	0.64 ± 0.02	0.35 ± 0.04	0.37 ± 0.04
		(3.0–3.9)	(0.62–0.67)	(0.29–0.42)	(0.30–0.43)
COLORADO RIVER BASIN					
Upper Green River (E)	9	4.31 ± 0.77	0.64 ± 0.02	0.38 ± 0.04	0.34 ± 0.03
		(3.2–6.0)	(0.61–0.67)	(0.33–0.45)	(0.29–0.37)
Yampa River (E)	65	4.30 ± 0.82	0.66 ± 0.03	0.35 ± 0.04	0.36 ± 0.03
		(2.8–6.0)	(0.60–0.73)	(0.25–0.44)	(0.28–0.45)
Yampa River (S)	23	3.63 ± 0.51	0.63 ± 0.03	0.31 ± 0.05	0.38 ± 0.04
		(2.5–4.3)	(0.56–0.67)	(0.24–0.42)	(0.31–0.45)
Sabino Canyon, AZ (S)	4	3.33	0.59	0.31	0.22
		(3.0–3.8)	(0.53–0.62)	(0.29–0.33)	(0.19–0.28)
San Pedro (E)	13	3.27 ± 0.56	0.53 ± 0.03	0.32 ± 0.03	0.27 ± 0.03
		(2.6–4.6)	(0.49–0.60)	(0.27–0.38)	(0.22–0.32)
F. rivularis ANSP 21982	2	5	0.68	0.38	0.34
		(1)	(0.66–0.69)	(0.35–0.40)	(0.33–0.35)
F. fragilis ANSP 22011	1	3.9	0.48	0.31	0.32
F. parallelus ANSP 21996	3	4.0	0.57	0.25	0.35
		(3.6–4.5)	(0.56–0.58)	(0.24–0.26)	(0.31–0.38)
F. walkeri ANSP 87479	7	3.96 ± 0.54	0.64 ± 0.02	0.26 ± 0.02	0.30 ± 0.03
		(3.6–5.1)	(0.61–0.66)	(0.23–0.29)	(0.24–0.32)
Queen Charlotte UU 14239	8	6.57 ± 0.90	0.62 ± 0.02	0.32 ± 0.0	0.37 ± 0.3
		(5.2–7.7)	(0.59–0.66)	(0.29–0.37)	(0.35–0.42)