

# Biogeography of Great Basin Aquatic Snails of the Genus *Pyrgulopsis*

Robert Hershler and Donald W. Sada

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## ABSTRACT

Snails of the genus *Pyrgulopsis* (Caenogastropoda: Hydrobiidae) are among the richest elements of aquatic biodiversity in the Great Basin (80 Holocene species), with most species endemic to single springs, spring systems, or drainage basins. *Pyrgulopsis* is an old Great Basin group, with a fossil record extending into the late Miocene (Truckee Formation). These tiny, gill-breathing gastropods (commonly known as springsnails) are obligately aquatic throughout their life cycle which, together with the above features, suggests that their biogeographic patterns are highly informative with respect to late Cenozoic hydrographic history.

Distributions of *Pyrgulopsis* species define seven regions of endemism within the Great Basin. Five of these correspond to drainages harboring concentrations of other endemic aquatic biota (Death Valley system, Lahontan Basin, Bonneville Basin, Railroad Valley, upper White River basin), whereas snail endemism in Dixie and Steptoe basins appears to be unique. Each of the three largest regions (Death Valley system, Lahontan Basin, Bonneville Basin) contains two or three subregions of *Pyrgulopsis* endemism, most of which are not paralleled by other aquatic biota.

*Pyrgulopsis* biogeography in part conforms to currently accepted interpretations of pluvial drainage in the Great Basin, but locally suggests different, presumably older relationships. Various historical relationships with adjacent external drainages are implied, although snail biogeography provides surprisingly little evidence of prior linkage with the Sacramento and upper Colorado River basins. In contrast to the fish-hook track, which is attributed to various mollusks and fishes and links the Snake River basin with the eastern Bonneville and western Lahontan Basins, *Pyrgulopsis* provides evidence of more continuous prior drainage integration across the northern boundary of the Great Basin.

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## Introduction

Gastropods of the family Hydrobiidae (commonly known as springsnails) are a highly suitable group for biogeographic evaluation of historical relationships among drainages of the Great Basin. These gill-breathing snails are obligate to permanent waters and disperse only through their habitat (Taylor and Bright, 1987).<sup>1</sup> Because of the antiquity (late Miocene) of these snails and their tight linkage with aquatic habitats, their patterns of phylogenetic relationships and distributions likely reflect late Cenozoic regional hydrographic history. Native distributions of these snails in the Great Basin appear to have been little affected by introduced species in contrast to fishes (particularly salmonids; Behnke, 1992). The diverse hydrobiid fauna of the Great Basin includes many locally endemic forms, suggesting a complex evolutionary history that can provide a rich source of biogeographic information.

For this contribution we focus on the hydrobiid *Pyrgulopsis*, the most speciose genus of aquatic snails in North America. Our purposes are to describe the regions of endemism defined by Holocene *Pyrgulopsis* species in the Great Basin and to review the distributions and the inferred phylogenetic relationships of these snails as they relate to current interpretations of drainage history.

*Pyrgulopsis* is a North American group of 131 described species that are considered valid, 61% of which live in the Great Basin. Members of the genus are found throughout much of western North America from the Rio Grande basin west to the California coast and from the Snake River–Columbia River basin south to the Bolsón de Mapimí depression in Chihuahua and Coahuila states, northern Mexico (Figure 1).<sup>2</sup> The scope of *Pyrgulopsis* remains incompletely known because many species are undescribed, including sizable faunas in northern Mexico and the northwestern United States. The Great Basin contains the greatest diversity of *Pyrgulopsis* (80 species), followed by a far smaller fauna in the Colorado River drainage (20 species). Allopatry of congeners is typical, although two or three species occasionally are sympatric, usually in large springs.

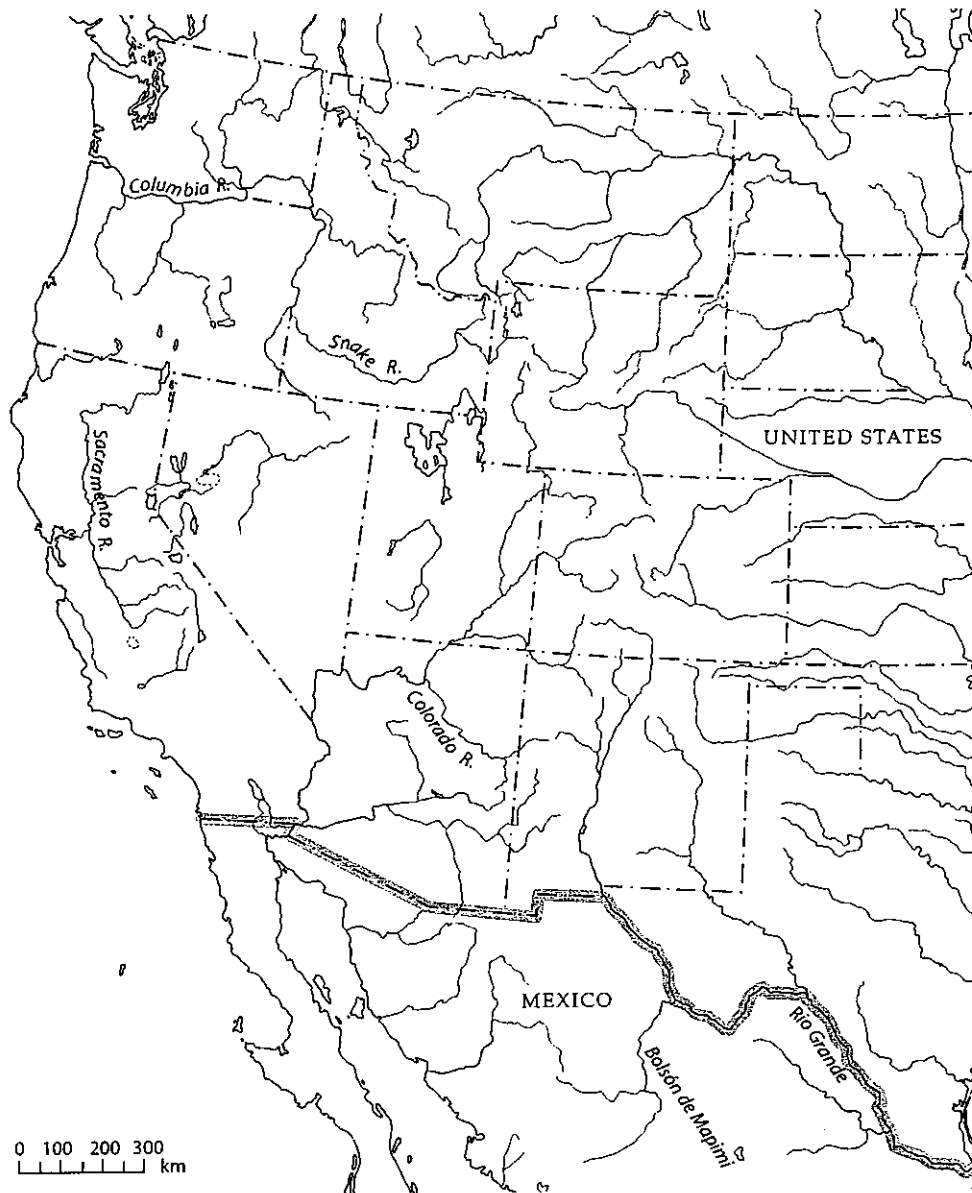
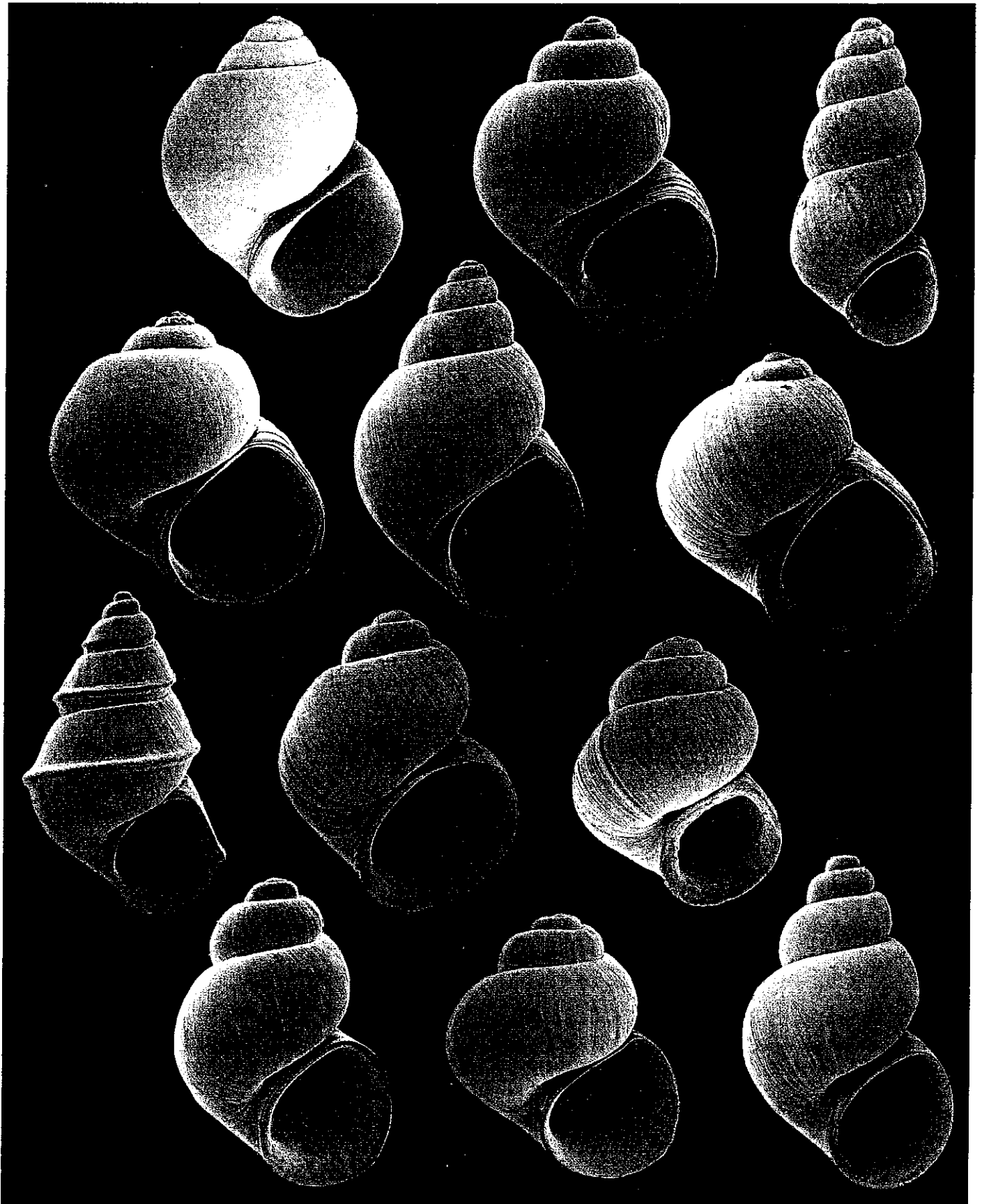


FIGURE 1.—The general distribution of *Pyrgulopsis* (shaded area) throughout the western United States and northern Mexico. The southern limit of the genus in Mexico is uncertain.

*Pyrgulopsis* is composed of small snails (1–8 mm in maximum shell dimension) having a smooth or weakly sculptured shell that ranges from low trochiform to narrow-conic in shape (Figure 2). Throughout the West *Pyrgulopsis* is a locally abundant member of benthic communities, living on rock or aquatic vegetation and grazing on periphyton (Mladenka, 1992). Females are oviparous and deposit egg capsules on hard substrates. Larval development is direct, with “crawl-away” young emerging from the egg capsules. *Pyrgulopsis* typically lives in springs ranging from tiny seeps to large rheocrenes and limnocrenes. Snails generally are concentrated near spring sources, with their density declining downflow (e.g., Noel, 1954)—a pattern that surely contributes to their tendency for local differ-

entiation. A few species live in lakes, rivers, and larger streams. Although some species live only in basin floor habitats, many others live in middle- and high-elevation springs and streams along montane slopes, suggesting that faunal

FIGURE 2 (opposite).—Scanning electron micrographs of shells of selected *Pyrgulopsis* species. Top row (left to right): *P. breviloba* (USNM 873174, shell height 1.8 mm), *P. bryantwalkeri* (USNM 874305, 2.3 mm), *P. dixensis* (USNM 874391, 2.0 mm); second row: *P. erythropoma* (USNM 857864, 2.2 mm), *P. hendersoni* (USNM 874386, 5.1 mm), *P. merriami* (USNM 873395, 2.5 mm); third row: *P. nevadensis* (USNM 590364, 4.6 mm), *P. notidicola* (USNM 873215, 1.8 mm), *P. orbiculata* (USNM 873196, 1.4 mm); bottom row: *P. owensensis* (USNM 857955, 2.3 mm), *P. papillata* (USNM 873185, 2.0 mm), *P. turbatrix* (USNM 883978, 2.9 mm).



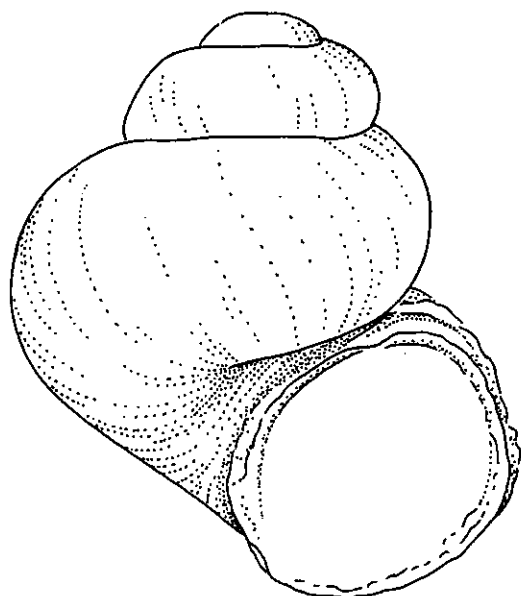


FIGURE 3.—*Pyrgulopsis truckeensis*, from the Truckee Formation (late Miocene), Churchill County, Nevada (holotype, USNM 560438). Shell height 2.2 mm.

movement has been achieved by upland headwater transfers (e.g., stream capture) as well as by basinal integration.

Whereas extant species typically live in small springs, fossil shells referable to the genus routinely are found in late Cenozoic lacustrine deposits (Taylor, 1966a). Paleocological studies that delineate habitat use by these snails are lacking. The known ecology of extant congeners allows us to conjecture that *Pyrgulopsis* was not widely dispersed in paleolakes but instead was restricted to well-oxygenated littoral zones or lived in springs or wetlands closely associated with these lakes. The fossil record of *Pyrgulopsis* is limited in utility because of the weak phylogenetic signal provided by the simple shells of these snails (Taylor, 1987:5). Nevertheless, the occurrence of *P. truckeensis* (Figure 3) in the Truckee Formation (stratigraphy discussed by Firby, 1993) in the northwest Great Basin suggests that the genus dates at least to the late Miocene (Yen, 1950; see Gregg and Taylor, 1965, for assignment of this species to *Fontelicella* (= *Pyrgulopsis*)).<sup>3</sup> It has been suggested that Holocene (presumably cold-water) species in the genus generally may be Pliocene in origin and that western hydrobiids living in thermal springs (which include many *Pyrgulopsis* species) are generally ancient, perhaps middle Tertiary in age (Taylor, 1987:5, as *Fontelicella*). The antiquity of this group suggests that, as in the case of Great Basin fishes (e.g., Smith, 1978; Minckley et al., 1986), ancestral biotic ranges were affected not only by extensive integration and subsequent fragmentation of Late Quaternary pluvial drainage, but also by the spectrum of tectonic and volcanic events that shaped the modern regional landscape during the past 17–18 My.

## Methods

A rigorous biogeographical analysis (e.g., Wiley, 1988) of Great Basin *Pyrgulopsis* is precluded by the paucity of phylogenetic information concerning these snails, and although we discuss morphological groupings of species (as summarized in Appendix), biogeographic conclusions derived from distributions of these snails must be refined in the future. Most of the Great Basin *Pyrgulopsis* fauna was described during the past decade (Hershler and Sada, 1987; Hershler, 1989, 1995, 1998; Hershler and Pratt, 1990), and the study of these snails lags well behind that of regional aquatic vertebrates. Taxonomic re-analysis of relatively widespread and/or morphologically variable forms will be necessary, as evidenced by a recent allozymic study of *P. wongi* from the southwestern Great Basin; this study revealed fixed-allele differences among populations from different drainages (Hamlin, 1996), suggesting the presence of cryptic species. The only published phylogenetic analysis of *Pyrgulopsis* species provided little resolution (Hershler, 1994, fig. 31) and did not establish monophyly of the genus within the subfamily Nymphophilinae.<sup>4</sup> Morphological diversity among species assigned to *Pyrgulopsis* is pronounced, particularly with respect to glandular penial ornament (Figure 4). Species groupings in use are based on very few characters (mostly from penial form and ornament) that often are noncongruent, and many snail species are strongly differentiated by autapomorphies.

We thus rely heavily on the technique of inferring past drainage relationships on the basis of biotic distributions, although we acknowledge the inherent limitations of this method (Platnick and Nelson, 1978). A biotic distribution encompassing several now-isolated drainages may suggest previous integration or connection of these waters (and/or relatively vagile organisms), but this assumes that biotic components automatically expand or contract their ranges in concert with potential habitat. The extent to which this assumption is realistic depends greatly on ecological characteristics of species in question. Biotic distributions do not reveal relative timing of historical relationships among inhabited areas, whereas fossils and/or a well-resolved cladogram might provide this information. Relatively broadly distributed taxa are useful within this context, but locally endemic forms provide no information in the absence of phylogenetic resolution. (In contrast, broadly distributed taxa have little utility for vicariance biogeography.) Despite these drawbacks, earlier efforts using this methodology often have been insightful for Great Basin aquatic biogeography, as exemplified by seminal works on fishes (Hubbs and Miller, 1948; Hubbs et al., 1974).

We follow King's (1982) definition of the Great Basin (which, in turn, was based on that of Frémont, 1845) as all contiguous areas of currently internal drainage between the Sierra Nevada and Rocky Mountains. Thus, areas that may have had recent external drainage but now are endorheic, such as the Salton Trough and disrupted drainage of the Colorado River in southeast Nevada, are treated as Great Basin. Drainage maps

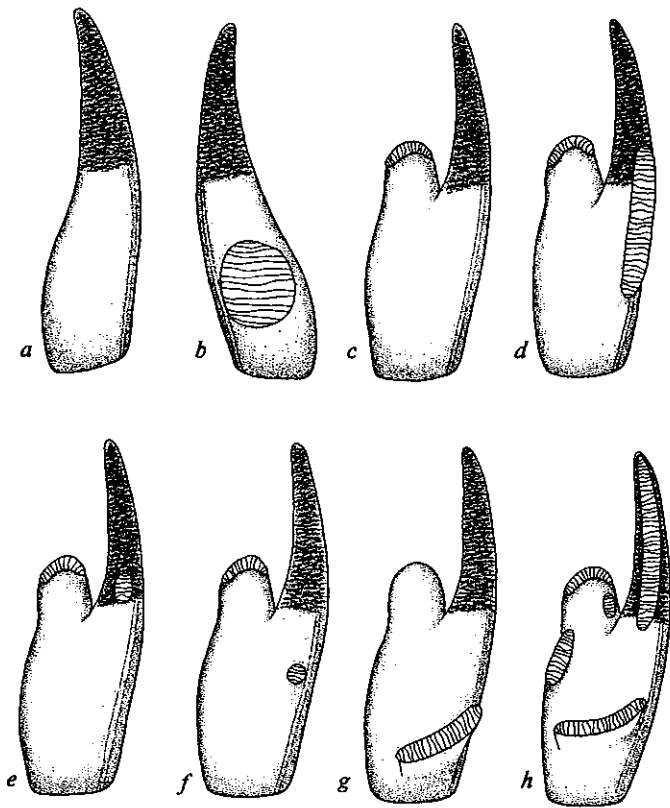


FIGURE 4.—Representative variation in penial glandular ornament among *Pyrgulopsis* species groups (see Appendix for names of species exhibiting each form): a, simple penis lacking glands (group 1); b, ornament of a superficial ventral gland (group 2); c, ornament of a terminal gland (group 3); d, ornament of a terminal gland and elongate Dg1 abutting filament (group 4); e, ornament of a terminal gland and small, basal penial gland (group 5); f, ornament of a terminal gland and weak, dot-like Dg1 (group 6); g, ornament of a raised Dg1 (group 8); h, ornament of a full complement of glands (group 9). The schematic drawings are not to scale.

were constructed by using United States Geological Survey (USGS) 1:2,000,000 line graph data as base. Drainage basins and their boundaries were digitized from USGS 1:500,000 (state) hydrologic unit maps. The fit of hydrographic boundaries onto the drainage base is not exact because these two sets of data were originally of different scales and map projections. Final maps were prepared using Adobe Illustrator (version 7.0). Regions of endemism refer to drainages having two or more endemic species and should not be confused with “areas of endemism,” which imply congruence of distributional and phylogenetic pattern among taxa (Harold and Mooi, 1994).

#### Acknowledgments

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row (NMNH) inked anatomical drawings and assisted with preparation of plates. Fiscal support was provided by two awards from the Smithsonian Institution Scholarly Studies Program. This paper benefited from detailed and very useful criticisms from Marith Reheis, Richard Vari, and two anonymous reviewers. We also acknowledge an intellectual debt to Dwight W. Taylor, whose pioneering studies of western American freshwater molluscan biogeography (notably Taylor, 1960, 1966a, 1985; Taylor and Smith, 1981; Taylor and Bright, 1987) paved the way for the present work.

#### Biogeography

*Pyrgulopsis* is widespread in the Great Basin (Figure 5) and even occurs in some poorly watered, fishless regions such as the “area of sterile basins” of southern Nevada (Hubbs and Miller, 1948:45). We know of no major sampling gaps, although distributions of many species may be imprecisely known because of nonexhaustive local fieldwork and probable undocumented extinctions in historic time.

Distributions of Great Basin species are given in Table 1. Most of the fauna is endemic to single springs, spring complexes, or drainage basins. Only 16 of the 80 species range across major drainage divides and, as mentioned above, a re-evaluation of the purported conspecificity of populations is necessary in these cases. *Pyrgulopsis* species describe seven major regions of endemism within the Great Basin (Figure 6), five of which correspond to drainages harboring other endemic biota (e.g., fishes; Smith, 1978; Minckley et al., 1986). On the other hand, snail endemism in Dixie and Steptoe Basins is not matched by any other aquatic organism. Species of *Pyrgulopsis* also define subregions of endemism within the largest of these drainages (Bonneville Basin, Lahontan Basin, Death Valley system); most of these subregions have no parallel among other aquatic biota.

**DEATH VALLEY SYSTEM.**—Treatment of this fauna partly reiterates that of Hershler and Pratt (1990). The three components (Owens Valley, Amargosa River basin, and Mohave Desert) of the Death Valley hydrographic system contain a total of 14 species of *Pyrgulopsis*, all but four of which are endemic. Endemic species are concentrated in two subregions, upper Owens Valley and the Amargosa River basin (Figure 7), both of which harbor other endemic biota (Sada et al., 1995).

The upper Owens Valley subregion contains an endemic flock of three species—*P. aardahli*, *P. owensensis*, *P. perturbata*—that are most similar to the widespread Lahontan species *P. gibba*. The distribution of another species from this subregion, *P. wongi* (Figure 8a), suggests prior integration among upper Owens Valley—the southeastern Lahontan region (Carson and East Walker River basins); Mono Valley, which comprised the uppermost segment of the pluvial Owens River drainage (Putnam, 1949); and several valleys to the east (Deep Springs Valley, Huntoon Valley, Fish Lake Valley, Teels Salt Marsh). Reheis et al. (2002) present shoreline evidence that

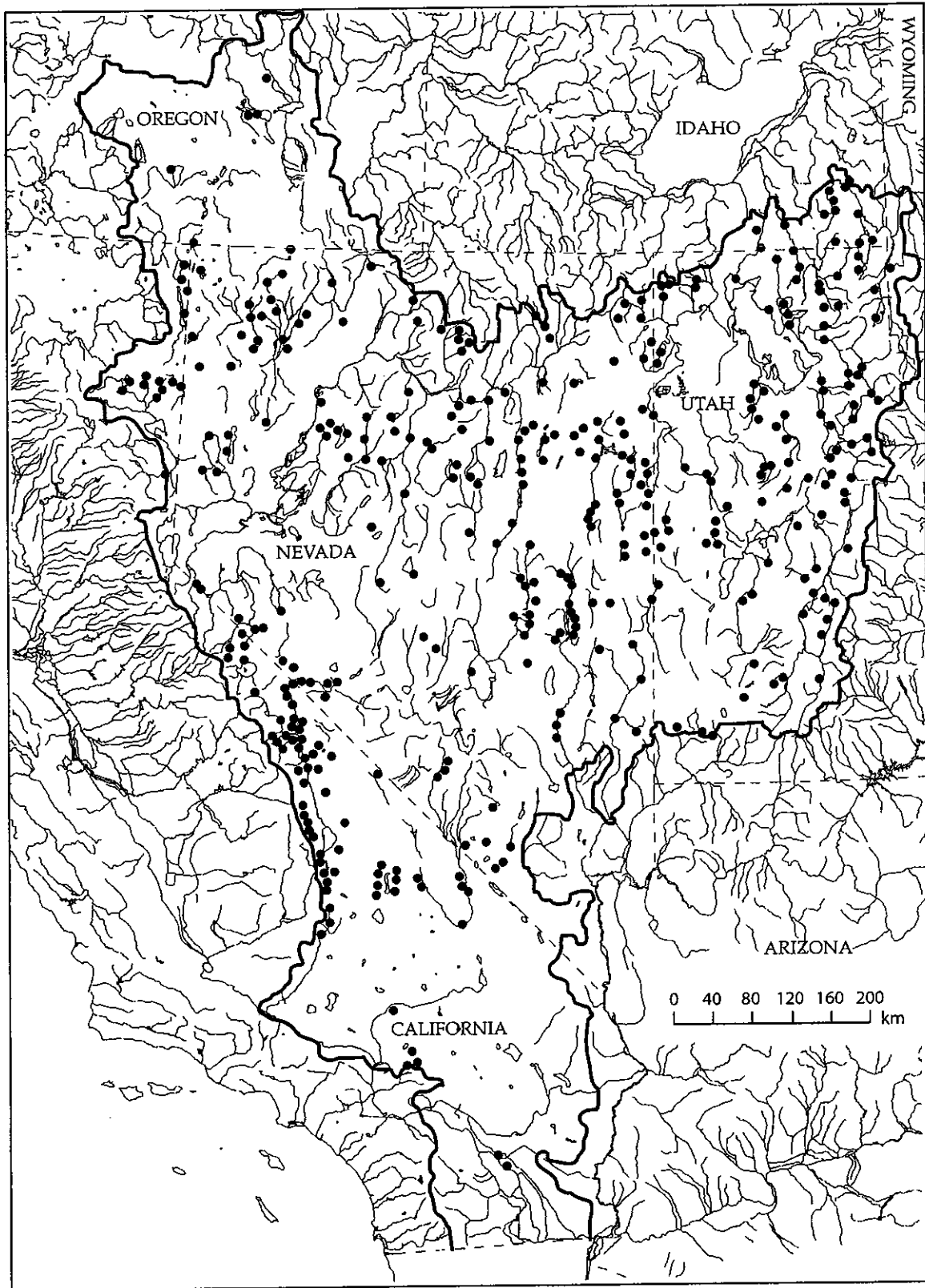


FIGURE 5.—Distribution of *Pyrgulopsis* in the Great Basin of the western United States. Dots often represent more than one locality. The heavy line shows the boundary of the Great Basin hydrographic system.

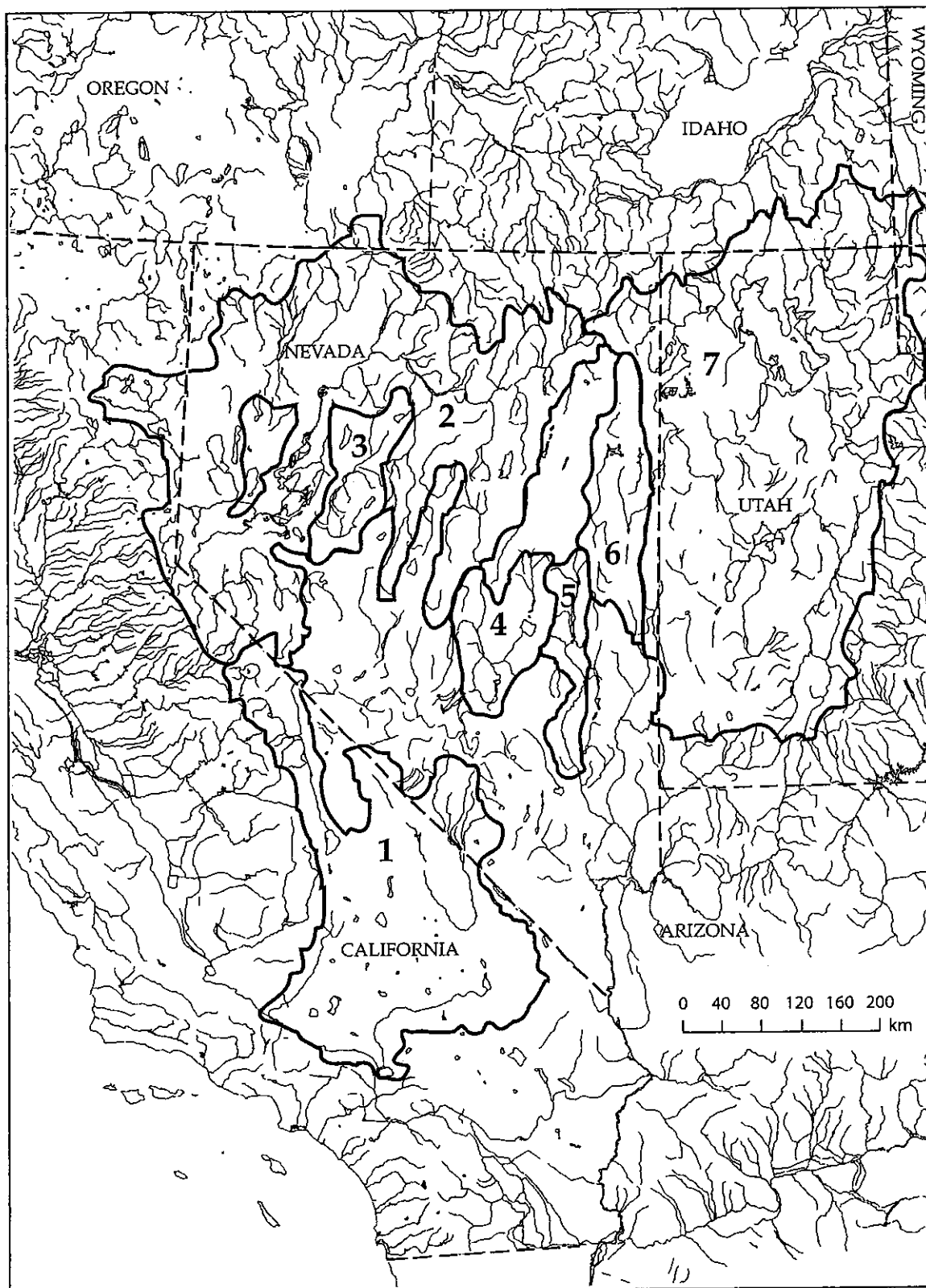


FIGURE 6.—Regions of endemism represented by *Pyrgulopsis* in the Great Basin. 1, Death Valley system; 2, Lahontan Basin; 3, Dixie Basin; 4, Railroad Valley; 5, upper White River basin; 6, Steptoe Basin; 7, Bonneville Basin.

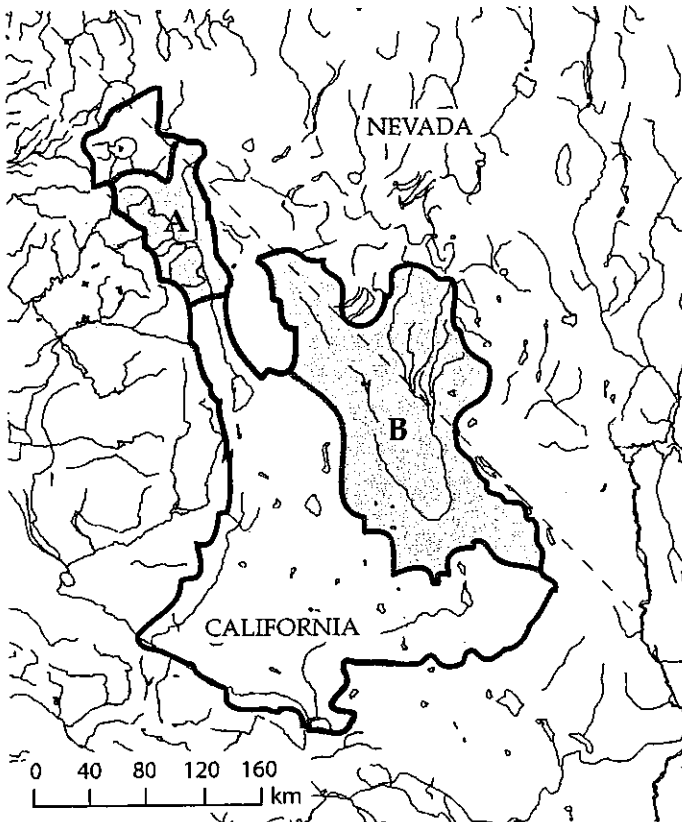




TABLE 1.—Continued.

Species	Drainage												
	Great Basin									Extralimital			
	DV	LA	RB	ST	DX	WR	IB	BO	OL	SA	CA	SN	CO
<i>papillata</i>	-	-	X	-	-	-	-	-	-	-	-	-	-
<i>peculiaris</i>	-	-	-	-	-	-	-	X	-	-	-	-	-
<i>pellita</i>	-	X <sup>1</sup>	-	-	-	-	-	-	-	-	-	-	-
<i>perturbata</i>	X	-	-	-	-	-	-	-	-	-	-	-	-
<i>pictilis</i>	-	X <sup>1</sup>	-	-	-	-	-	-	-	-	-	-	-
<i>pilsbryana</i>	-	-	-	-	-	-	-	X	-	-	-	-	-
<i>pisteri</i>	X	-	-	-	-	-	-	-	-	-	-	-	-
<i>planulata</i>	-	-	-	X <sup>1</sup>	-	-	-	-	-	-	-	-	-
<i>plicata</i>	-	-	-	-	-	-	-	X <sup>1</sup>	-	-	-	-	-
<i>ruinosa</i>	-	-	-	-	-	-	Y <sup>1</sup>	-	-	-	-	-	-
<i>sadai</i>	-	X	-	-	X	-	-	-	-	-	-	X	-
<i>sathos</i>	-	-	-	-	-	X	-	-	-	-	-	-	-
<i>saxatilis</i>	-	-	-	-	-	-	-	X <sup>1</sup>	-	-	-	-	-
<i>serrata</i>	-	-	-	X	-	-	-	-	-	-	-	-	-
<i>sterilis</i>	-	-	-	-	-	-	X	-	-	-	-	-	-
<i>sublata</i>	-	-	-	-	-	-	X <sup>1</sup>	-	-	-	-	-	-
<i>sulcata</i>	-	-	-	X	-	-	-	-	-	-	-	-	-
<i>transversa</i>	-	-	-	-	-	-	-	X	-	-	-	-	-
<i>turbatrix</i>	X	-	-	-	-	-	X	-	-	-	-	-	X
<i>umbilicata</i>	-	X	-	-	-	-	-	-	-	-	-	-	-
<i>variegata</i>	-	-	-	-	-	-	-	X	-	-	-	X	-
<i>villacampae</i>	-	-	X	-	-	-	-	-	-	-	-	-	-
<i>vinyardi</i>	-	X	-	-	-	-	-	-	-	-	-	-	-
<i>wongi</i>	X	X	-	-	-	-	X	-	-	-	-	-	-

<sup>1</sup>Species is endemic to a single spring.



Mono Valley's pluvial Lake Russell may have had an interval of northern drainage to the East Walker River basin, and Russell (1889:299-301) implied earlier integration of Mono Valley and the Lahontan Basin prior to disruption by Quaternary volcanics. Perhaps early integration between Mono and Huntoon Valleys also occurred, because their divide is only slightly above the highest shoreline (~2257 m; Reheis et al., 2002) documented for Lake Russell. Distribution of *P. wongi* in isolated valleys to the east of the Owens Valley trough correlates, in part, with an emerging concept that Lake Lahontan may have extended sufficiently south of Walker Lake to integrate with Fish Lake Valley (Mifflin and Wheat, 1979; Reheis and Morrison, 1997; Reheis et al., 2002). However, integration of this conjectured drainage with Deep Springs Valley would have been unlikely, because pluvial Deep Spring Lake was isolated by very high divides during the late Pleistocene (Miller, 1928). A fossil *Pyrgulopsis* (*Fontelicella* sp.; Taylor, 1966a:67) was recorded from the Waucoba Lake beds (fide Walcott, 1897), which contain tephra layers from 2.22-2.17 Ma (A. Sarna-Wojcicki, in litt., August, 1998) that are now uplifted above

FIGURE 7 (left).—Regions of endemism by *Pyrgulopsis* within the Death Valley system. A, upper Owens Valley (north of Tinemaha Reservoir); B, Amargosa River basin (including its terminus, the Death Valley trough). The heavy line shows the boundary of the Death Valley pluvial drainage system.

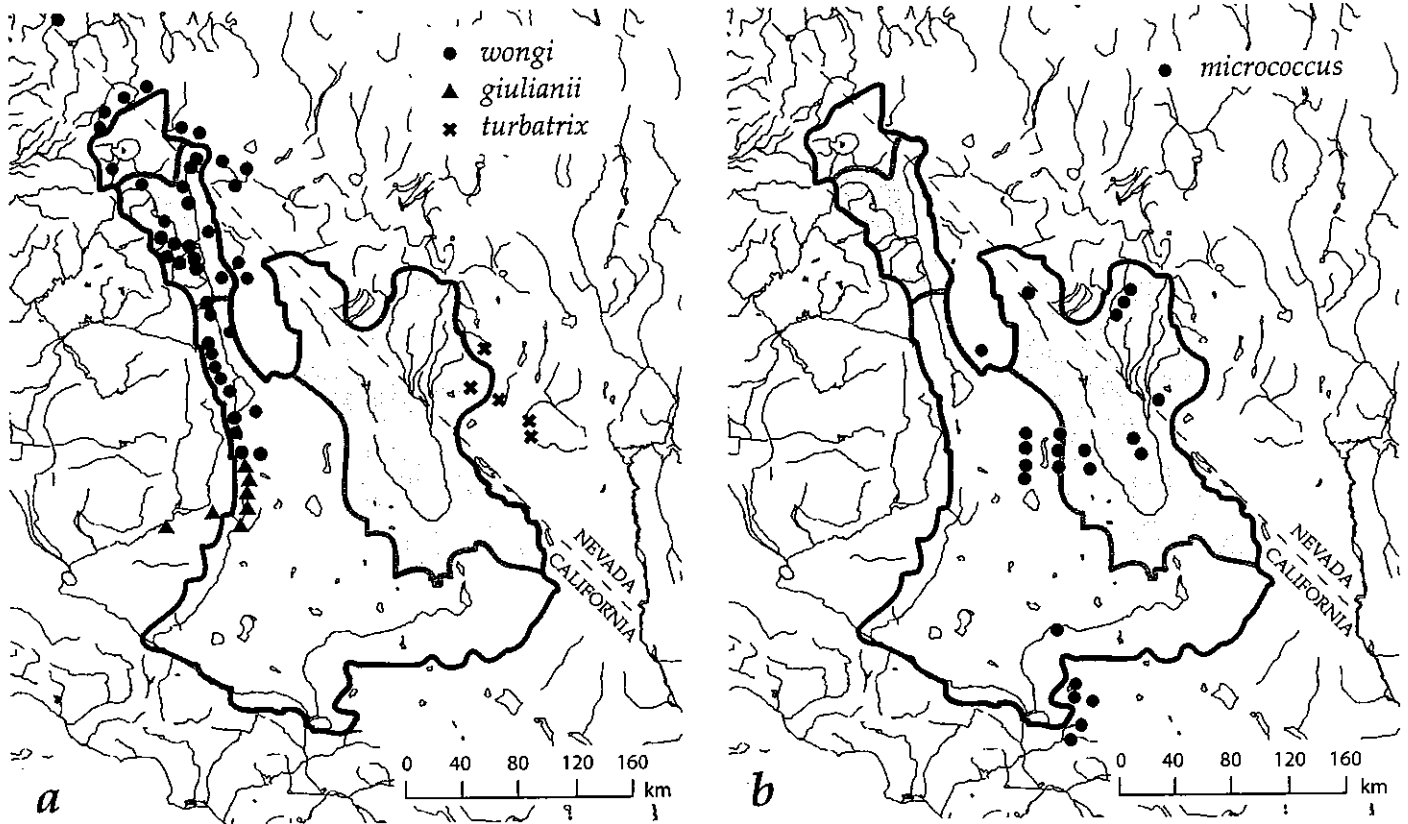


FIGURE 8.—Distributions of selected *Pyrgulopsis* species of the Death Valley System: a, *P. giulianii*, *P. turbatix*, *P. wongi*; b, *P. micrococcus*. Shading indicates the regions of endemism (from Figure 7).

eastern Owens Valley. This record suggests that *P. wongi* may have dwelled early in the proto-Sierra Nevada/White Mountain block and attained current distribution as a result of later tectonic events that created Owens, Deep Springs, and Fish Lake Valleys during the past 2.3 My (Bachman, 1978; Reheis and Sawyer, 1997; also see Lueddecke et al., 1998). This hypothesis is supported by allozyme evidence that *P. wongi* populations of Deep Springs Valley are more similar to snails of Owens Valley than to samples from upper segments of the pluvial Owens River drainage (Hamlin, 1996).

*Pyrgulopsis giulianii* (Figure 8a), which is morphologically very similar to the upper Owens Valley species flock described above, lives in Sierra Nevada streams that drain to Indian Wells Valley, into which pluvial Lake Owens spilled. Records of this species along the south fork of the Kern River west of the Sierra Nevada suggest prior transmontane drainage across the Sierra Nevada divide (also indicated by Dibblee, 1967, figs. 79, 80), which presumably was disrupted by uplift and westward tilting of the southern portion of this range since the late Neogene (Loomis and Burbank, 1988; Unruh, 1991; Christiansen and Yeats, 1992).<sup>5</sup>

Of the seven species endemic to the Amargosa River basin, six are restricted to the Ash Meadows spring oasis, several of which (*P. crystalis*, *P. erythropoma*, *P. pisteri*) form a putative

clade closely similar to *P. avernalis* from Moapa Valley in southeast Nevada (Colorado River basin).<sup>6</sup> The seventh species endemic to the Amargosa River basin, *P. amargosae*, lives in springs along the lower Amargosa River and most closely resembles a species from the Snake River basin (*P. bruneauensis*). This putative relationship is suggestive of the fish-hook distributional pattern described for various freshwater mollusks and fishes (Taylor 1960, 1966a), although this possibility would be bolstered by presence of linking populations or species in the large intervening area.<sup>7</sup>

The distribution of another snail, *P. turbatix* (Figure 8a), also implies that the Amargosa River basin had a previous drainage relationship with the Colorado River basin as well as with several isolated valleys to the east. *Pyrgulopsis turbatix* lives along slopes of the Spring Mountains in Amargosa Flat (which drains to Ash Meadows), isolated Indian Springs and Pahrump Valleys, and Las Vegas Valley (Colorado River basin). (Note that another congener, *P. deaconi*, also lives along the western and eastern flanks of the Spring Mountains in Pahrump and Las Vegas Valleys, respectively.) *Pyrgulopsis turbatix* also lives in a single spring in Frenchman Flat, a small, isolated basin west of Indian Springs Valley. Many have speculated that the Death Valley system had a past connection with the Colorado River basin (see Miller, 1946); although an

oft-postulated connection via spilling of the integrated pluvial lake system to the south (through Bristol, Cadiz, and Danby Lake basins) is unlikely (Brown and Rosen, 1995; Hooke, 1998), other forms of integration may have occurred. Distribution of *P. turbatrrix* conforms in part to previous integration of the Amargosa River basin and Las Vegas Valley around the north flank of the Spring Mountains, as proposed by Hubbs and Miller (1948:101–102; also see Nolan in Gilluly, 1929:682). This integrated system presumably was disrupted as a result of stream captures across the low, largely alluvial divides in the region. Hubbs and Miller (1948:85) argued that “Lake Pah-rump” spilled to the Amargosa River basin, but Mifflin and Wheat (1979) denied existence of a late Pleistocene pluvial lake in this valley. Integration of the drainage postulated above with that of Frenchman Flat may have occurred via the low divides separating the Amargosa River basin from Rock and Mercury Valleys to the west (which in turn are weakly separated from Indian Springs Valley). Alternatively, drainage integration may have been disrupted by the several kilometers of movement along local, northeast-trending strike-slip faults, at least some of which occurred after the Miocene (Carr, 1984; Stewart, 1988). Distribution of *P. turbatrrix* along flanks of the Spring Mountains also could have arisen via transmontane stream capture, perhaps associated with late Cenozoic tilting of this range (Burchfiel et al., 1983).

*Pyrgulopsis micrococcus* (Figure 8b) lives in all three components of the Death Valley hydrographic system, although it is found in only a lower segment of the pluvial Owens River drainage, Panamint Valley. The distribution of this snail provides a possible exception to the assertion by Taylor (1985: 317–318) that “spillover from Lake Panamint into Death Valley, and into Lake Manly in Death Valley, had no recognizable effect on mollusc distribution.” However, this species lives in high-elevation springs in the Panamint Mountains, and its distribution across this divide may reflect headwater transfer as opposed to pluvial dispersal. Distribution of this snail also implies early (before the late Pleistocene) drainage integration of the Death Valley system with both Saline Valley (northwest of Panamint Valley) and the California coastal drainage south of the Transverse Ranges. Saline Valley, a small, profoundly closed basin that lacked a pluvial lake, perhaps integrated with Panamint Valley before the faulting that was responsible for basinal development during the past 3.0 My (Burchfiel et al., 1987). The distribution of *P. micrococcus* is paralleled by another prosobranch snail, *Assimineia infima*, which lives in Saline (Hershler, unpublished) and Panamint Valleys (as Holocene fossil; Taylor, 1966b:208), as well as in the Amargosa River basin (Hershler, 1987). The transmontane distribution of *P. micrococcus* in the San Bernardino Mountains implies early presence in the region—before the late Miocene to early Pliocene uplift, which truncated and reversed the southward Mojave drainage (Meisling and Weldon, 1989).<sup>8</sup>

*Pyrgulopsis* biogeography (1) implies various prior drainage connections between the Death Valley system and other,

mostly adjacent, areas and (2) suggests that the upper Owens Valley and Amargosa River basin subregions of endemism do not share a close historical relationship. Interestingly, early drainage integration between the northwest portion of the Death Valley system and the Sacramento Valley before the late Cenozoic Sierra Nevada uplift (e.g., Huber, 1981) is not well reflected in *Pyrgulopsis* biogeography. The complete absence of species overlap and the entirely different sets of historical drainage relationships implied by the *Pyrgulopsis* faunas of Owens Valley and the Amargosa River basin are striking, given the pluvial integration of these drainages, yet they agree with the distribution patterns of other mollusks (Taylor, 1985) and of fishes (Minckley et al., 1986; also see Echelle and Dowling, 1992). Taylor (1985:317) suggested that the disparity of freshwater mollusks from west and east of Death Valley may reflect a dispersal barrier provided by extension of the Miocene proto-Gulf of California into the area. Although fossils may imply presence of a late Cenozoic estuary in portions of the Mojave Desert (Durham and Allison, 1960; Smith, 1970; disputed by Spencer and Patchett, 1997), no physical record of such conditions has been found in the Death Valley region (Buising, 1990, fig. 1), and the local fossil record is equivocal in this regard.<sup>9</sup> Physical evidence of middle Pleistocene integration of the Owens and Amargosa River basins is clear (Smith, 1976; Jan-nik et al., 1991; Fitzpatrick and Bischoff, 1993), yet hydro-graphic conditions nonetheless may have provided a barrier to aquatic dispersal (Miller, 1981) that perhaps was positioned between Indian Wells and Panamint Valleys.

LAHONTAN BASIN.—This large region harbors 22 species of *Pyrgulopsis*. Four endemic species of fishes also live in this basin (Hubbs et al., 1974; Deacon and Williams, 1984). The 16 endemic species of *Pyrgulopsis* are concentrated in four subregions (Figure 9), only one of which, the Black Rock Desert, harbors other endemic aquatic biota. *Pyrgulopsis* biogeography implies considerable prior drainage integration within the Lahontan Basin and between this and several adjacent drainages.

A southwest extension of Reese River Valley (Antelope Valley) contains two endemic species (*P. augustae*, *P. pictilis*) that are morphologically very similar to other Lahontan snails. Basin floor springs in the Carico Lake basin (part of the middle segment of the Humboldt River basin) harbor two endemic species (*P. basiglans*, *P. bifurcata*) that form a putative clade similar to the group of snails from the Amargosa and White River basins discussed above. Two snails (*P. bryantwalkeri*, *P. humboldtensis*) belonging to large groups of similar species are endemic to the upper Humboldt River basin. The distribution of another snail, *P. leporina* (Figure 10a), implies that drainage of the upper Humboldt River basin (Lamoille Valley) was previously integrated (before the late Pleistocene) with that of northern Ruby Valley, perhaps reflecting spill of pluvial Lake Franklin into Lake Lahontan via Lake Clover as suggested by Snyder et al. (1964; but disputed by Mifflin and Wheat, 1979:57). Soldier Meadows, a prominent zone of thermal springs that drains south to the floor of Black Rock Desert via Mud Meadows

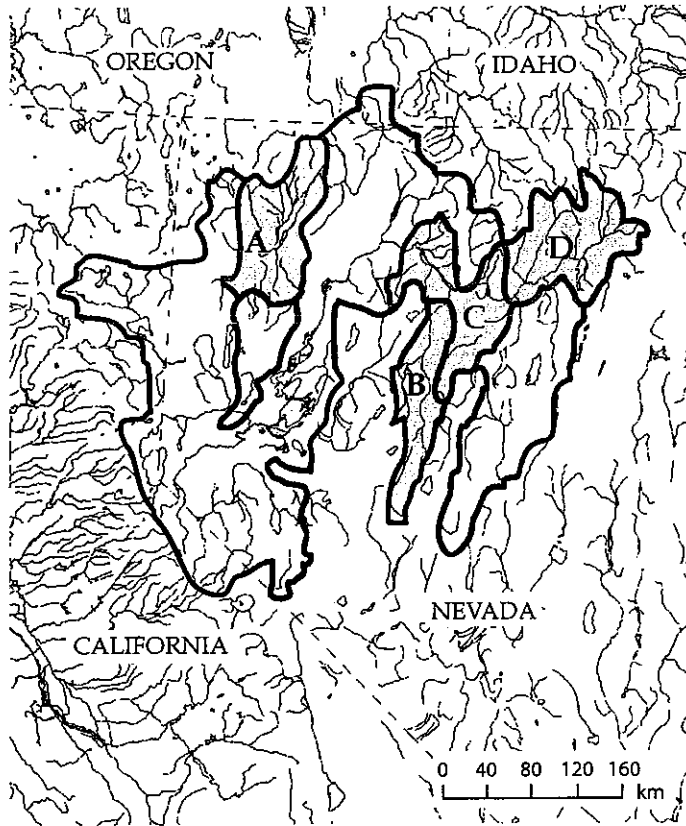
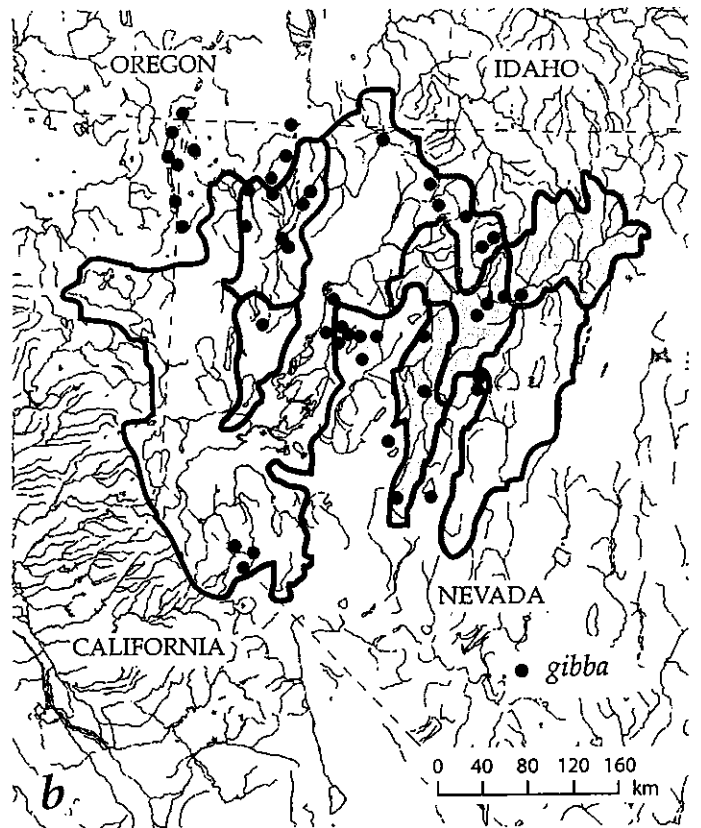
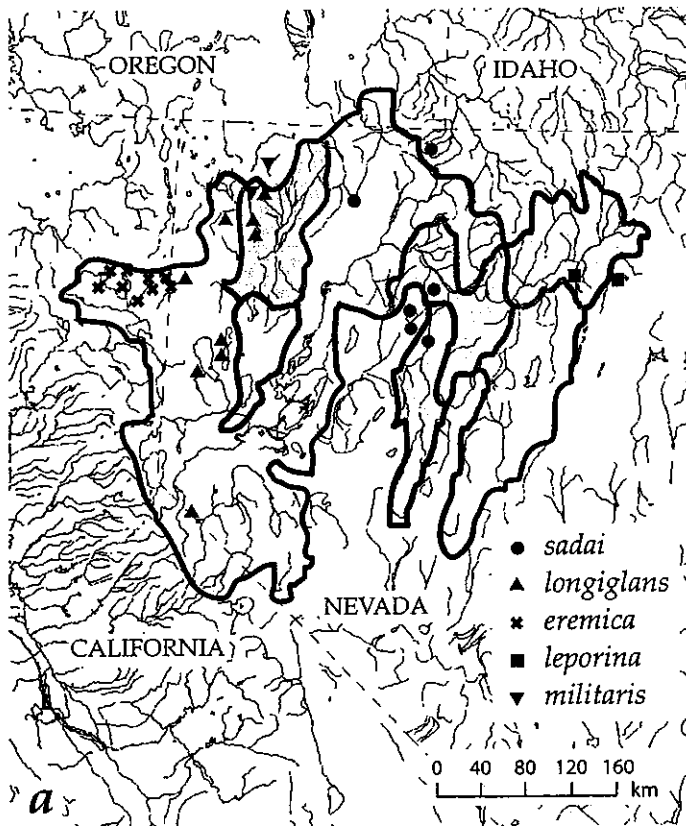


FIGURE 9 (left).—Regions of endemism by *Pyrgulopsis* within the Lahontan system. A, Black Rock Desert; B, Reese River basin; C, middle Humboldt River basin (includes the section of river from Palisade to Golconda Summit; also Carico Lake, Crescent, and Pumpnickel Valleys); D, upper Humboldt River basin (includes Marys River drainage). The heavy line shows the boundary of the Lahontan pluvial drainage system.

FIGURE 10 (below).—Distributions of selected *Pyrgulopsis* species of the Lahontan system: a, *P. eremica*, *P. leporina*, *P. longiglans*, *P. militaris*, *P. sadai*; b, *P. gibba*. Shading indicates the regions of endemism (from Figure 9).



Creek, contains a presumed flock of three endemic species (*P. limaria*, *P. notidicola*, *P. umbilicata*), which closely resemble an eastern Lahontan (Squaw Valley) species. Soldier Meadows also contains an endemic species of desert dace (Nyquist, 1963). Distribution of a fourth snail (*P. militaris*) belonging to this local group implies earlier drainage integration between Soldier Meadows and Alvord Basin to the north (Figure 10a), which in turn had (at least temporarily) a pluvial connection with the Snake River basin during the late Pleistocene (Lindberg and Hemphill-Haley, 1988). Snail transfer also could have been mediated through intervening Summit Lake basin, which Mifflin and Wheat (1979:27, 30) suggested had a complex Quaternary history that included intervals of drainage to Soldier Meadows and Alvord Basin. Note that Soldier Meadows springs are associated with a lineament extending through the Alvord Basin, which Garside and Schilling (1979:38–39, fig. 28) interpreted as a fault trace.

In addition to the endemic faunas described above, the Lahontan Basin harbors scattered locally endemic species. Of particular note is *P. nevadensis*, which lived in several western Lahontan lakes but is now probably extinct (Hershler, 1994). This snail is closely similar to *P. archimedis* from Klamath Lake basin, and the implied historical drainage relationship between these areas is part of the fish-hook track described by Taylor (1960, fig. 1; 1985, fig. 17) for these and other species having similar shell sculpture. We are not confident, however, that other components of this track, consisting of fossil taxa from the Snake River region and southern California, are closely related to these living species because development of carinate shell sculpture has been subject to homoplasy in this group (Hershler, 1994, 1998).

Several widespread snails also reflect considerable past connectivity of drainage in the Lahontan region. *Pyrgulopsis wongi*, discussed above, lives in both the Carson River and East Walker River basins (Figure 8a). *Pyrgulopsis longiglans* (Figure 10a) is distributed in a north–south manner in the western portion of the Lahontan Basin (overlapping the Black Rock Desert) whereas *P. sadai* (Figure 10a) is distributed in a similar fashion in the central Lahontan area (overlapping the Reese River and the middle Humboldt subregions). Distribution of this species also implies prior drainage integration between the Lahontan Basin and the Snake River basin in northeast Nevada, although the single locality in the Snake River drainage (at the base of the Santa Rosa Range) is suggestive of a headwater transfer. The distribution of *P. eremica* (Figure 10a) in the western Lahontan Basin conforms to interpretations that Eagle Lake and Horse Lake basins (north of Honey Lake Valley), both of which contained pluvial lakes, overflowed to Lake Lahontan (Gester, 1962; Snyder et al., 1964; Morrison, 1991). In the Eagle Lake basin, this snail lives along Willow Creek, which may have drained pluvial Lake Acaps'kati to the south before the damming caused by Quaternary basalt flows (Gester, 1962). *Pyrgulopsis gibba* lives throughout much of the western Lahontan Basin, including all of the subregions of endemism (Figure 10b). Distribution of this snail implies past connections be-

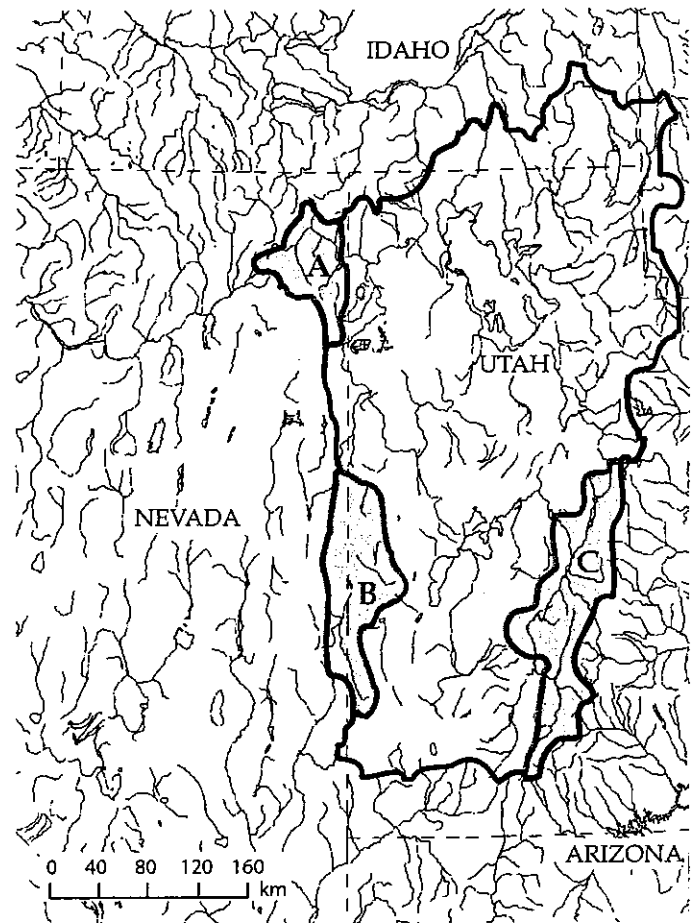


FIGURE 11.—Regions of endemism by *Pyrgulopsis* within the Bonneville Basin. A, Thousand Springs basin (includes Pilot Creek, Tecoma, and Thousand Springs Valleys); B, Snake Valley (includes Hamlin and Snake Valleys); C, upper Sevier River basin (extending to Sevier Bridge Reservoir above Gunnison; exclusive of the West Fork Sevier River below Piute Reservoir). The heavy line shows the boundary of the Bonneville pluvial drainage system.

tween the Lahontan Basin, several closely proximate Nevadan valleys (Big Smokey, Dixie, Granite Springs, and Grass Valleys), and the “Oregon Lakes” region, although the northern component of this distribution also may be attributed to drainage disruption caused by tens of kilometers of right-lateral slip (Miocene to Holocene) along the Eugene–Denio fault zone (Lawrence, 1976).

**BONNEVILLE BASIN.**—Taylor and Bright (1987) previously discussed the aquatic molluscan biogeography of this region (although not focusing on *Pyrgulopsis*), which constitutes the largest drainage unit in the Great Basin. The Bonneville Basin harbors 17 species of *Pyrgulopsis*, 14 of which are endemic. This basin also contains eight endemic species of fishes (Smith, 1978). The *Pyrgulopsis* fauna is very distinct from that of the Lahontan Basin (paralleling that of fishes), and only a single species ranges across both regions. Endemic species are concentrated in three subregions (Figure 11), of which only the Snake Valley (along the Nevada–Utah border, east of the Snake

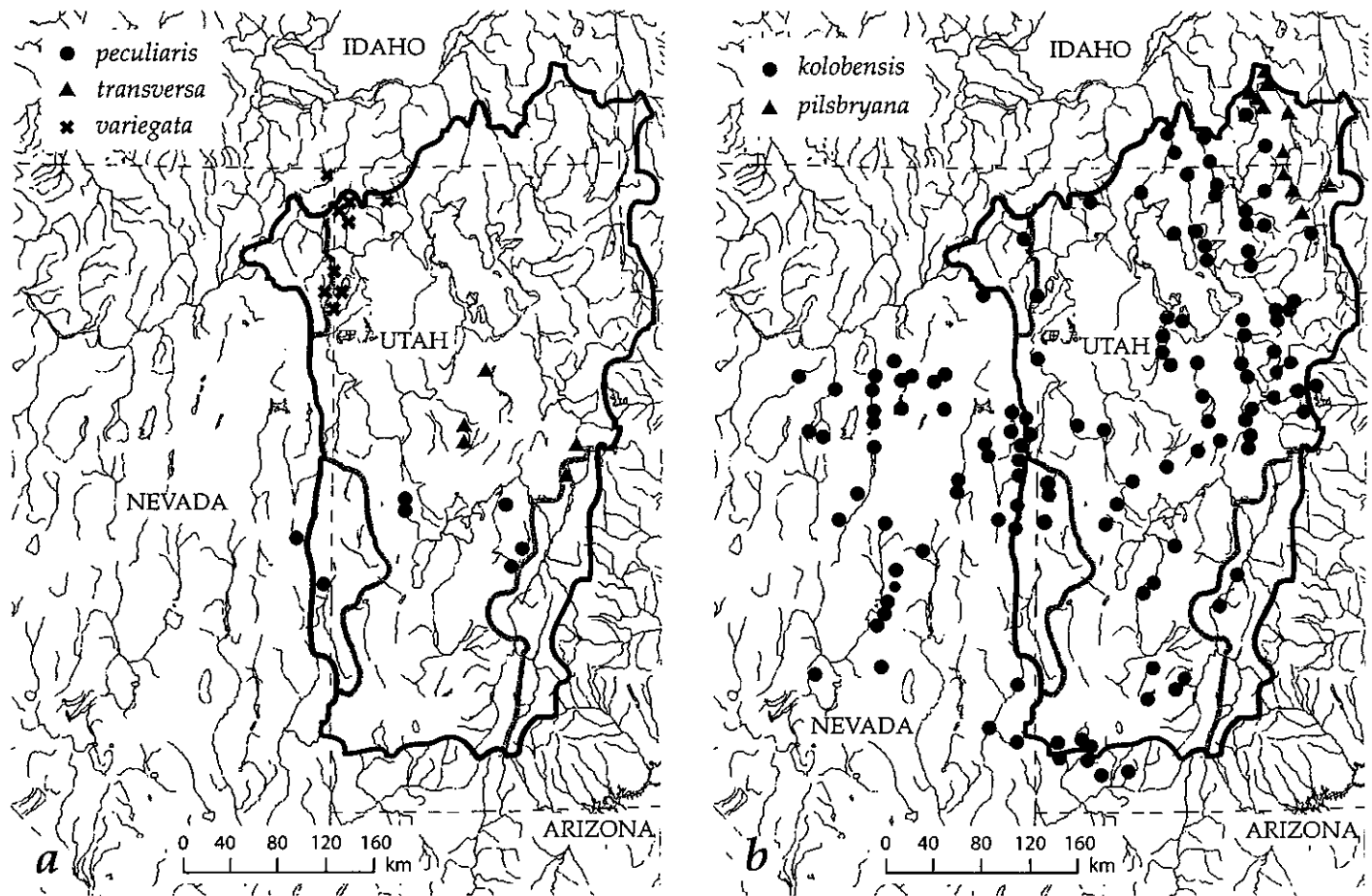


FIGURE 12.—Distributions of selected *Pyrgulopsis* species of the Bonneville Basin: a, *P. peculiaris*, *P. transversa*, *P. variegata*; b, *P. kolobensis*, *P. pilsbryana*. Shading indicates regions of endemism (from Figure 11).

Range; not to be confused with the Snake River basin to the north) contains other endemic biota.

The Thousand Springs subregion harbors five species, including three endemics (*P. hovinghi*, *P. lentiglans*, *P. millenaria*) distributed along segments of the Thousand Springs Creek drainage. Although relationships of these endemic snails are uncertain, the distribution of another snail, *P. variegata* (Figure 12a), suggests a prior drainage relationship existed with an adjacent portion of the northwest Bonneville Basin and Goose Creek, which is in the Snake River basin to the north. Physical evidence also suggests that Goose Creek was part of the Bonneville drainage basin before the late Miocene drainage reversal that was associated with passage of the Yellowstone Hot Spot (Hildebrand and Newman, 1985; Rodgers et al., 1991).

Three species are locally endemic in the Snake Valley subregion (see Figure 11). One of these, *P. hamlinensis*, is closely similar to *P. montana*, which lives in the uppermost portion of Meadow Valley Wash (a disrupted segment of Colorado River drainage) just over the White Rock Mountain divide to the west. Distributions of these species may reflect past historic upland stream capture between these drainages. *Pyrgulopsis*

*saxatilis* is most similar to a species from the White River valley to the west (*P. lata*), whereas the third endemic, *P. anguina*, is most similar to *P. chamberlini* from the Sevier River basin to the east. Prior drainage integration with areas to the west and east is also implied by the distribution of *P. peculiaris* (Figure 12a), which lives in the Snake Valley as well as in the lower segment of the Sevier River basin and the isolated Spring Valley in eastern Nevada. Five species are endemic in the upper segment of the Sevier River basin in southern Utah, confirming the distinctiveness of this fauna as noted by Taylor and Bright (1987). Affinities of these species imply prior historical relationships with other segments of the Bonneville Basin, as does the distribution of *P. transversa* (Figure 12a).

The distribution of *P. kolobensis* suggests extensive prior connectiveness of Bonneville Basin drainage (this snail overlaps all three subregions of endemism) as well as integration with the eastern Lahontan Basin, isolated valleys situated between these two regions, and the Colorado River basin (Figure 12b). (This snail exhibits considerable morphological differentiation across its broad range and almost certainly represents a species complex.) Past integration with the Colorado River ba-

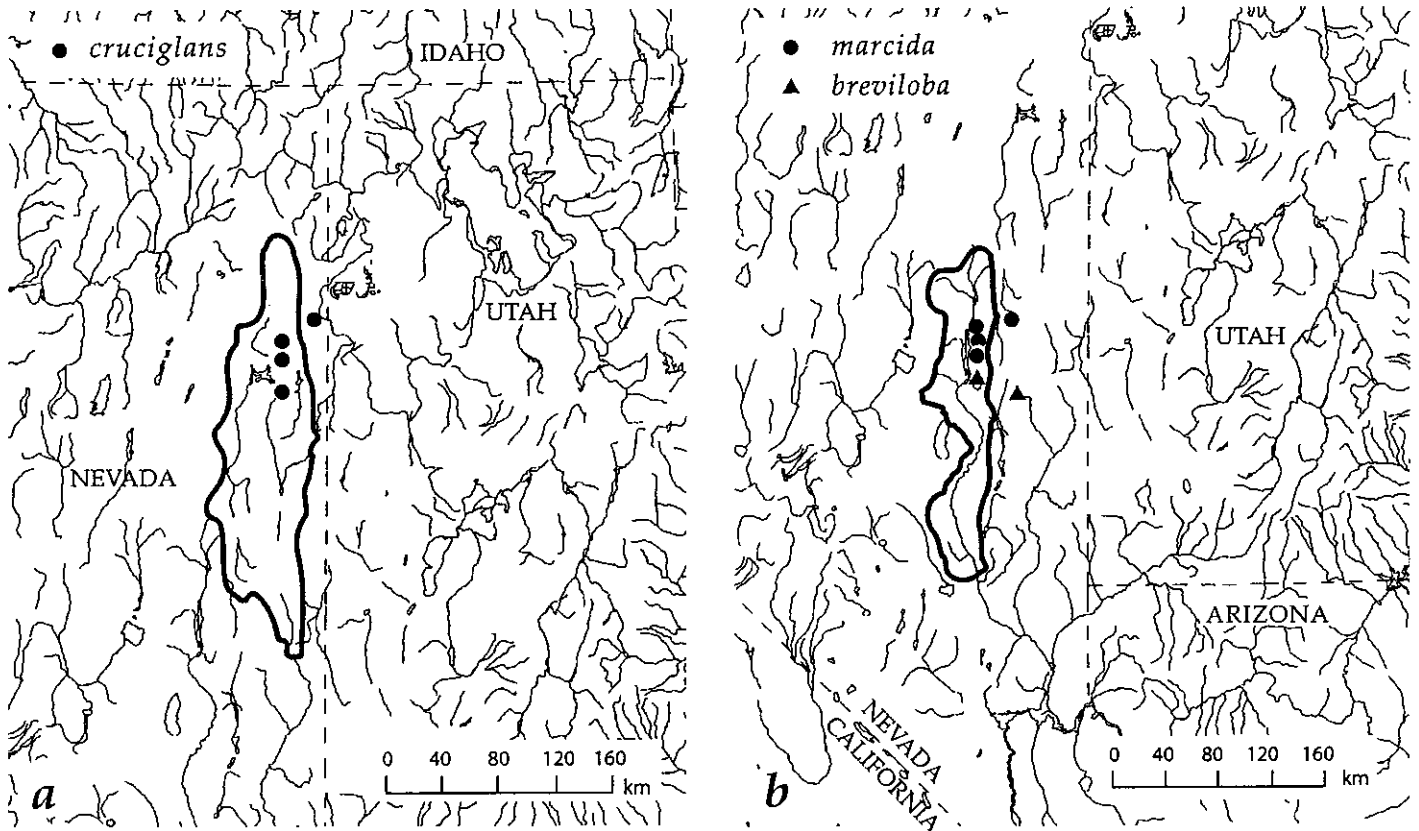


FIGURE 13.—Distributions of selected *Pyrgulopsis* species in Steptoe Basin (a, *P. cruciglans*) and in the upper White River basin (b, *P. marcida*, *P. breviloba*). The heavy lines show the boundaries of these drainage basins.

sin (in southern Utah) probably represents headwater transfers, for which there is also ichthyological evidence (Hubbs and Miller, 1948:29–30) as well as physical evidence (Averitt, 1962; Anderson and Mehnert, 1979). Undescribed material (USNM collection) from the Snake River basin of southeast Idaho is closely similar to or possibly conspecific with this snail, conforming with the physical record of early southerly drainage of southeast Idaho basins (Ore, 1982; Bobo, 1991; Osier, 1995).<sup>10</sup> The distribution of *P. pilsbryana* reflects integration of the Bear Lake and Bear River basins (Figure 12b) and is noteworthy in that this snail does not range below the Oneida Narrows, which comprised the divide between pluvial Lake Thatcher and the Bonneville Basin (Bright, 1963).

**STEPTOE BASIN.**—This large Nevadan basin (which includes Antelope, Goshute, Spring, and Steptoe Valleys) contains eight species, six of which are endemic. Endemic species are concentrated in the northern and southern segments of this drainage, and only the widespread *P. kolobensis* lives in both areas. Five of the endemic species are localized in a large basin floor spring province along the east flank of the Egan Range north of Ely. These snails are united by several unique features and probably represent a species flock, the affinities of which are not clear. The distribution of *P. cruciglans* in the northern segment of Steptoe Basin (Figure 13a) and in the adjacent western

Bonneville Basin is enigmatic because shorelines indicate that although pluvial Lake Waring was relatively deep, its high stand was well below basal sills, and it did not integrate with Lake Bonneville during the late Pleistocene (Hubbs et al., 1974; Currey et al., 1984). Note that the sole native fish living in the Steptoe Basin, *Relictis solitarius*, does not cross the Bonneville divide but instead ranges to the west and south (Butte and Ruby Valleys; Hubbs et al., 1974; Deacon and Williams, 1984).

**UPPER WHITE RIVER BASIN.**—This large area includes Pahranaagat and White River Valleys (above Pahranaagat Wash) but excludes Moapa Valley (the lowermost segment of the White River basin), which maintains external drainage to the Colorado River basin. DiGuseppi and Bartley (1991) suggested that the White River drainage was internally drained before capture by the Colorado River during the Quaternary. This region contains eight species (five endemic); this fauna neither overlaps nor shows affinities with the two species living in Moapa Valley, which instead have affinities with snails in the Amargosa River basin (*P. avernalis*) and Colorado River basin of northern Arizona (*P. carinifera*). The upper White River basin also contains an endemic species of cyprinid fish (Miller and Hubbs, 1960). Of the endemic snails for which affinities are clear, *P. merriami* is most similar to fauna of the Rio Grande and upper



Gila River basins, whereas *P. lata* is most similar to *P. saxatilis* from the Bonneville Basin.

Distributions of two nonendemic species (Figure 13b) suggest prior relationships between the White River region and two fishless valleys to the east (Cave and Dry Lake Valleys) despite physical evidence that the pluvial lakes of these small valleys did not overflow during the late Pleistocene (Mifflin and Wheat, 1979). The distribution of *P. marcida* supports the contention of Hubbs et al. (1974:65) that, although Cave Valley appears to be part of a structural trough including Steptoe Valley to the north, Cave Valley instead probably drained early (i.e., prior to the late Quaternary pluvial period) to the White River valley. We were unable to confirm the assertion of Hubbs and Miller (1948:98) that there may be a low, alluvial saddle separating the southern portion of Cave Valley from the White River valley; maps indicate that these valleys instead are separated in this area by middle Tertiary andesite flows. The distribution of *P. breviloba* (Figure 13b) conforms to an interpretation (Hubbs and Miller, 1948:98) that Dry Lake valley (therein referred to as Bristol Valley) may have drained early, south to the White River valley via Delamar Valley. Drainage integration between these valleys may have been disrupted by significant late Cenozoic lateral slip along the northeast-trending Pahrangat Fault Zone (Rowan and Wetlaufer, 1981; Jayko, 1990).

**RAILROAD BASIN.**—Railroad Valley in south-central Nevada is closed to the east, north, and west principally by the Grant, White Pine, and Pancake Ranges, respectively, but it opens to the southwest into a large basin comprising Reveille, Hot Creek, and Little Fish Lake valleys (Figure 6). Mifflin and Wheat (1979:30) suggested that Big Sand Springs Valley also may have opened southeast to Railroad Valley before the Late Quaternary emplacement of the Lunar Crater Volcanic Field (see Scott and Trask, 1971; Luedke and Smith, 1991). The northern segment of Railroad Valley harbors six endemic species of *Pyrgulopsis*, and widespread *P. kolobensis* also occurs locally, both in Railroad and Reveille Valleys. Four of the local endemics—*P. aloba*, *P. carinata*, *P. lockensis*, *P. papillata*—belong to a group represented in western California and the Lahontan Basin, northern Bonneville Basin, Snake River basin, and Colorado River basin. Three of these snails compose a morphologically distinct subgroup confined to thermal limnocrenes.

**DIXIE BASIN.**—This large, Nevada basin includes Buffalo, Buena Vista, Dixie, Edwards Creek, Fairview, and Pleasant Valleys. It contains two dissimilar endemic species—*P. aurata*, *P. dixensis*—that closely resemble other Lahontan forms. The only endemic fish in this drainage is an undescribed subspecies of *Gila bicolor*, which Hubbs and Miller (1948) suggested was closely related to Lahontan taxa. In support of these connections, Reheis et al. (2002) infer that a high stand of Lake Lahontan flooded into Dixie Basin during the middle Pleistocene.

**OREGON LAKES.**—*Pyrgulopsis* is poorly represented in this large region, which consists of a series of valleys and pluvial lakes in northeast California and southeast Oregon. Only four

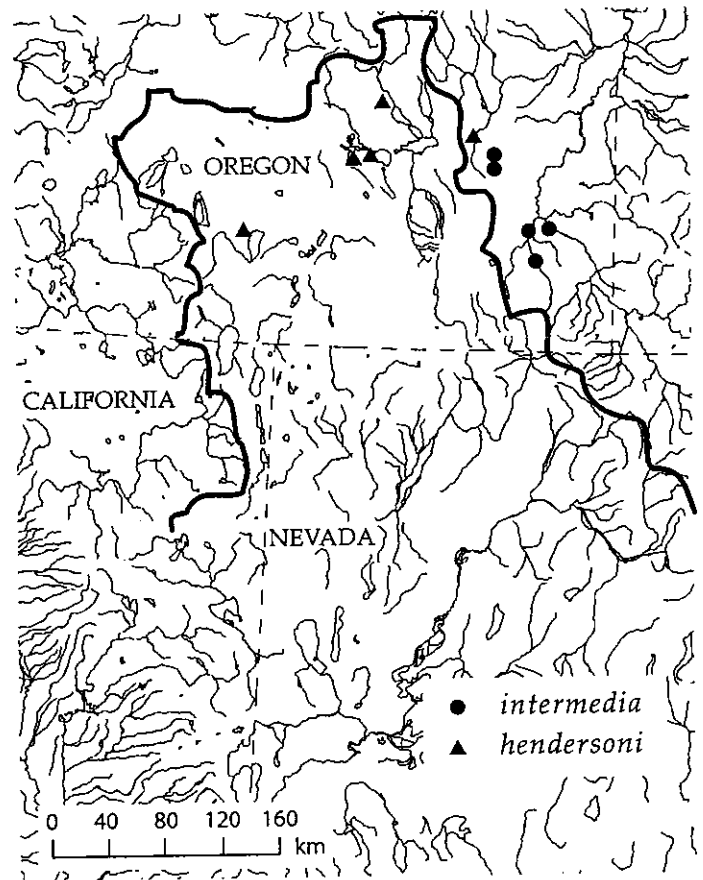


FIGURE 14.—Distributions of *Pyrgulopsis intermedia* and *P. hendersoni* of the "Oregon Lakes" region. The heavy line shows the northwest boundary of the Great Basin.

species are present, none of which are endemic, and relatively large areas (e.g., Goose Lake and Fort Rock basins) apparently lack *Pyrgulopsis*. Biogeographic patterns of these snails, nevertheless, are informative, suggesting past integration of component valleys as well as relationships with both the Lahontan Basin (as discussed above) and the Snake River basin. The distribution of *P. gibba* (Figure 10b) suggests prior integration of Long and Surprise Basins, whose pluvial lakes apparently did not overflow during the late Pleistocene (Mifflin and Wheat, 1979; Allison, 1982, respectively). The snail also lives in Coleman Valley, a small endorheic basin that Hubbs and Miller (1948:65) suggested was flooded by an arm of pluvial Lake Warner. However, Weide's (1974, fig. 19) map of the lake indicates that this did not occur in the late Pleistocene. The distribution of *P. hendersoni* (Figure 14) suggests prior integration of the widely separated Lake Abert and Malheur Lake basins, which is also suggested by the distribution of the fish *Gila bicolor* (Minckley et al., 1986). This snail also lives in springs along the Malheur River, conforming to the oft-postulated prior drainage relationship between the Oregon Lakes region and the Snake River basin (e.g., Wheeler and Cook, 1954; Taylor and Smith, 1981; disputed by Repenning et al., 1995). Shoreline



evidence suggests that pluvial Lake Malheur probably spilled east to the Malheur River (Gehr and Newman, 1978), and a similar eastward drainage through Malheur or Crane Gaps may have occurred earlier, before late-Pleistocene emplacement of lava flows (Piper et al., 1939; Bisson and Bond, 1971; Baldwin, 1976). The distribution of *P. intermedia* also suggests a prior relationship between regional drainage and the Snake River basin. This snail lives in Crooked Creek, a tributary to the Owyhee River (Snake River basin), as well as in Barren Valley, a small basin often depicted on maps as draining to the Snake River basin (e.g., Snyder et al., 1964; Williams and Bedinger, 1984) but which, in fact, is endorheic and seemingly a northern extension of the Alvord Basin trough. Snail populations from the Pit River and Klamath Lake basins are similar to *P. intermedia*—although probably not conspecific, as suggested by Taylor (1985:309).

### Conclusions

*Pyrgulopsis* biogeography within the Great Basin conforms in part to current interpretations of pluvial drainage configurations, but in many cases it defines additional or more complicated patterns that presumably reflect older relationships. Various drainage relationships between the Great Basin and adjacent regions also are implied by these data, although there is surprisingly little evidence of past integration between the Great Basin and the Sacramento River basin to the west and the

upper Colorado River basin to the northeast. This may partly reflect inadequate sampling of these extra-limital areas. In contrast to previous suggestions that the Great Basin had prior connections along its northeast and northwest boundaries with the Snake River basin (Taylor, 1966a, 1985; Minckley et al., 1986; Taylor and Bright, 1987), *Pyrgulopsis* biogeography suggests a more continuous pattern of northern integration.

As mentioned above, a more rigorous biogeographic analysis of *Pyrgulopsis* must await preparation of a well-corroborated phylogeny for its species, which will prove difficult using morphological criteria alone and thus will probably require the use of DNA sequence data. Determination of cladistic structure among Holocene species of this group can provide a hierarchical depiction of historical relationships among drainages, but the fossil record also must be better utilized to constrain the chronology more tightly. Given that hydrobiids are difficult to identify at the species and, often, generic ranks based on traditional shell characters, new methods will be needed to extract a phylogenetic signal from fossils, perhaps from details of shell structure or composition of preserved organic shell components. Ecological characteristics of fossil *Pyrgulopsis* also must be better understood if we are to determine, for instance, whether interbasinal patterns reflect vicariance of pluvial lake biota or transmontane headwater transfers. This information may perhaps be obtained from a combination of environmentally sensitive isotopes preserved in shell fabric and more detailed study of sedimentary facies.

## Appendix

### Species Groups of *Pyrgulopsis*

The informal groups described below are defined mostly by characters of penial form and ornament. We follow the terminology of Hershler, 1994.

1. A small number of species, mostly from the Great Basin, share a simple penis bereft of distal lobe and glands (Figure 4a). These snails otherwise closely resemble typical *Pyrgulopsis*, and a close relationship is inferred, although separate generic status for some or all of these may be suggested upon cladistic analysis. Subgroups are discernable on the basis of shape of shell and penial filament. Species included are *aloba*, *augustae*, *carinata*, *coloradensis* (Virgin River basin), *dixensis*, *eremica*, *greggi* (Kern River basin), *lockensis*, *millenaria*, and *papillata*.
2. Snails of this group have a glandular ornament of a single, superficial ventral unit (Figure 4b). This gland differs in appearance from the narrow, raised ventral gland typical of *Pyrgulopsis* and resembles that of eastern American *Birgella* (Thompson, 1984, figs. 81, 82) and *Rhaphinema* (Thompson, 1970, fig. 3D,E). With the exception of *P. arizonae*, the snails of this group also lack a penial lobe, per-

haps indicating a close relationship with the group described above. Subgroups are recognizable on the basis of shell shape and gland position and size. Species included are *arizonae* (Gila River basin), *avernalis* (Colorado River basin), *basiglans*, *bernardina* (Río Yaqui basin), *bifurcata*, *crystalis*, *erythropoma*, and *pisteri*.

3. A large number of species share a relatively narrow, distally bifurcate penis ornamented with a terminal gland along the distal edge of the rather small lobe (Figure 4c). Other dorsal glands are absent in these snails, although some species have a single ventral gland. The terminal gland is often oriented longitudinally rather than transversely, as in groups described below. In some species the terminal gland is weakly developed (e.g., *stearnsiana*) or often absent (*bryantwalkereri*). This group conforms in large part to the "*Fontelicella stearnsiana* series" described by Taylor (1987:10). Subgroups are recognizable on the basis of shell shape, shape of penial lobe and filament, and development of the terminal gland. Species included are *amargosae*, *aurata*, *bacchus* (Colorado River basin), *brandi* (Río Casas Grandes basin), *breviloba*, *bruneauensis* (Snake River basin), *bryantwalkereri*, *carinifera* (Colorado River basin), *conica* (Colo-

- rado River basin), *fairbanksensis*, *hamlinensis*, *hubbsi*, *imperialis*, *isolata*, *lentiglans*, *manantiali* (Cuatro Ciénegas basin), *micrococcus*, *montana*, *morrisoni* (Verde River basin), *nanus*, *nonaria*, *sathos*, *simplex* (Verde River basin), *sola* (Verde River basin), *stearnsiana* (California coastal drainage), *thompsoni* (Gila River basin), and *transversa*.
4. A medium-sized group comprises species in which the outer edge of the dorsal penis has an elongate gland (Dg1) abutting or slightly overlapping the filament (Figure 4d). Penial ornament in this group is otherwise variable, although most species have a terminal gland, ventral gland, and sometimes additional dorsal glands. The penial lobe of these snails often is enlarged relative to the filament. This group includes the large snails allocated to the subgenus *Natricola* Gregg and Taylor, 1965, except for *intermedia*. Species included are *glandulosa* (Verde River basin), *hendersoni*, *hovinghi*, *idahoensis* (Snake River basin), *inopinata*, *montezumensis* (Verde River basin), *pecosensis* (Rio Grande basin), *pellita*, *robusta* (Snake River basin), and *sublata*.
  5. Another large group consists of snails in which the penis has a short penial gland at the base of the filament and generally no other dorsal glands other than a terminal gland and occasionally a ventral gland (Figure 4e). Subgroups are recognizable on the basis of shell sculpture, shape of penial lobe and filament, development of terminal gland, presence of additional dorsal glands, and position of ventral gland. Species included are *anatina*, *archimedis* (Klamath Lake basin), *diablensis* (Sacramento River basin), *fusca*, *humboldtensis*, *kolobensis*, *lata*, *leporina*, *limaria*, *longae*, *marcida*, *militaris*, *nevadensis*, *notidicola*, *pictilis*, *pilsbryana*, *saxatilis*, *serrata*, *sterilis*, *taylori* (California coastal drainage), *trivialis* (Gila River basin), *turbatrix*, *umbilicata*, *variegata*, and *vinyardi*.
  6. Six species have a penis with a well-developed terminal gland, a ventral gland, and a weakly developed additional dorsal gland corresponding to Dg1 (Figure 4f). Species

included are *aardahli*, *gibba*, *giulianii*, *owensensis*, *perturbata*, and *ruinosa*.

7. The five species locally endemic in southwestern Steptoe Valley are united by strong protoconch microsculpture, a broadly conical or subglobose shell, and unique features of the central radular teeth (fused lateral cusps, basal cusps absent or very weakly developed, elongate basal tongue). Although penial form and ornament varies considerably among these species, we nevertheless interpret the group as a strongly differentiated clade based on the synapomorphic radular features. Species included are *landyei*, *neritella*, *orbiculata*, *planulata*, and *sulcata*.
8. Two Great Basin species share a distinctive pattern of penial ornament consisting of a large, raised, proximal dorsal unit (Figure 4g). These species are *cruciglans* and *plicata*.
9. A large number of species share a massive penis having a long gland on the dorsal surface of the penial filament (Pg); typically they also share a terminal gland (typically transverse, and often U-shaped), one or two ventral glands, and one or more additional dorsal glands (Figure 4h). Members of this group usually have an enlarged, pyriform bursa copulatrix and a narrow bursal duct. The seminal receptacle is often very small relative to the bursa copulatrix and usually is well posterior in position, broadly overlapping the bursa copulatrix. This group corresponds, at least in part, to the "californiensis series," as defined by Taylor (1987). Subgroups are recognizable from the presence of secondary dorsal glands and from the shape and multiplication of penial glands. Species included are *anguina*, *californiensis* (California coastal drainage), *chamberlini*, *chihuahua* (Rio Carmen basin), *chupaderae* (Rio Grande basin), *davisi* (Rio Grande basin), *deaconi*, *deserta* (Virgin River basin), *fausta* (Colorado River basin), *gracilis*, *intermedia*, *longiglans*, *longinqua*, *metcalfi* (Rio Grande basin), *neomexicana* (Rio Grande basin), *peculiaris*, *roswellensis* (Rio Grande basin), *sadai*, *thermalis* (Gila River basin), *ventricosa* (Sacramento River basin), *villacampae*, and *wongi*.

## Notes

1. Ponder et al. (1994) suggested that passive dispersal on birds may be a significant factor in biogeography of some Australian hydrobiids.
2. Twelve eastern American species currently are allocated to the genus (Hershler and Thompson, 1987; Hershler, 1994; Thompson, 1995); recent morphological studies indicate that this fauna is a distinct clade that is not closely related to *Pyrgulopsis* (Thompson and Hershler, In press).
3. Tall-spined western Paleogene hydrobiids, usually allocated to *Hydrobia* or *Micropyrgus* (e.g., from Flagstaff Formation; La Rocque, 1960), approach the range of shell variation of modern *Pyrgulopsis*, but they probably represent other clades (Taylor, 1975).
4. Other genera in the subfamily are *Birgella*, *Cincinnatia*, *Notogillia*, *Nymphophilus*, *Rhaphinema*, *Spilochlamys*, and *Stiobia* (Thompson, 1979).
5. These and other early concepts of extent and timing of late Cenozoic uplift of the Sierra Nevada (e.g., Axelrod, 1962; Huber, 1981) have recently been dis-

puted (Small and Anderson, 1995; Wernicke et al., 1996; Wolfe et al., 1997).

6. An earlier conjecture (Hershler and Pratt, 1990:292) that all of the endemic *Pyrgulopsis* in Ash Meadows were derived from taxa in the White River Valley (whose lowermost segment is Moapa Valley) to the east was premature.

7. This refers to a distributional track encompassing the Bonneville Basin, the middle Snake River drainage, the Lahontan Basin, and the Death Valley system.

8. Nagy and Murray (1996) suggested that this drainage reversal may not have occurred before 0.5 Ma.

9. Late Cenozoic fossil Foraminifera from Panamint Valley may have lived in a saline lake instead of in an estuary (Smith, 1960).

10. Whether or not the late Pleistocene Bonneville Flood (Malde, 1968; O'Connor, 1993) also contributed to snail exchange with the Snake River basin is conjectural.

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