

A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States. Part I. Genus *Pyrgulopsis*

ROBERT HERSHLER

Department of Invertebrate Zoology (Mollusks), NHB STOP 118, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

Abstract. A recently completed field survey of springs throughout the Great Basin yielded collections of hydrobiid snails from more than 500 sites, and revealed a wealth of undescribed diversity of these small gastropods. In this, the first of a two-part taxonomic series treating this material, 58 new species of *Pyrgulopsis* Call & Pilsbry, 1886, are described; and new records are provided for 10 previously described members of this genus. Assignment of these novelties to *Pyrgulopsis* is done with the acknowledgement that this large genus, as currently constituted, is probably not monophyletic, but a more refined classification of these snails reflecting evolutionary relationships must await preparation of a phylogenetic analysis, which is beyond the scope of this work. *Pyrgulopsis* occur in a variety of spring-fed water bodies in the Great Basin, including brackish and/or thermal habitats. Although a few species are widespread in the region, local endemism is prevalent and 22 of the new species are known only from single localities. Several areas contain concentrations of locally endemic snails which may represent species flocks, notably Duckwater Valley (seven species) and southern Steptoe Valley (five species). This fauna is largely distributed in an allopatric fashion, although a few springs harbor two or three species. Most of the springs inhabited by hydrobiids in the region are small, fishless, and have been ignored by state and federal land management agencies. However, many of these sites are degraded by livestock grazing, water withdrawal, and other activities and will require protection in order to conserve snails and other native aquatic biota. Two of the novelties described herein have become extinct during the past two decades.

... the western states appear to present a set of conditions that should encourage isolation and speciation, especially in certain taxa containing macroscopic forms and the West should theoretically have a unique population of freshwater invertebrates. ... Indeed, there is already evidence to show that the western aquatic invertebrate fauna is much richer and more varied than is indicated in the literature. (Pennak, 1958:224)

INTRODUCTION

Pennak's assertion that the aquatic invertebrate fauna of the western United States is undersampled was accompanied by a plea for colleagues to pursue more field, laboratory, and zoogeographic work in the region and publish the results of these endeavors. Although his prediction has been affirmed by the unabated publication of new taxa from the region over the past 28 years (e.g., Holsinger, 1974; Holsinger & Longley, 1980; Taylor, 1987), large areas in the West still have not been comprehensively surveyed and various aquatic invertebrate groups remain poorly known. Among the latter are the ubiquitous, locally abundant (Noel, 1954), small freshwater gastropods of the family Hydrobiidae, which total about 100 described species in the West. These snails are tightly linked with their aquatic habitat and often are endemic to single water bodies (particularly springs) or local drainage systems, features which render the group eminently suitable for zoogeographic inquiry (Taylor & Bright, 1987) and also thrust them into prominence with respect to ongoing efforts to conserve and manage western aquat-

ic ecosystems. Much of this snail fauna now is imperiled—although a few species have been added to the Federal List of Threatened and Endangered Wildlife, a more telling indication of the status of the fauna is the fact that until recently, when the U.S. Fish and Wildlife Service discontinued designation of Category 2 species as candidates (USDI, 1996), most of these snails were candidates for addition to this list (e.g., USDI, 1994).

Although western hydrobiids are poorly known, the fauna of the Great Basin, in particular, has been neglected. This huge (500,000 km²), remote and relatively rugged region is composed of more than 100, typically isolated, drainage basins (Mifflin, 1988:fig. 3) that were variously integrated during the wetter or pluvial period of the Late Quaternary (11,000–13,000 ybp) when many large lakes or wetlands were present (Figure 1). Although about 40 nominal species of hydrobiids have been recorded from the region, the group has not figured prominently in the few faunal surveys of the region (e.g., Brues, 1928, 1932), and published collections are from relatively few, widely scattered locales. Field coverage has been extremely uneven as, for instance, the Great

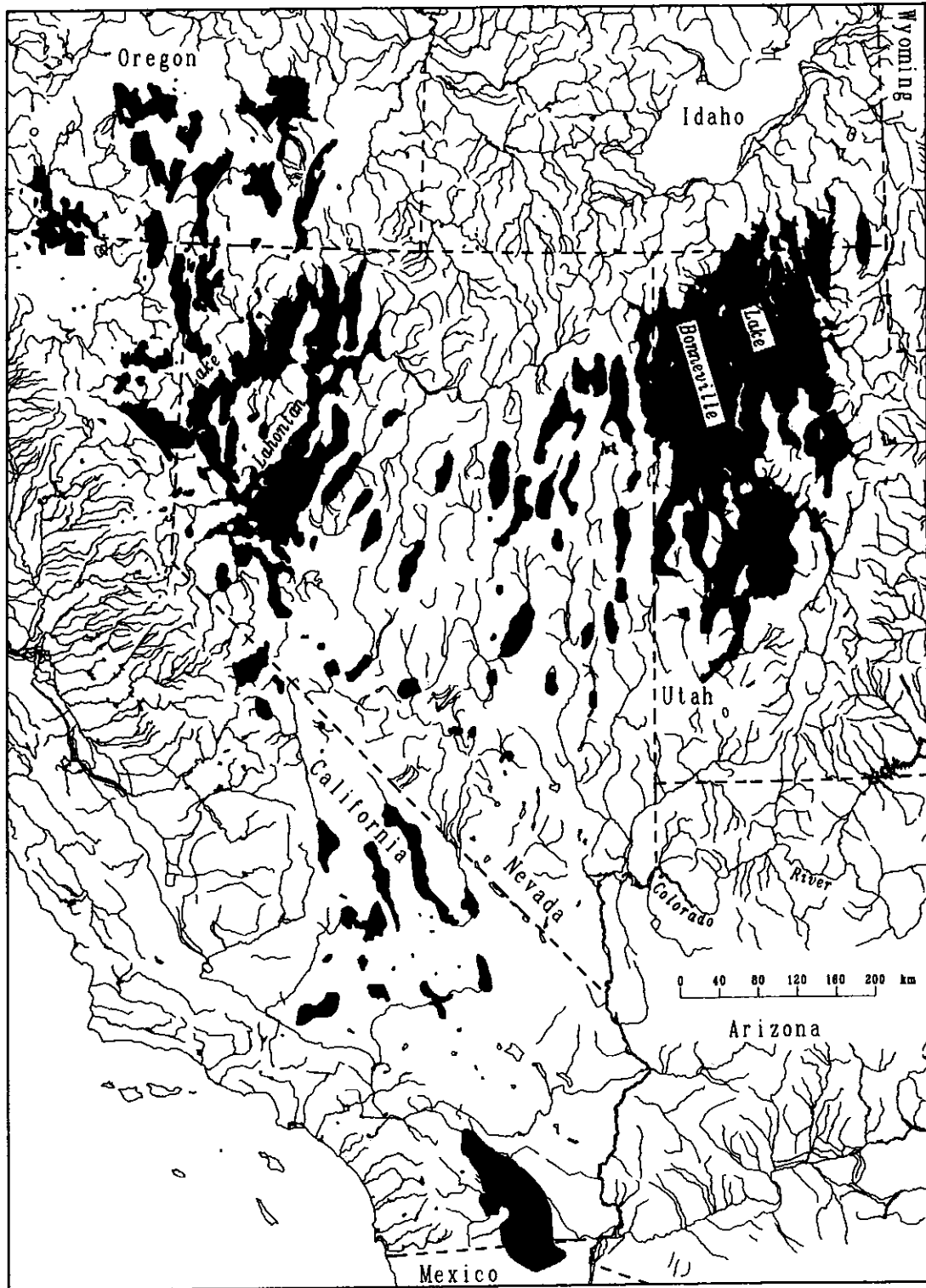


Figure 1

Map showing pluvial lakes (black) of the Great Basin superimposed on modern drainage (lake distribution from Miffin & Wheat, 1979; King, 1982; Currey et al., 1983; Williams & Bedinger, 1984).

Basin of Utah was relatively well surveyed by Chamberlin, Jones, and other workers, while Nevada scarcely has been touched. However, the literature also provides indications that much fauna remains to be described (e.g., Deacon et al., 1980; J. E. Williams et al., 1985; Taylor & Bright, 1987:241). The paucity of collecting activity has important biogeographic implications as, for instance, the widely cited "fish hook" pattern, a distributional track attributed to various mollusks (and fishes) and extending from the eastern Bonneville Basin via the middle Snake River and western Lahontan basin to the Death Valley system (Taylor, 1960:figs. 1-3; Taylor, 1966a:fig. 7; Smith, 1981) may reflect inadequate sampling in the Great Basin of northern Nevada. Furthermore, most of the previous work on this fauna was published prior to the advent of modern approaches to gastropod systematics, and consisted of descriptions of single species based on empty shells. Many shell characters have proven unreliable, and hence these treatments are of limited utility today. The minimal attention paid to the hydrobiid snails of the Great Basin may be partly attributable to an impression that the desert basins of this region are largely devoid of aquatic biota: note that a large, fishless portion of south-central Nevada was named the "area of sterile basins" by Hubbs & Miller (1948:45).

There is an urgent need for discovery and documentation of these snails, as the typical habitats of Great Basin hydrobiids, very small springs that are often less than 1 m wide and 1 cm deep, are fragile, unprotected, and prone to extreme degradation owing to water development in the region, particularly livestock grazing. To fulfill this need and generate a biogeographic database I began field survey in 1985 of the Death Valley system, a large pluvial drainage in southwestern Nevada and southeastern California. Completion of this survey led to the description of 19 new species of hydrobiids from the region (Hershler & Sada, 1987; Hershler, 1989; Hershler & Pratt, 1990). Field survey then shifted to the remaining portions of the Great Basin in California, which led to discovery of an additional three new species (Hershler, 1995). From 1991-1995, a survey of the rest of the hydrographic Great Basin¹ was conducted. This included portions of Idaho, Nevada (exclusive of previously visited portions of the Death Valley system), Oregon, Utah, and Wyoming. Drainages of the Colorado River and Snake River in Nevada also were visited. During the survey more than 2000 sites were visited. Hydrobiid snails were collected from more than 500 springs, and many new taxa were discovered. The purpose of this paper, the first of a two-part taxonomic series, is to describe the new material of *Pyrgulopsis* Call & Pilsbry, 1886, the largest genus of hydrobiids in North America. In a recent review (Her-

shler, 1994), I recognized 65 Recent species in *Pyrgulopsis*; eight more new species have since been introduced (Hershler, 1995; Thompson, 1995). Herein an additional 58 new species are described, as are numerous new records for 10 previously described members of this genus.

Novelties described herein are allocated to *Pyrgulopsis* in the broad sense utilized by Hershler (1994). Note that a preliminary phylogenetic hypothesis for species in this genus (Hershler, 1994:fig. 31) permitted recognition of several well-supported clades within this group, which may be better treated as separate genera in the future. (Monophyly of *Pyrgulopsis* was not well tested as only a single outgroup was used.) Several additional morphologically cohesive groups are described herein, but allocation of these to new genera is tabled until a more comprehensive phylogenetic review of *Pyrgulopsis* is prepared. Fauna described herein includes not only several distinct, well-delineated groups, some of which may represent local "species flocks" (e.g., in Railroad and Step-toe Valleys), but also a large number of relatively similar yet geographically scattered species of uncertain affinities. Although the latter are contrasted principally on the basis of penial form and ornament, the reader should be aware that characters derived from these features are probably subject to homoplasy and may be misleading with regard to phylogenetic signal. Thus, for instance, it is difficult to confidently ascertain whether some of the new species modestly endowed with glandular ornament on the penis are allied with snails having similar penes or, alternatively, should be interpreted as reduced forms derived from either of two regionally widespread species, *P. gibba* Hershler, 1995, and *P. kolobensis* (Taylor, 1987). Given the large number of species and relatively small number of characters used in the descriptions, it will be difficult to unravel the phylogenetic relationships among these taxa using morphological criteria alone. In any event, such an analysis is beyond the scope of this paper, as it will require additional study of the many other congeners (encompassing characters not utilized in my earlier review) as well as re-evaluation of concepts of character discrimination and state coding based on information derived from the current study.

MATERIALS AND METHODS

This work was principally based on study of material (dry shell and anatomical components) collected during the recent field survey (and now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.), as other museum material from the region is scarce and almost always of empty shell, which usually cannot be confidently identified to species in this group. Identification of springs to be surveyed was facilitated by study of United States Geological Survey topographic maps (1:100,000 scale) and communications from various colleagues (see Acknowledgments). Mate-

¹ This restricts the Great Basin to the region characterized by internal drainage. Other definitions (physiographic or floristic) outline slightly different regions (see D'Azevedo, 1986:fig. 2).

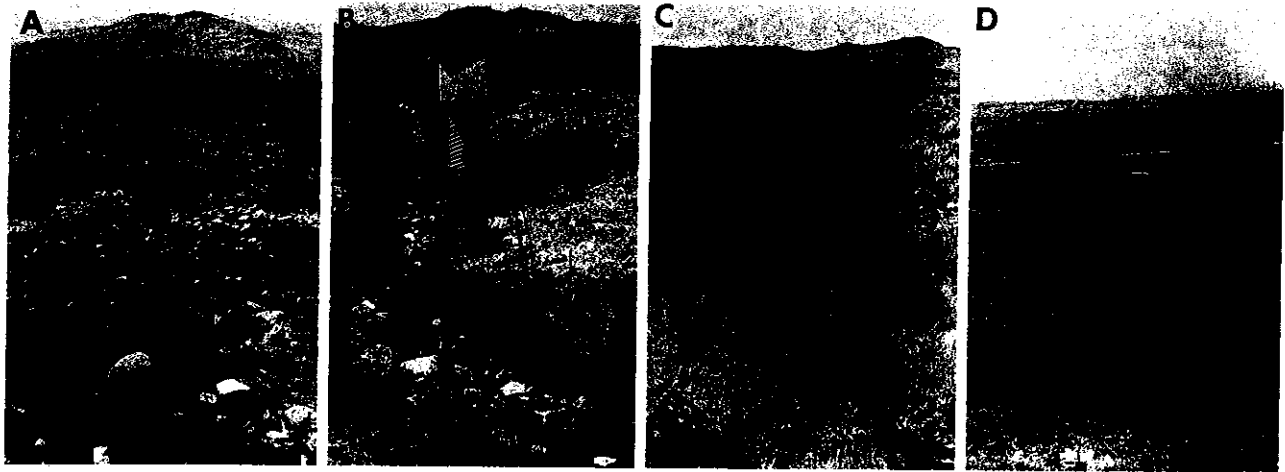


Figure 3

Representative Great Basin springs. A. Horseshutem Springs, nestled along the western flank of the Spring Mountains (1480 m elevation) in southeast Nevada. This small rheocrene, severely impacted by cattle, is the type locality of *P. turbatix*. Photograph by D. Sada, July, 1995. B. One of many small, thermal rheocrenes in the Mud Meadow drainage in northwest Nevada. Water temperature at this site was 39°C, and *P. notidicola* was found living in a moistened zone just outside the water. Note the artificial impoundment and old gauge box at the source of this spring. Photograph by G. Vinyard, August, 1991. C. Unnamed spring in Park Valley, northwest Utah. One of many highly mineralized springs in the Bonneville Basin inhabited by *P. kolobensis*. Photograph, August, 1993. D. Unnamed springs in the Simpson Mountains (1779 m elevation), overlooking the Old River Bed in southern Utah. These small, mineralized (1126 micromhos/cm) rheocrenes compose the type locality of *P. transversa*. Photograph, May, 1993.

number, size, position, orientation, apparent fusion of glands on penis; shape, position of penial duct.

Previously described species are treated only when new records were obtained from the field survey. Literature compilations pertaining to these snails are in Taylor (1975) and my recent review of *Pyrgulopsis* (Hershler, 1994). Synonymies for these taxa are not intended to be complete, but instead detail original citation of species (and synonyms), assignment to *Pyrgulopsis*, treatments of material from the study area, and pertinent references to the broader works listed above. A common name is proposed for each new species to facilitate their reference by governmental agencies.

NATURAL HISTORY

Pyrgulopsis are widespread within the Great Basin where they occur in a variety of relatively small, usually fishless, spring-fed water bodies (Figures 3–5). These animals also historically occurred in a few of the Great Basin lakes, with the main example provided by *P. nevadensis* (Stearns, 1883), which lived in Pyramid Lake (of the Lahontan Basin) until becoming extinct around the turn of the century. Members of this genus have not been found in any of the rivers of the Great Basin. The most common habitat for these snails is a rheocrene, or a spring which emerges from the ground as a flowing stream. *Pyrgulopsis* also occur in limnocrenes, in which the headspring forms a natural pool (which is drained by a flowing

stream), and helocrenes, springs that comprise marshlike situations. Waters harboring *Pyrgulopsis* range from small seeps with miniscule discharge and depth of 1 cm or less, to large springs such as those feeding Clear Lake in southern Utah, whose discharge is about 6.8 m³/sec (Mundorff, 1971:62). While most of these springs are of medium temperature (e.g., 10–21°C.), snails were also found in more than 50 thermal springs (e.g., those having temperature greater than 21°C.; per Garside & Schilling, 1979:1). While most of these springs were in the 22–35° range, it is worth noting that in the two cases in which even warmer (ca. 39°C.) water was involved (i.e., springs in Mud Meadows harboring *P. notidicola*; described below), most of the snails seen were macicolous, inhabiting a moistened zone around the margins of the spring. While most of the springs were of low to medium conductivity (e.g., 200–600 micromhos/cm), *Pyrgulopsis* were collected from more than 50 brackish springs (having greater than 1 gm/l total dissolved solids; Todd, 1980), most of which were along the margins of the Great Salt Lake Desert (and harbored *P. kolobensis*).

Pyrgulopsis often decline dramatically in density downflow from spring sources, presumably reflecting their requirement for the well-known stable temperature, chemistry, and flow regime characterizing headsprings (Deacon & Minckley, 1974). This pattern of distribution is most pronounced in smaller springs, while in larger habitats *Pyrgulopsis* may occur far downstream from spring sources.

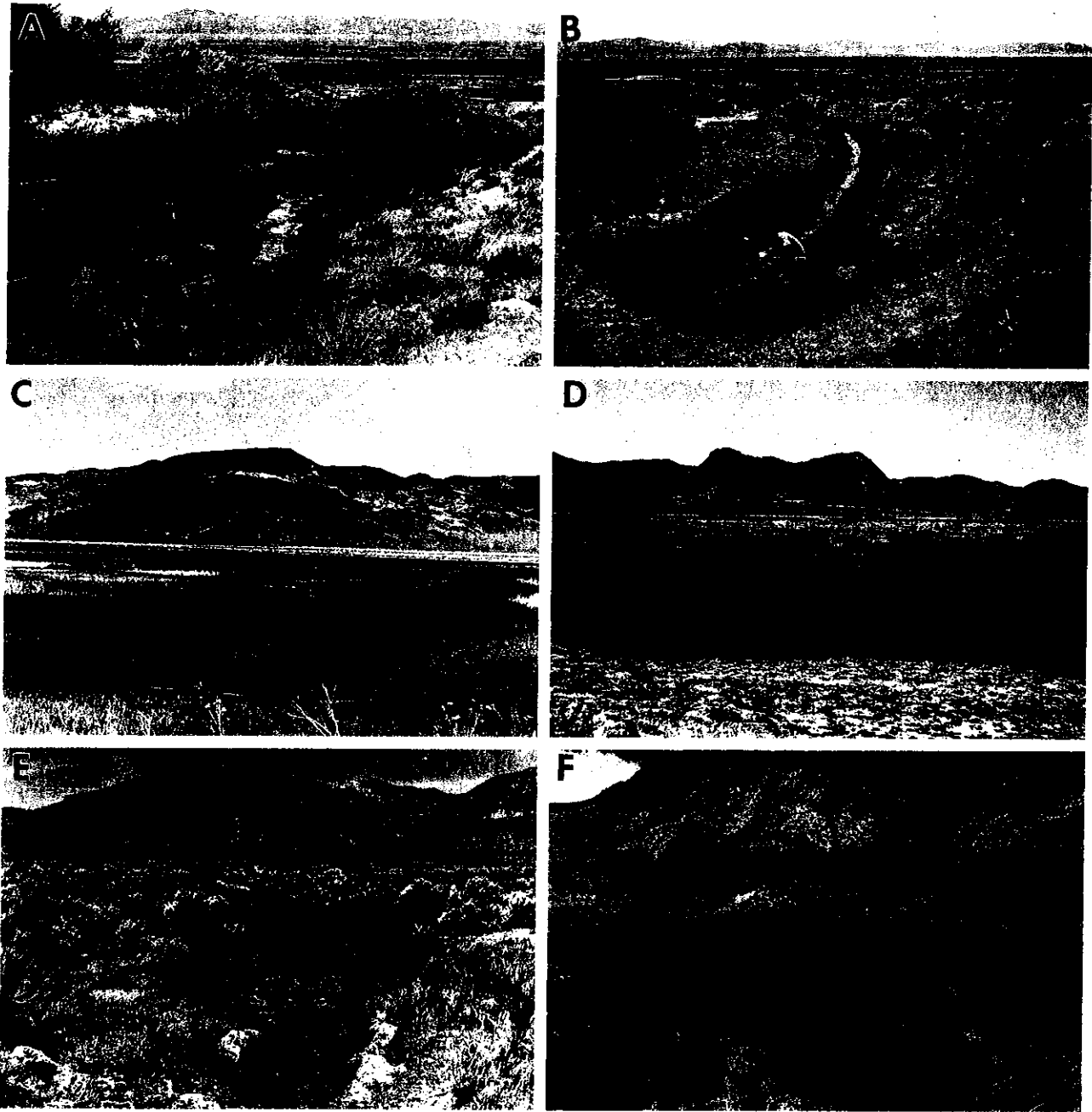


Figure 4

Representative Great Basin springs. A. The northernmost spring in the Flag Spring complex, White River Valley, Nevada. This limnocrene (pool diameter about 15 m) is the type locality of *P. sathos*, which was collected along the margins of the 14 m diameter pool. *Pyrgulopsis breviloba* was abundant in the outflow channel below the pool. Photograph, June 1992. B. The southernmost spring in the Emigrant Springs complex, White River Valley, Nevada. *Pyrgulopsis gracilis* and *P. marcida* co-occur in this small rheocrene, which is highly impacted by cattle. Photograph, June 1992. C. Unnamed basin floor spring in Fish Lake Valley, Nevada. The source of this spring is a small (2 m diameter), thermal (26°C.) limnocrene. The narrow outflow is the type locality of *P. ruinosa*, now believed to be extinct. Photograph, July 1988. D. Big Warm Spring, a large, thermal (30.5°C.) limnocrene in Duckwater Valley, Nevada. This is the type locality of *P. papillata*, and *P. villacampae* also is present. Photograph, D. Sada, October 1992. E. One of many small rheocrenes that compose a large wetland along the southeastern edge of Steptoe Valley near Ely, Nevada, which contains a series of locally endemic snail species (as well as *P. kolobensis*). This site is the type locality of *P. sulcata*. Photograph, August 1991. F. Series of small rheocrenes along Pine Creek, Humboldt River drainage, Nevada, which harbor *P. gibba*. Photograph, July 1991.

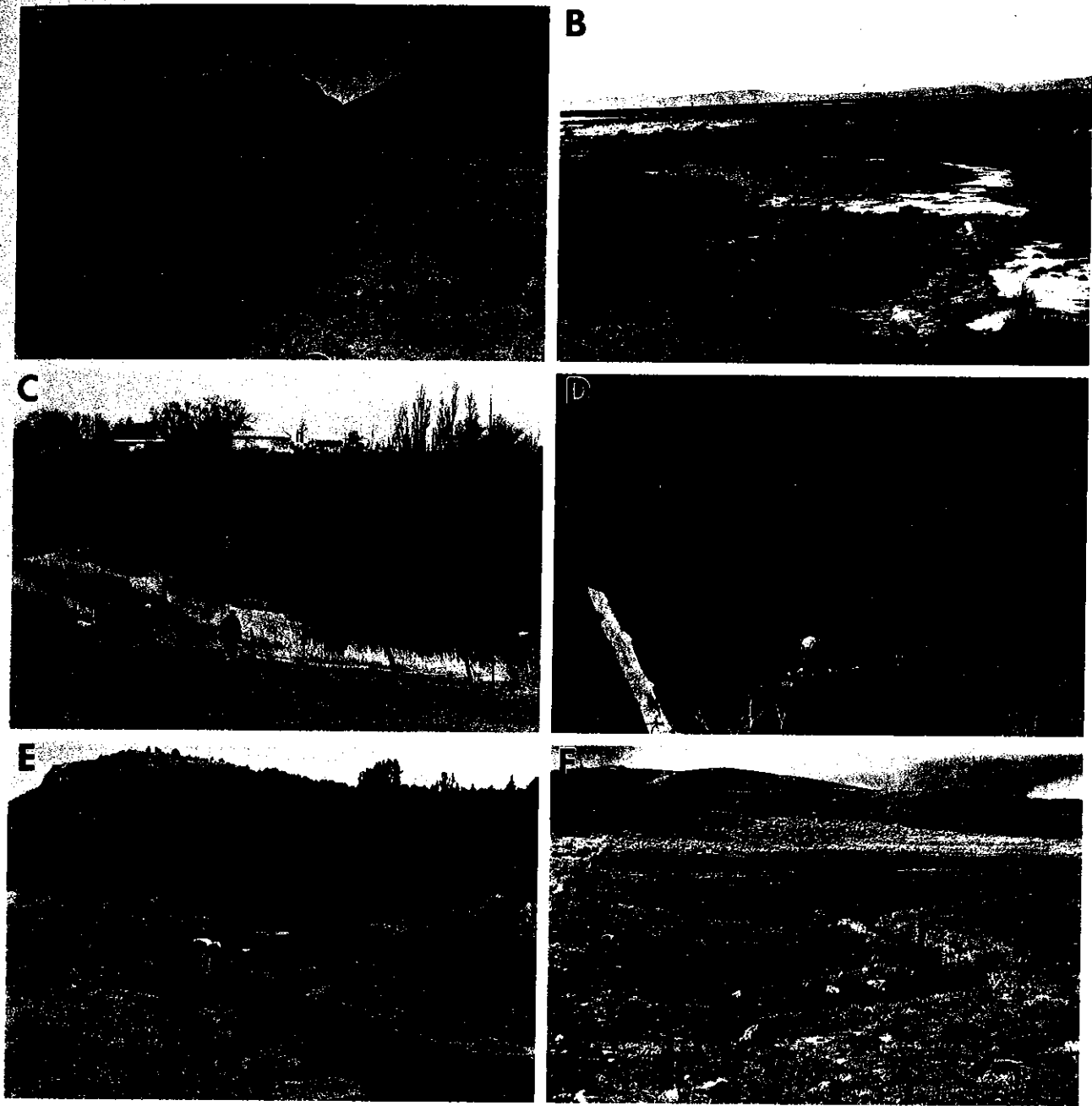


Figure 5

Representative Great Basin springs. A. Wetland fed by a series of small, mineralized (ca. 1000 micromhos/cm) springs, perched in the Shoshone Range above Reese River Valley, Nevada. This is the type locality of *P. sadai*, which was found in only one of these springs (in a small area of about 1 m²), all of which were highly degraded by cattle. Photograph, July 1994. B. Bar M Spring, one of the many brackish springs along the northern edge of the Great Salt Lake (Utah) that harbors *P. kolobensis*. Photograph, July 1993. C. Salt Spring, another brackish spring in northern Utah harboring *P. kolobensis*. Photograph, May 1993. D. Unnamed springs along the eastern flank of the White Rock Mountains (2180 m elevation), overlooking Hamlin Valley, Utah. This is the type locality of *P. hamlinensis*, which occurred abundantly in the dense stand of watercress lining the small stream. Photograph, May 1993. E. Broad (8 m), shallow, spring-fed stream tributary to Etna Reservoir, Grouse Creek Valley, Utah, harboring *P. variegata*. Photograph, July 1993. F. Series of small rheocrenes, Thousand Springs Creek drainage, Nevada, comprising the type locality of *P. millenaria*. Photograph, August 1992.

Pyrgulopsis are most commonly found among aquatic vegetation, especially Cress (*Rorippa*²), which often forms dense mats lining outflows of small springs. In larger limnocrenes (which often are thermal), snails may be found on other aquatic plants such as Bladderwort (*Utricularia*), or on the bases of riparian Spike rush (*Eleocharis*) or Tule (*Scirpus*). Snails are also often found on hard substrates such as bedrock or pieces of travertine. *Pyrgulopsis* are rarely found on or in soft sediment. Although quantitative sampling of snails was not pursued during this project, the densities of 1000–10,000 snails/m² reported for several limnocrene springs in eastern Nevada by Deacon et al. (1980) are probably typical for that habitat in the Great Basin, and considerably less than those of snails inhabiting the smaller rheocrenes. As an indication of the typical local abundance of these animals, a few minutes of sampling at a site usually yielded several hundred living individuals.

Pyrgulopsis are not only found in basin floor springs, which often line the perimeter of dry lake beds and whose outflows coalesce to form large marshes, but also in springs farther up the mountain slopes as well as in spring brooks and streams coursing along well-defined canyons. The snails were collected from sites ranging up to about 2440 m elevation, but appeared to "drop out" in higher alpine situations. For the most part, members of this fauna are distributed in an allopatric fashion. Sympatry of two (and rarely three) congeners was documented at only 14 of the more than 400 sites listed herein, most of which were springs in Duckwater and Steptoe Valley where series of locally endemic species occur. Although the fauna includes several widespread species, notably *P. gibba* and *P. kolobensis*, local endemism is a more common feature. Note that 22 of the 58 new species appear to be restricted to single localities. Details of biology have not been studied for *Pyrgulopsis* of the Great Basin. In the sole detailed study of biology of any species of the genus, Mladenka (1992) determined that *P. bruneauensis*, which is endemic to thermal springs in the Snake River drainage of southern Idaho, is a non-selective grazer of algae and diatoms. As with other congeners, the Great Basin species are oviparous, with females depositing single, small egg capsules on hard substrates.

Two of the species described herein (*P. carinata* and *P. ruinosa*) apparently have become extinct during the past one or two decades. Relatively few of the collecting sites are in pristine condition, with livestock grazing being the predominant source of disturbance. Smaller, basin floor springs in particular were often profoundly disturbed by cattle, which modify the habitat both physically and chemically by trampling, removing aquatic and riparian vegetation, and depositing urine and feces. The resulting habitat often is largely unsuitable for *Pyrgulopsis*, al-

though snails may persist in a small, upflow "refuge" of clean, flowing water which cows cannot reach. Additional, but less prevalent sources of disturbance are related to human residential and recreational activities, notably diversion and/or withdrawal of water. Exotic biota also may pose a serious threat to these populations, particularly crayfish, which have been widely introduced into the region's waters (Bouchard, 1978; Johnson, 1986) and, although omnivorous, often feed on small gastropods (Covich, 1978; Vermeij & Covich, 1978). An Asiatic gastropod, *Melanoides tuberculata* (Müller, 1774), now thrives in many of the warm springs of the Great Basin and may be displacing native prosobranch snails here and elsewhere in the West (see Murray, 1970; Williams et al., 1985), although rigorous documentation of this phenomenon and elucidation of its mechanism are lacking.

SYSTEMATICS

Family HYDROBIIDAE Troschel, 1857

Pyrgulopsis Call & Pilsbry, 1886

Type species: *Pyrgula nevadensis* Stearns, 1883; original designation.

Diagnosis: A North American freshwater genus distinguished from other taxa assigned to the subfamily Nymphophilinae by the combination of small size, relatively thin, and generally ovate to ovate-conic shell, and penis having relatively few glands. Differs from similar *Nymphophilus* Taylor, 1966b (locally endemic in northern Mexico) in several features of the radular teeth (e.g., narrower central teeth, narrower basal tongue on the central teeth, narrower central cusps on the central and lateral teeth), simpler gonadal morphology, longitudinal (not transverse) bursa copulatrix, and superficial (not raised) position of the vas deferens on the neck.

Remarks: Phylogenetic relationships among the new taxa described herein are not known. Thus, for sake of convenience and to aid the reader attempting to identify material, these species instead are treated according to their geographic distributions, which are grouped into major hydrographic units as indicated below. Note that although local endemism is frequent in this fauna, several species occur in more than one of these drainages.

(a) Death Valley system. The hydrobiid fauna of this large drainage, which may or may not have emptied into the Colorado River during the Quaternary (Brown & Rosen, 1995), was recently reviewed by Hershler & Pratt (1990). During the current survey, new material was obtained from a few portions of the drainage in southwestern Nevada.

(b) Colorado River basin. This includes the current Colorado River drainage in southern Nevada as well as several large basins in the eastern half of the state that drained to the Colorado in pluvial times (Hubbs & Miller, 1948).

² Note that the widespread Watercress is often segregated as *Nasturtium* (Nelson, 1992).

reflexed loop. Penis (Figure 31B, C) large; base rectangular, often folded along inner edge; filament short, medium width, tapering to point, slightly oblique; lobe short, squarish, broad, slightly oblique. Terminal gland large, narrow, curving, transverse, largely on ventral surface. Dg1 small, rarely dotlike, absent, or fragmented into two units, usually longitudinal, medial or positioned slightly proximal to filament. Dg2 and Dg3 usually fused into single, large, curved unit (rarely fused with Dg1) transversely positioned near distal edge of lobe; gland sometimes accompanied by one to two small units positioned alongside (sometimes abutting or fused to) proximal edge. Ventral gland large, rarely absent or accompanied by second, dotlike unit; borne on prominent swelling, longitudinal-transverse, positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Spring, southwest of The Crossing, Fish Lake Valley, Esmeralda County, Nevada, T. 1 N, R. 36 E, SW $\frac{1}{4}$ section 16 (Figure 50). Holotype, USNM 873407 (Figure 18M), collected by R. Hershler and D. Giuliani, 16 July 1988; paratypes, USNM 860700. The type locality, a small, thermal (26°C.) limnocrone, is the northernmost of a series of five springs on a large ranch (Figure 4C). Snails were collected in the shallow outflow, and were absent both in the spring pool and in other springs of this complex. This species has not been collected on subsequent visits to this now degraded area and is probably extinct.

Remarks: Although not closely similar to any congener, this species resembles *P. gibba* and a group of species found in the Owens Valley region in that its penis is relatively well ornamented with glands, but lacks a penial gland. *Pyrgulopsis ruinosa* differs from the above species in having a relatively large Dg1, long, fused Dg2-3, and short penial filament.

Material examined: NEVADA. *Esmeralda County:* Spring, southwest of The Crossing (Figure 4C), USNM 860700, USNM 873407.

Pyrgulopsis sublata Hershler, sp. nov.

Lake Valley pyrg

(Figures 7B, 12E, 18N, O, 31D-F)

Etymology: From *sublatus* (Latin), raised aloft; referring to the prominently raised or frilled opercular whorls characterizing this species.

Diagnosis: Medium-sized, with broadly to ovate-conic shell. Penis large, filament and lobe short. Penial ornament a large terminal gland, large Dg1, and small Dg2.

Description: Shell (Figures 7B, 18N, O) broadly to ovate-conic, width/height, 66-78%; height, 2.2-2.7 mm; width, 1.4-2.0 mm; whorls, 4.5-5.0. Protoconch 1.4

whorls, diameter 0.35 mm; surface smooth except for very weak wrinkling around apex and faint spiral striae on later portion. Teleoconch whorls medium to highly convex, shoulders weak or absent; sculpture including occasional faint spiral striae. Aperture ovate, adnate or slightly disjunct. Inner lip usually thin; columellar shelf very narrow or absent. Outer lip usually thin, orthocone or weakly prosocline, weakly sinuate. Umbilicus rimate or shallowly perforate. Periostracum tan.

Operculum (Figure 12E) ovate, multispiral, amber, nuclear region reddish; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar thick along most of perimeter, broadly so between nucleus and inner edge; whorl outlines strongly bulging.

Radula 645 \times 100 μ m, with 63 rows of teeth. Central tooth 22 μ m wide, with highly indented dorsal edge; lateral cusps, 7-9; central cusp rounded; basal cusps medium-sized, sometimes accompanied by weak thickening to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-5(6); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 26-32 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 27-34 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium grey. Snout, foot light to medium grey. Opercular lobe having black smear all around. Neck unpigmented to medium grey. Pallial roof, visceral coil medium grey-brown to black, pigment not uniform. Penial filament and adjacent portion of base darkly pigmented.

Ctenidial filaments, 17, pleated; pericardium overlapping ctenidium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 31D. Albumen gland with medium-large (30-40%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two slightly or greatly overlapping posterior-oblique loops; proximal loop often weakly developed, usually having weak pigment streak on proximal arm. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix 67% as long and often as wide as albumen gland, elongate-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at midline, medium length, medium width. Seminal receptacle small, pouchlike, overlapping anteriormost bursa, extending to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland large, bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 31E, F) large, broadly rectangular, weakly folded or smooth; filament short, narrow, tapering to point, oblique; lobe short (usually as long as filament), square (rarely club-like), slightly oblique. Terminal gland large, narrow, rarely ovate or bifurcate; transverse, largely ventral. Dg1 extending from base of filament (sometimes slightly overlapping filament) along outer edge to medial position and then curving inward a short distance; proximal portion borne on low swelling; gland occasionally split into two similarly sized, abutting units. Dg2 small, ovate, medial (or slightly basal to middle of penis), borne along inner edge (often protruding slightly), usually longitudinal or slightly oblique, sometimes curving transversely toward Dg1. Penial duct straight, near outer edge.

Type locality: Wambolt Springs, Lake Valley, Lincoln County, Nevada, T. 9 N, R. 65 E, NE ¼ section 23 (Figure 50). Holotype, USNM 874681 (Figure 18N), collected by R. Hershler and P. Hovingh, 26 June 1992; paratypes, USNM 860724. The type locality is a shallow, but broad (8 m) helocrene, slightly disturbed by livestock.

Remarks: Among the group of species whose penes have an elongate Dg1, *P. sublata* resembles several species from Verde River drainage (see Hershler & Landye, 1988) and some populations herein referred to *P. kolobensis* in also having a well-developed Dg2 along the inner edge of the penis. *Pyrgulopsis sublata* differs from these species in lacking a ventral gland on the penis and in having a very strongly frilled, multispiral operculum.

Material examined: NEVADA, Lincoln County: Wambolt Springs, Lake Valley, T. 9 N, R. 65 E, NE ¼ section 23, USNM 860724, USNM 874681.

Pyrgulopsis lockensis Hershler, sp. nov.

Lockes pyrg

(Figures 7C, 12F, 14G-I, 19A, 32A-C)

Etymology: Referring to endemism of this species at Lockes, Duckwater Valley.

Diagnosis: Small, with sub-globose to ovate-conic shell. Penis large, filament very short, lobe absent. Penial ornament absent.

Description: Shell (Figures 7C, 19A) sub-globose to ovate-conic, width/height, 80–93%; height, 1.6–1.9 mm; width, 1.4–1.6 mm; whorls, 3.25–4.5. Protoconch 1.2 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex, later portion smooth, with a few weak spiral striations. Teleoconch whorls highly convex; shoulders narrow or absent. Aperture sub-circular, usually adnate, rarely disjunct.

Inner lip medium thickness, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum tan.

Operculum (Figure 12F) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula (Figure 14G-I) 570 × 90 μm, with 47 rows of teeth. Central tooth 20 μm wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp narrow, daggerlike; basal cusps medium-sized. Basal process U-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4); neck weakly flexed; outer wing 190% of cutting edge length. Inner marginal teeth with 21–24 cusps, including large near basal cusp offset from others; cutting edge occupying 46% of length of tooth. Outer marginal teeth with 25–31 cusps; cutting edge occupying 29% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles, snout unpigmented or light grey-brown. Foot unpigmented or light grey-brown, darker along anterior edge. Opercular lobe black along inner edge. Neck unpigmented except for internal grey granules. Pallial roof, visceral coil usually light-medium grey-brown, rarely black, pigment usually darker on anterior mantle. Penis unpigmented.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium medium-sized, narrow, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary a little less than 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 32A. Albumen gland having very short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; rectal furrow weakly developed. Ventral channel overlapping capsule gland to medium extent; longitudinal fold well developed. Genital aperture a short slit opening near middle of capsule gland; anterior extension short. Coiled oviduct a tight, circular loop kinked proximally or at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, narrowly-ovate, often curved, usually oblique, with 33% of length posterior to albumen gland, anterior edge often shallowly embedded in gland. Bursal duct originating from or near anterior edge at mid-line, short, medium width. Seminal receptacle very small, pouchlike, overlapping anteriormost portion of bursa, often shallowly embedded in albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 32B, C) large; base elongate, smooth, sometimes having sub-terminal bulge; filament very

large, filament short, lobe medium length. Penial ornament a large terminal gland, large Dg1, small Dg2, small Dg3, and small ventral gland.

Type locality: South of Burns, Oregon.

Remarks: The Abert Lake Basin population (Figure 53), although disjunct from the previously known range of *P. hendersoni* (Harney Lake and Malheur River basins to the northeast), closely conforms to this species, differing principally in having a smaller ventral gland on the penis. The large-snail collected by Taylor & Smith (1981:352; *F[ontelicella]*. sp.) from near the north end of Lake Abert also may be referable to this species.

Material examined: OREGON. *Lake County:* Springs, northwest corner Lake Abert, T. 33 S, R. 21 E, SW ¼ section 16, USNM 883547.

Pyrgulopsis intermedia (Tryon, 1865)

- Pomatiopsis intermedia* Tryon, 1865, 1865, pl. 22, fig. 8.
Fontelicella intermedia (Tryon, 1865), Taylor, 1975: 104 [literature compilation].—Taylor, 1985:308–310.
Pyrgulopsis intermedia (Tryon, 1865), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:42, 44 [figures].

Diagnosis: Large, with ovate-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament a large terminal gland, medium-sized penial gland, and large ventral gland.

Type locality: Owyhee River, southeast Oregon.

Remarks: Taylor (1985) earlier noted on the occurrence of this snail in Barren Valley (Figure 53), a small endorheic drainage positioned between South Fork Malheur River and Owyhee River. Barren Valley populations closely resemble snails from the type locality area, but are slightly smaller and have squatter shells.

Material examined: OREGON. *Malheur County:* Sky-light Spring, Barren Valley, T. 28 S, R. 38 E, SW ¼ section 8, USNM 854126.—Spring, Dowell Ranch, Barren Valley, T. 27 S, R. 38 E, SW ¼ section 33, USNM 874179.

Species from the Bonneville Basin

Pyrgulopsis kolobensis (Taylor, 1987)

- Paludestrina longinqua* (Gould, 1855), Pilsbry, 1899:122 [not Gould, 1855; in part].—Hannibal, 1912a:34 [in part].—Hannibal, 1912b:186 [in part].—Henderson & Daniels, 1916:322, 334 [in part].—Henderson & Daniels, 1917:64, 71, 72, 76.—Henderson, 1924:190.—Chamberlin & Jones, 1929:176–178, fig. 82 [in part].—Berry, 1931:114.—Jones, 1935:228 [in part?].—Jones, 1940a:42 [in part].—Jones, 1940b:29 [in part].—Woolstenhulme, 1942a:14 [in part].—Woolstenhulme, 1942b:55 [in part].

Amnicola (Cincinnati) cincinnatiensis (Anthony, 1840), Henderson, 1924:190 [not Anthony, 1840].

Cincinnati cincinnatiensis (Anthony, 1840), Chamberlin & Jones, 1929:175–176 [not Anthony, 1840].

Amnicola longinqua Gould, 1855, Call, 1884:20–21 [not Gould, 1855; in part].—Henderson, 1936:137 [in part].—Chamberlin & Roscoe, 1948:11.—E.G. Berry, 1948:69.

Fontelicella longinqua (Gould, 1855), Russell, 1971:232–233, fig. 4 (penis) [not Gould, 1855].

Fontelicella kolobensis Taylor, 1987:19, fig. 8.

Fontelicella pinetorum Taylor, 1987:20, fig. 9.—Hershler, 1994 [placed in synonymy with *Pyrgulopsis kolobensis*].

Pyrgulopsis kolobensis (Taylor, 1987), Hershler, 1994:44, 46 [figures; transfer to *Pyrgulopsis*].

Diagnosis: Medium-sized to large, shell usually ovate-conic. Penis large, filament short, lobe medium-long. Penial ornament variable, but typically a large terminal gland, small penial gland, and large ventral gland.

Type locality: Toquerville Springs, Washington County, Utah, T. 40 S, R. 13 W, section 35.

Remarks: This species (and its junior synonym, *Fontelicella pinetorum*) had been previously recorded only from the upper Virgin River basin in southwest Utah. However, *Pyrgulopsis kolobensis* is clearly conspecific with the widespread snail of the eastern Great Basin, which is found as far south as the northern flank of the mountain range composing the Great Basin-Virgin River divide, and which has been identified as *Paludestrina longinqua* Gould, 1855 in the literature. As explained elsewhere (Hershler, 1994:47), *Pyrgulopsis longinqua* (Gould, 1855) is restricted to its type locality area in the Salton Trough of southern California and, although these two species share some presumably derived penial features, they do not appear to be closely related (Hershler, 1994, fig. 31).

The range of *P. kolobensis* is herein extended to include much of the Bonneville Basin (including the Sevier River sub-basin and a few localities from both upper and lower Bear River drainage), as well as various isolated drainages of eastern Nevada and portions of the Colorado River basin (Meadow Valley Wash in southern Nevada, Strawberry River drainage in the Wasatch Mountains of Utah) (Figure 54).

Variation is considerable within this broadly distributed species. Although typically ovate-conic, the shell also may be either broadly conical (such as in populations from southern Steptoe Valley) or narrow-conic (Independence Valley). The terminal gland of the penis is usually fairly large and curved, but may also be short, and either ovate or (rarely) circular. The penial gland often is small (and is absent in one population from the Virgin River drainage) and confined to the base of the filament, but also may be long, filling most of the filament and often extending a short or long distance onto the base. In some populations the penial gland appears to be split and/or

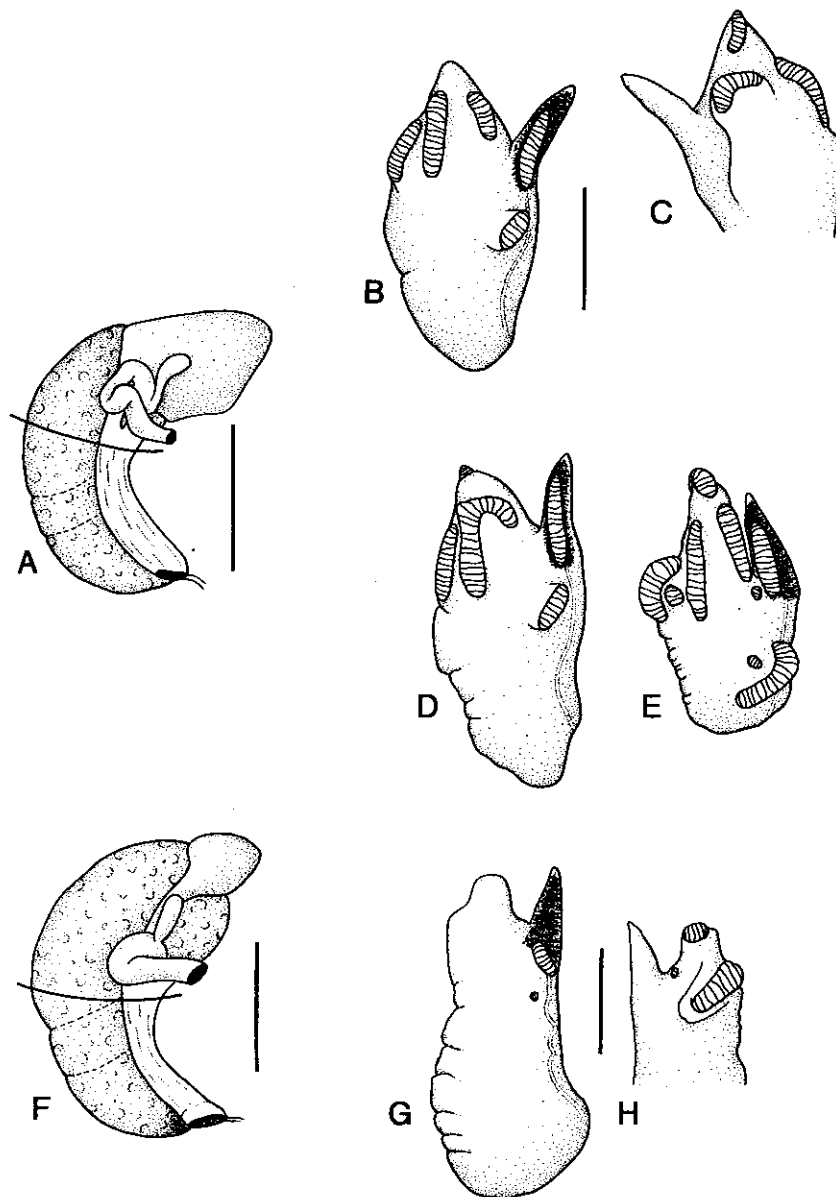


Figure 44

Genitalia of *Pyrgulopsis* species (A–E, *P. anguina*, USNM 860725; F–H, *P. saxatilis*, USNM 860726). A–E. Bars = 0.5 mm. F–H. Bars = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. anguina*.

accompanied by a more proximal, longitudinal Dg1. In many populations Dg1 is well developed, and may be raised on a pedicel and/or have a decidedly transverse orientation. A Dg2 often is present as a narrow, distal unit (sometimes raised). A proximal gland, also found along the inner edge, may also be present (notably in populations from Huntington, Newark, and Ruby Valleys), either instead of or in addition to the typical Dg2.

In a few populations, the ventral gland is multiple (Mound Valley). Penial variation can be considerable even within a single population or among those of a small drainage and unusual forms are linked with typical morphology by intermediates in all cases, hence I choose not to sub-divide this taxon at this time.

Material examined: IDAHO. *Bannock County*: Heart

Mountain Spring (outflow), Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883681.—Spring, north of road along Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883691.—Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883536, USNM 883894. *Franklin County*: Spring, upper Cub River, Bear River drainage, T. 15 S, R. 41 E, NW ¼ section 8, USNM 874697, USNM 883568. *Oneida County*: Big Malad Spring, Malad Valley, T. 14 S, R. 35 E, NW ¼ section 10, USNM 883480.—Twin Springs, Curlew Valley, T. 13 S, R. 32 E, NW ¼ section 30, USNM 883595.—Springs, southeast of Stone Reservoir, Curlew Valley, T. 16 S, R. 33 E, NW ¼ section 7, USNM 883390. **NEVADA.** *Elko County*: Springs, north-northwest Denton Canyon, Butte Valley, T. 28 N, R. 62 E, SW ¼ section 3, USNM 874308.—Spring, north-northwest of The Narrows, Butte Valley, T. 28 N, R. 61 E, SW ¼ section 36, USNM 874283.—Springs, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, SW ¼ section 5, USNM 874339.—Spring, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, NW ¼ section 10, USNM 874257.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 18, USNM 873337, USNM 874316.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, section 7, USNM 873341.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 10, USNM 873328, USNM 874282.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, NE ¼ section 16, USNM 873338.—Gamble Spring, Thousand Springs Creek, T. 40 N, R. 69 E, NW ¼ section 8, USNM 874717.—Hellman Spring, Huntington Valley, T. 27 N, R. 55 E, NE ¼ section 36, USNM 874078, USNM 874337.—Springs, South Fork Twin Creek, Huntington Valley, T. 27 N, R. 56 E, SE ¼ section 6, USNM 874071, USNM 874317, USNM 874674.—Big Springs, Independence Valley, T. 36 N, R. 66 E, NE ¼ section 33, USNM 874330. *Eureka County*: upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, NW ¼ section 35, USNM 874333.—upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873336.—Spring, upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873410.—Fish Creek Springs, Fish Creek Valley, T. 16 N, R. 53 E, NW ¼ section 8, USNM 874764, USNM 874875.—Simpson Springs, Diamond Valley, T. 19 N, R. 54 E, NW ¼ section 22, USNM 874324.—Springs, Roberts Creek, Kobeh Valley, T. 23 N, R. 50 E, NE ¼ section 35, USNM 874334.—Pratt Springs, Pine Valley, T. 27 N, R. 52 E, SE ¼ section 10, USNM 874301.—Tonkin Spring, Denay Valley, T. 23½ N, R. 49 E, SW ¼ section 1, USNM 874313, USNM 874716.—Hand-Me-Down Creek, Crescent Valley, T. 28 N, R. 49 E, SE ¼ section 3, USNM 874302. *Lincoln County*: Spring, Kershaw-Ryan State Park, Meadow Valley Wash, T. 4 S, R. 67 E, NE ¼ section 19, USNM 854170, USNM 873184, USNM

873455, USNM 874039, USNM 874761.—North Spring, Clover Valley, Meadow Valley Wash, T. 5 S, R. 69 E, SW ¼ section 11, USNM 874768.—Spring, Spring Valley State Park, Meadow Valley Wash, T. 2 N, R. 70 E, NE ¼ section 7, USNM 874675, USNM 874777.—Spring, west-northwest of Cottonwood Wash, Spring Valley, Meadow Valley Wash, T. 2 N, R. 70 E, NW ¼ section 5, USNM 874679, USNM 874766. *Nye County*: Butterfield Springs, White River Valley, T. 7 N, R. 57 E, NE ¼ section 28, USNM 873155.—Springs below Black Spring, Sand Creek, Garden Valley, T. 3 N, R. 57 E, NW ¼ section 27, USNM 874661.—Butterfield Springs, Railroad Valley, T. 8 N, R. 57 E, SE ¼ section 27, USNM 873155.—Thorn Spring (north), Railroad Valley, T. 7 N, R. 57 E, SW ¼ section 28, USNM 883854.—Thorn Spring, Railroad Valley, T. 7 N, R. 57 E, section 28, USNM 874087.—Spring, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, SW ¼ section 28, USNM 883845.—Stream, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, NE ¼ section 34, USNM 883247.—Spring, northeast of Tom Spring, Railroad Valley, T. 8 N, R. 57 E, SW ¼ section 1, USNM 873169.—Springs, ca. 2.4 km north-northwest of Currant, Railroad Valley, T. 11 N, R. 58 E, NW ¼ section 32, USNM 873171.—Spring, south of Cottonwood Canyon, Reveille Valley, T. 2 N, R. 50 E, NE ¼ section 28, USNM 883546. *White Pine County*: Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, NW ¼ section 17, USNM 874670.—Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, section 16, USNM 873430.—Willow Patch Spring, Snake Valley, T. 15 N, R. 68 E, SE ¼ section 36, USNM 854169, USNM 874281, USNM 874669.—Spring, southwest of Caine Spring, Snake Valley, T. 15 N, R. 17 E, NE ¼ section 31, USNM 874277.—Spring, Minerva, Spring Valley, T. 11 N, R. 67 E, SE ¼ section 12, USNM 874668.—Spring, 1.6 km north of Minerva, Spring Valley, T. 11 N, R. 67 E, SW ¼ section 1, USNM 874665.—Spring, 3.2 km north of Minerva, Spring Valley, T. 12 N, R. 67 E, NW ¼ section 36, USNM 873217, USNM 874676.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 32, USNM 874332.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873229.—Springs, southeast of Cleve Creek (0.3 km east of above), Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873199.—Spring, lower Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 20, USNM 873225.—Springs, Stonehouse, Spring Valley, T. 22 N, R. 66 E, SW ¼ section 17, USNM 874309.—Cane Spring, Pleasant Valley, T. 21 N, R. 70 E, SW ¼ section 22, USNM 874279.—Lower Sanford Spring, Deep Creek Valley, T. 23 N, R. 69 E, NE ¼ section 25, USNM 874274.—Springs, West Deep Creek, Deep Creek Valley, T. 24 N, R. 70 E, NE ¼ section 3, USNM 874278.—Tippett Springs, Antelope Valley, T. 23 N, R. 67 E, NW ¼ section 14, USNM 874338, USNM 883592.—Chin Creek, Antelope Valley, T. 25 N, R. 67 E, NE ¼ section

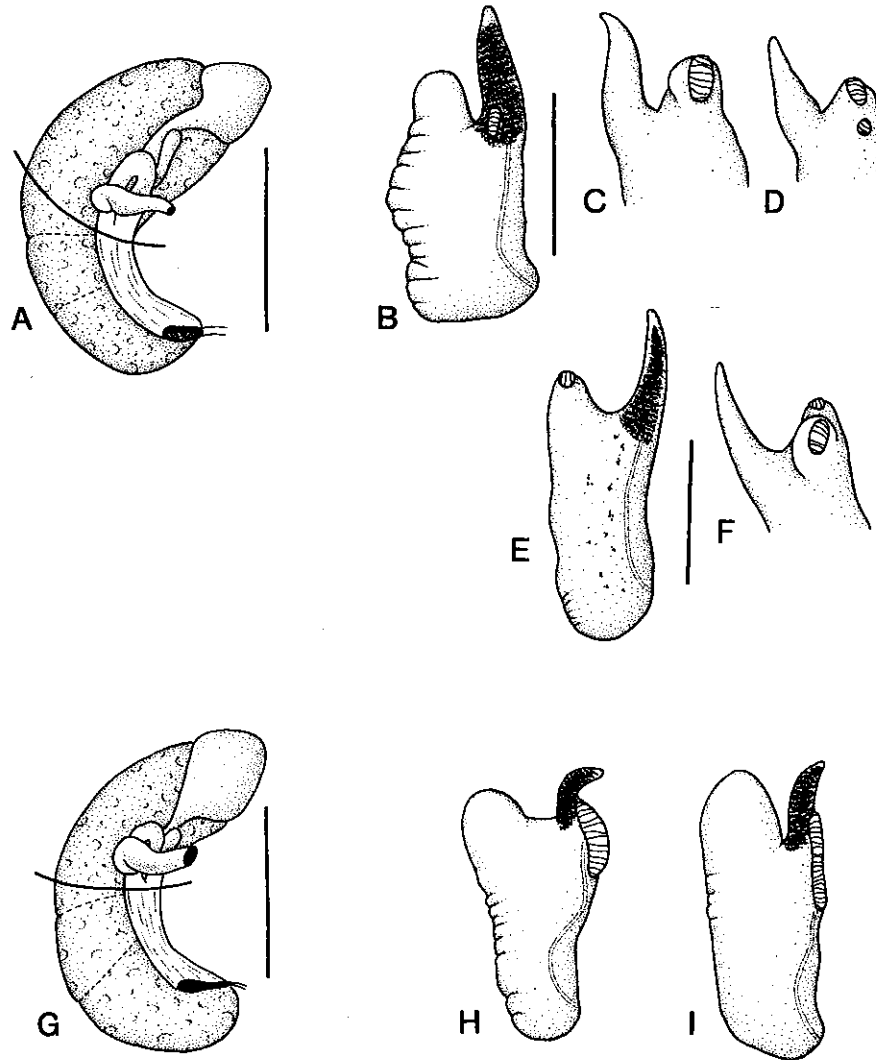


Figure 45

Genitalia of *Pyrgulopsis* species (A–D, *P. variegata*, USNM 860723; E, F, *P. variegata*, USNM 883599; G–I, *P. hovinghi*, USNM 874715). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. hovinghi*, which lacks ventral ornament). Two sets of penes (B, C; E, F) and a third example of the ventral penis (D) are shown for *P. variegata*.

26, USNM 874323.—Spring, west side HWY 318, ca. 9.6 km south of Lund, White River Valley, T. 11 N, R. 62 E, USNM 873161.—Spring, west side HWY 6, west-northwest of Preston, White River Valley, T. 13 N, R. 61 E, SW ¼ section 31, USNM 873330, USNM 874680.—Spring, Bull Creek, Railroad Valley, T. 14 N, R. 56 E, SE ¼ section 14, USNM 874774, USNM 874881.—Green Springs, Railroad Valley, T. 15 N, R. 57 E, SW ¼ section 33, USNM 874773, USNM 874874.—Bennett Spring, Steptoe Valley, T. 19 N, R. 63 E, SE ¼ section 33, USNM 874303.—Springs, northwest of Clark Spring,

Steptoe Valley, T. 19 N, R. 63 E, NE ¼ section 32, USNM 873220.—Springs, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 20, USNM 874691, USNM 883937.—Springs, Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5, USNM 892017.—Springs, Steptoe Ranch, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 5, USNM 873221.—Spring, north of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5, USNM 873206.—Spring, Schell Creek, Steptoe Valley, T. 22 N, R. 65 E, NE ¼ section 7,

USNM 874325.—Springs, Schell Creek, ca. 1 km below Schellbourne Pass, Steptoe Valley, T. 22 N, R. 65 E, SE $\frac{1}{4}$ section 5, USNM 873236.—Owens Springs, Butte Valley, T. 26 N, R. 62 E, NW $\frac{1}{4}$ section 33, USNM 874321.—Springs, southwest side of Newark Lake, Newark Valley, T. 20 N, R. 55 E, sections 4, 5, 8, USNM 873332.—Minoletti Spring, Newark Valley, T. 22 N, R. 55 E, NW $\frac{1}{4}$ section 11, USNM 874328.—Cold Spring, Newark Valley, T. 23 N, R. 55 E, NW $\frac{1}{4}$ section 26, USNM 874320, USNM 874901.—Station Spring, Ruby Valley, T. 25 N, R. 57 E, NE $\frac{1}{4}$ section 13, USNM 874311.—Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, SW $\frac{1}{4}$ section 2, USNM 874307.—Springs, northwest of Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, NE $\frac{1}{4}$ section 3, USNM 873335. \textit{UTAH. Box Elder County:} Blue Creek Spring, Blue Creek Valley, T. 13 N, R. 5 W, NW $\frac{1}{4}$ section 29, USNM 883625.—Spring, ca. 3.5 km east-northeast of Portage, Malad Valley, T. 15 N, R. 3 W, NE $\frac{1}{4}$ section 4, USNM 883490, USNM 883577.—Spring, ca. 1.6 km north of Promontory Point, Promontory Mountains, Great Salt Lake Desert, T. 6 N, R. 5 W, NE $\frac{1}{4}$ section 21, USNM 883611.—Shaw Spring, Promontory Mountains, Great Salt Lake Desert, T. 7 N, R. 5 W, NE $\frac{1}{4}$ section 9, USNM 883607.—Springs, ca. 1.6 km south of Sweetwater Spring, Promontory Mountains, Great Salt Lake Desert, T. 8 N, R. 5 W, center section 5, USNM 883632.—Spring, east of Rozel Flat, Promontory Mountains, Great Salt Lake Desert, T. 9 N, R. 6 W, NE $\frac{1}{4}$ section 31, USNM 854782.—Spring, ca. 0.8 km north of Mantua Reservoir, Great Salt Lake Desert, T. 9 N, R. 1 W, NE $\frac{1}{4}$ section 16, USNM 883569.—Salt Spring, Point Lookout, Salt Creek, Great Salt Lake Desert (Figure 5C), T. 11 N, R. 3 W, SE $\frac{1}{4}$ section 6, USNM 874067, USNM 883216.—Spring, Painted Rock, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 4 W, NW $\frac{1}{4}$ section 11, USNM 883209, USNM 883399.—Spring, Jesses Knoll, Salt Creek, Great Salt Lake Desert, T. 11 N, R. 4 W, SE $\frac{1}{4}$ section 34, USNM 874069, USNM 883234, USNM 883400.—Springs, west-southwest of Connor Springs, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 5 W, NW $\frac{1}{4}$ section 12, USNM 883198, USNM 883401.—Spring, southwest of Lampo Junction, Great Salt Lake Desert, T. 10 N, R. 5 W, NE $\frac{1}{4}$ section 4, USNM 854548, USNM 883388.—Bar M Spring, Great Salt Lake Desert (Figure 5B), T. 11 N, R. 10 W, SE $\frac{1}{4}$ section 1, USNM 883630.—Spring, east side HWY 30, west of Dove Creek Hills, Great Salt Lake Desert, T. 11 N, R. 15 W, NW $\frac{1}{4}$ section 14, USNM 883615.—So. Tremonton, FMNH 178357.—Spring, north of Plymouth, Malad Valley, FMNH 224314. \textit{Cache County:} Spring, below (west of) Porcupine Reservoir, Cache Valley, T. 9 N, R. 2 E, NW $\frac{1}{4}$ section 17, USNM 883853.—Pool alongside Logan River, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW $\frac{1}{4}$ section 27, USNM 883575.—Spring, Spring Hollow, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW $\frac{1}{4}$ section 27, USNM 858290.—Murray Spring;

Cache Valley, T. 10 N, R. 1 W, SW $\frac{1}{4}$ section 10, USNM 883476. \textit{Davis County:} Spring, ca. 1.6 km northeast of Mushroom Spring, Antelope Island, Great Salt Lake Desert, T. 2 N, R. 3 W, NW $\frac{1}{4}$ section 11, USNM 883219, USNM 883489. \textit{Iron County:} Spring, east of Summit, Parowan Valley, T. 34 S, R. 9 W, SE $\frac{1}{4}$ section 31, USNM 883612.—Spring, upper Little Creek, Parowan Valley, T. 34 S, R. 7 W, NE $\frac{1}{4}$ section 17, USNM 883616.—Kane Spring, Parowan Valley, T. 32 S, R. 9 W, NE $\frac{1}{4}$ section 12, USNM 883593.—Spring, Upper Bear Valley, T. 33 S, R. 7 W, NE $\frac{1}{4}$ section 23, USNM 883619.—West Spring, Lower Bear Valley, T. 32 S, R. 6 W, SW $\frac{1}{4}$ section 28, USNM 883589.—Big Swamp Springs, Lower Bear Valley, T. 32 S, R. 6 W, NW $\frac{1}{4}$ section 23, USNM 883601. \textit{Juab County:} Springs, McIntyre, Tintic Valley, T. 11 S, R. 3 W, SE $\frac{1}{4}$ section 28, USNM 883206.—Baker Hot Springs, Old River Bed, T. 14 S, R. 8 W, SE $\frac{1}{4}$ section 10, USNM 883238, USNM 883431.—Cherry Creek, below Indian Springs, Old River Bed, T. 12 S, R. 5 W, NW $\frac{1}{4}$ section 21, USNM 883197.—Spring, Mount Laird, Sevier Desert, T. 14 S, R. 11 W, center section 26, USNM 883226, USNM 883432.—Spring, northeast of Chicken Creek Reservoir, Juab Valley, T. 15 S, R. 1 W, NE $\frac{1}{4}$ section 16, USNM 883426, USNM 883438.—Springs, Hollow Creek, Juab Valley, T. 13 S, R. 2 E, NW $\frac{1}{4}$ section 5, USNM 883600.—Springs, Curiant Creek, Juab Valley, T. 12 S, R. 1 E, NW $\frac{1}{4}$ section 18, USNM 883195.—Spring, Mona, Juab Valley, T. 11 S, R. 1 E, NE $\frac{1}{4}$ section 31, USNM 874077, USNM 883240.—Spring, south of Starr, Juab Valley, T. 11 S, R. 1 E, SW $\frac{1}{4}$ section 8, USNM 874070, USNM 874072, USNM 883231.—“Percy Spring,” south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE $\frac{1}{4}$ section 26, USNM 858289, USNM 883473.—Spring, near south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE $\frac{1}{4}$ section 26, USNM 858280.—Spring, southwest of “Mallard Pool,” Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE $\frac{1}{4}$ section 23, USNM 883200.—North Springs, Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE $\frac{1}{4}$ section 3, USNM 883217.—“Leland Harris” Springs, Snake Valley, T. 14 S, R. 18 W, NE $\frac{1}{4}$ section 32, USNM 883223.—Spring (source), Spring Creek, Deep Creek Valley, T. 11 S, R. 19 W, SW $\frac{1}{4}$ section 19, USNM 874276. \textit{Millard County:} Coyote Spring, Beaver River drainage, T. 23 S, R. 9 W, NW $\frac{1}{4}$ section 33, USNM 883239.—Tie House Spring, Beaver River drainage, T. 24 S, R. 10 W, NE $\frac{1}{4}$ section 22, USNM 883212.—Spring Lake (Clear Lake), Sevier River drainage, T. 20 S, R. 7 W, NW $\frac{1}{4}$ section 11, USNM 883214.—Painter Spring, Tule Valley, T. 19 S, R. 14 W, NE $\frac{1}{4}$ section 5, USNM 883202.—Sinbad Spring, Tule Valley, T. 16 S, R. 13 W, NE $\frac{1}{4}$ section 33, USNM 883207, USNM 883424.—Spring, at corral, east of Horse Canyon, Snake Valley, T. 17 S, R. 19 W, NE $\frac{1}{4}$ section 29, USNM 883220.—Knoll

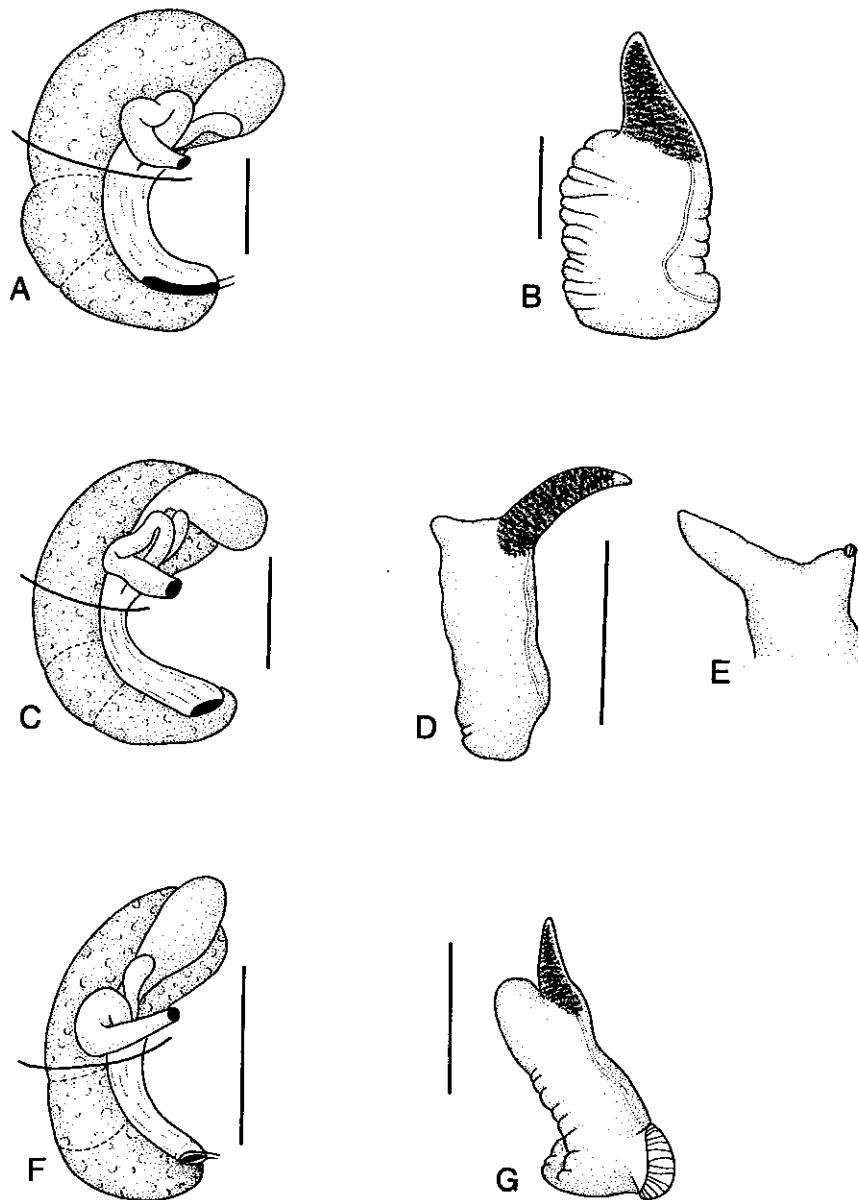


Figure 46

Genitalia of *Pyrgulopsis* species (A, B, *P. millenaria*, USNM 860721; C-E, *P. lentiglans*, USNM 860722; F, G, *P. plicata*, USNM 860727). A, B, Bars = 0.25 mm. C-G. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. millenaria* and *P. lentiglans*, which lack ventral ornament).

Springs, Snake Valley, T. 18 S, R. 18 W, NE $\frac{1}{4}$ section 16, USNM 883218.—Twin Springs, Snake Valley, T. 16 S, R. 18 W, SW $\frac{1}{4}$ section 22, USNM 883208.—Cold Spring, Snake Valley, T. 16 S, R. 19 W, NW $\frac{1}{4}$ section 2, USNM 883213. *Morgan County*: Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, NW $\frac{1}{4}$ section 14, USNM 883389.—Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, SE $\frac{1}{4}$ section 15, USNM

874074.—Dixie Spring, East Canyon Creek, Weber River drainage, T. 2 N, R. 3 E, NE $\frac{1}{4}$ section 1, USNM 883634.—Lost Creek near Devils Slide, Weber River drainage, T. 4 N, R. 4 E, SE $\frac{1}{4}$ section 19, USNM 883596.—Devils Slide, FMNH 179260, FMNH 179307. *Rich County*: Spring, lower Home Canyon, Bear River drainage, T. 8 N, R. 6 E, SW $\frac{1}{4}$ section 24, USNM 883485. *Salt Lake County*: Spring, Riverton, Jordan River

drainage, T. 3 S, R. 1 W, NW ¼ section 34, USNM 883236, USNM 883284.—Spring, HWY 80, Parleys Canyon (just below Parleys Summit), Jordan River drainage, T. 1 S, R. 3 E, SE ¼ section 8, USNM 858287, USNM 883628.—Spring, Emigration Canyon (near mouth), Jordan River drainage, T. 1 S, R. 1 E, NE ¼ section 11, USNM 883613.—Spring, (upper) City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, NW ¼ section 13, USNM 883606.—Spring, City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, section 30, USNM 874073, USNM 874374, USNM 874375, USNM 883588.—Spring, City Creek Canyon, USNM 31271.—Lambs Canyon, Great Salt Lake Desert, FMNH 178387.—Mill Creek Canyon, Jordan River drainage, FMNH 178363.—Liberty Park, Salt Lake City, FMNH 178516.—south Salt Lake City, FMNH 179664.—33rd and 7th Street E, Salt Lake City, FMNH 178372.—Emigration Canyon, Great Salt Lake Desert, FMNH 178444.—City Creek, Salt Lake City, FMNH 178874, FMNH 178392.—City Creek, north bridge, FMNH 178362.—Red Butte Canyon, Great Salt Lake Desert, FMNH 178368, FMNH 178384.—Red Butte, Great Salt Lake Desert, FMNH 178369.—Tarpeys Spring, Salt Lake City, USNM 199398.—Salt Lake City, USNM 414181, USNM 424340.—Clintons Cave (sub-fossil), FMNH 178385, FMNH 223987, FMNH 224407. *Sevier County*: Springs, Live Oak Canyon, Sevier River drainage, T. 26 S, R. 3 W, NW ¼ section 4, USNM 883581.—Spring, 2.2 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 12, USNM 883428, USNM 883934. *Summit County*: Spring, southwest of Francis, Provo River drainage, T. 2 S, R. 6 E, SE ¼ section 32, USNM 883620.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874384.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874076.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, SE ¼ section 14, USNM 883629.—Beard Spring, Weber River drainage, T. 3 N, R. 4 E, SE ¼ section 19, USNM 883580. *Tooele County*: Springs, Dog Hollow Creek, Rush Valley, T. 9 S, R. 4 W, SE ¼ section 20, USNM 883196.—Spring, south end Atherly Reservoir, Rush Valley, T. 7 S, R. 5 W, SW ¼ section 28, USNM 883488.—Springs, south of Rush Lake, Rush Valley, T. 5 S, R. 5 W, NW ¼ section 2, USNM 883483.—Spring, below Little Pole Canyon, Skull Valley, T. 3 S, R. 7 W, SW ¼ section 30, USNM 883626.—Springs (southernmost), west of Salt Mountain, Skull Valley, T. 3 S, R. 8 W, SW ¼ section 16, USNM 883233.—Horseshoe Springs, Skull Valley, T. 2 S, R. 8 W, SE ¼ section 26, USNM 858285, USNM 873436, USNM 883204.—Muskrat Spring, Skull Valley, T. 2 S, R. 8 W, UMMZ 219484.—Big Spring, Skull Valley, T. 1 S, R. 7 W, SE ¼ section 8, USNM 858282, USNM 883199, USNM 883282.—Spring, northwest of Flux, Tooele Valley, T. 1 S, R. 7 W, NE ¼ section 25, USNM 883225, USNM 883398.—Spring, Lake Point, Tooele Valley, T. 1 S, R. 4 W, SE ¼ section 24, USNM 883621.—Near Lake Point, Tooele Valley, USNM 47864.—“Redden Springs,” ca. 9.6 km north of Callao, Great Salt Lake Desert, T. 9 S, R. 16 W, SW ¼ section 31, USNM 883203.—Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SW ¼ section 6, USNM 883232.—Spring feeding Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SE ¼ section 6, USNM 883224, USNM 883633.—Stream, 3.2 km west of Bonneville Service Station, near Timpi (Timpie), FMNH 178400 (mixed with *Tryonia protea* [Gould, 1855]).—West side of Skull Valley (subfossil), FMNH 178423.—4.8 km south of Stockton, Rush Valley, FMNH 178380.—Spring before Josepha, Skull Valley, FMNH 178382 (mixed with *Tryonia protea*).—First spring south of Josepha, Skull Valley, FMNH 178381.—Southeast of Tooele, FMNH 224405. *Utah County*: Springs, Warm Springs Ditch, Goshen Valley (Utah Lake Basin), T. 10 S, R. 1 E, center section 8, USNM 883230.—Holladay Springs, Utah Lake Basin, T. 9 S, R. 1 E, NE ¼ section 25, USNM 883605.—Spring, Right Fork Hobbie Creek, Utah Lake Basin, T. 7 S, R. 4 E, SW ¼ section 24, USNM 883570.—“Clyde Spring,” Hobbie Creek, Utah Lake Basin, T. 8 S, R. 3 E, SE ¼ section 3, USNM 883935.—Spring, Diamond Fork, Utah Lake Basin, T. 8 S, R. 5 E, NE ¼ section 32, USNM 873331, USNM 883571.—Spring, South Fork Provo River, T. 5 S, R. 3 E, NE ¼ section 36, USNM 883609.—Spring (source), Spring Creek, below Mill Pond, Utah Lake Basin, T. 5 S, R. 1 E, SW ¼ section 15, USNM 883229, USNM 883285.—Big Spring, west of Fairfield, Cedar Valley, T. 6 S, R. 2 W, SE ¼ section 30, USNM 883235.—Spring, Cedar Fort, Cedar Valley, T. 6 S, R. 2 W, SW ¼ section 6, USNM 883281, USNM 883429.—Spanish Fork Canyon (sixth water canyon), FMNH 178370, FMNH 178376. *Wasatch County*: Spring, Willow Creek, Strawberry River drainage (Colorado River drainage basin), T. 6 S, R. 12 W, SE ¼ section 14, USNM 883617.—Spring Creek, Wallsburg, Provo River drainage, T. 5 S, R. 5 E, ¼ section 18, USNM 883618.—Cascade Springs, Provo River drainage, T. 4 S, R. 3 E, NE ¼ section 24, USNM 873339, USNM 883635.—Spring, along HWY 40–189, ca. 2.0 km north Heber City, Heber Valley, Provo River drainage, T. 3 S, R. 5 E, SW ¼ section 29, USNM 883623.—Hot Springs, northwest of Midway, Heber Valley, Provo River drainage, T. 3 S, R. 4 E, SW ¼ section 27, USNM 883794, USNM 883844.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 33, USNM 874372.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 33, USNM 873340.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 19, USNM 858284.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 19, USNM 873334.—Ross Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 18, USNM 883631.—Provo River, below Charleston, FMNH 179177. *Washington County*: Springs, west side Left Fork

of North Creek, Virgin River drainage, T. 40 S, R. 11 W, NE ¼ section 28, USNM 847248.—Leeds, Virgin River drainage, FMNH 178356.—Springs, Left Fork Santa Clara River, Pine Valley, T. 39 S, R. 14 W, SW ¼ section 20, USNM 847029, USNM 883258.—Spring, Pinto Creek, Escalante Desert, T. 38 S, R. 15 W, NE ¼ section 12, USNM 874735.—Pinto Spring, Escalante Desert, T. 38 S, R. 14 W, center section 6, USNM 883211.—Spring, southwest of Pinto, Pinto Creek, Escalante Desert, T. 37 S, R. 15 W, SE ¼ section 33, USNM 883228.—Springs, Calf Springs Creek, Escalante Desert, T. 38 S, R. 17 W, NE ¼ section 4, USNM 883201. *Weber County*: Spring, mouth of Ogden County, Ogden River drainage, T. 6 N, R. 1 W, SW ¼ section 23, USNM 883598.—Springs, North Fork Ogden River, T. 7 N, R. 1 E, NE ¼ section 18, USNM 883604.

Pyrgulopsis pilsbryana (Baily & Baily, 1952)

Ammicola pilsbryi Baily & Baily, 1951:50, pl. 4, fig. 3 [not *Ammicola pilsbryi* Walker, 1906].

Ammicola pilsbryana Baily & Baily, 1952:144 [new name for *Ammicola pilsbryi* Baily & Baily, 1951].

Fonticella pilsbryana (Baily & Baily, 1952), Taylor, 1975: 152 [literature compilation].

Fonticella pilsbryi (Baily and Baily, 1951), Taylor, 1975: 153 [literature compilation].

Pyrgulopsis pilsbryana (Baily & Baily, 1952), Hershler and Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:60 [figures].

Diagnosis: Medium-sized to large, with ovate- to narrow-conic shell. Penis large, filament and lobe medium length. Penial ornament a medium-sized terminal gland, very small-large penial gland, and minute Dg3.

Type locality: Lifton, Ideal Beach, Bear Lake, Idaho.

Remarks: The range of this species (previously restricted to the type locality area in Bear Lake basin) encompasses the Bear Lake basin and Bear River basin, both above and below (above Cache Valley) the Bear Lake outlet (Figure 55). The distribution of this species closely abuts that of *P. kolobensis*, a similar species which differs in having a ventral gland on the penis. Populations of *P. pilsbryana* vary principally in terms of shell shape and length of penial gland.

Material examined: IDAHO. *Bear Lake County*: Spring, St. Charles Canyon, Bear Lake Basin, T. 15 S, R. 43 E, SE ¼ section 17, USNM 858281, USNM 883444.—Spring, northeast side Merkley Lake, Bear Lake drainage, T. 14 S, R. 44 E, NE ¼ section 26, USNM 883585.—Spring, Stauffer Creek, Bear River drainage, T. 11 S, R. 43 E, NE ¼ section 27, USNM 883587. *Caribou County*: Ledger Creek, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, SE ¼ section 5, USNM 883537, USNM 883895.—Pond outflow, Kelly Park, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, NW ¼ section 5, USNM 883534, USNM 883535, USNM 883889.—Formation

Spring, Bear River drainage, T. 8 S, R. 42 E, section 28, USNM 874153.—Formation Spring (outflow), Bear River drainage, T. 8 S, R. 42 E, SE ¼ section 28, USNM 883567.—Kackley Spring, Gem Valley, Bear River drainage, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883538, USNM 883891.—Spring (source), Whiskey Creek, Gentile Valley, Bear River drainage, T. 11 S, R. 41 E, SE ¼ section 7, USNM 883441. *Franklin County*: Spring Creek, HWY 34 crossing, Mound Valley, Bear River drainage, T. 12 S, R. 41 E, NW ¼ section 18, USNM 883423. UTAH. *Rich County*: Jacobsen Springs, Big Creek, Bear River drainage, T. 10 N, R. 6 E, SW ¼ section 1, USNM 883578.—Big Spring, Bear Lake Basin, T. 12 N, R. 5 E, NE ¼ section 4, USNM 883586.—Spring, ca. 0.8 km north of Lakota, Bear Lake Basin, T. 15 N, R. 5 E, SE ¼ section 32, USNM 883574. WYOMING. *Lincoln County*: Springs, Bear River drainage, T. 22 N, R. 120 W, section 26, USNM 883896.

Pyrgulopsis hamlinensis Hershler, sp. nov.

Hamlin Valley pyrg
(Figures 9I, 22K, 43A–C)

Etymology: Referring to endemism of this snail in Hamlin Valley, Utah.

Diagnosis: Small, with narrow-conic shell. Penis small to medium-sized, filament medium length, lobe short to medium length. Penial ornament a medium-sized terminal gland.

Description: Shell (Figures 9I, 22K) narrow-conic, width/height, 59–69%; height, 1.6–2.0 mm; width, 1.0–1.3 mm; whorls, 4.25–5.0. Protoconch 1.25 whorls, diameter 0.34 mm, smooth except for small area of very weak wrinkling at apex. Teleoconch whorls low-medium convexity, narrowly shouldered, often having pronounced angulation at base; body whorl often broadly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 560 × 95 μm, with 62 rows of teeth. Central tooth 23 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp narrow, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets deep. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having very light grey pigment proximally. Snout medium grey. Foot light

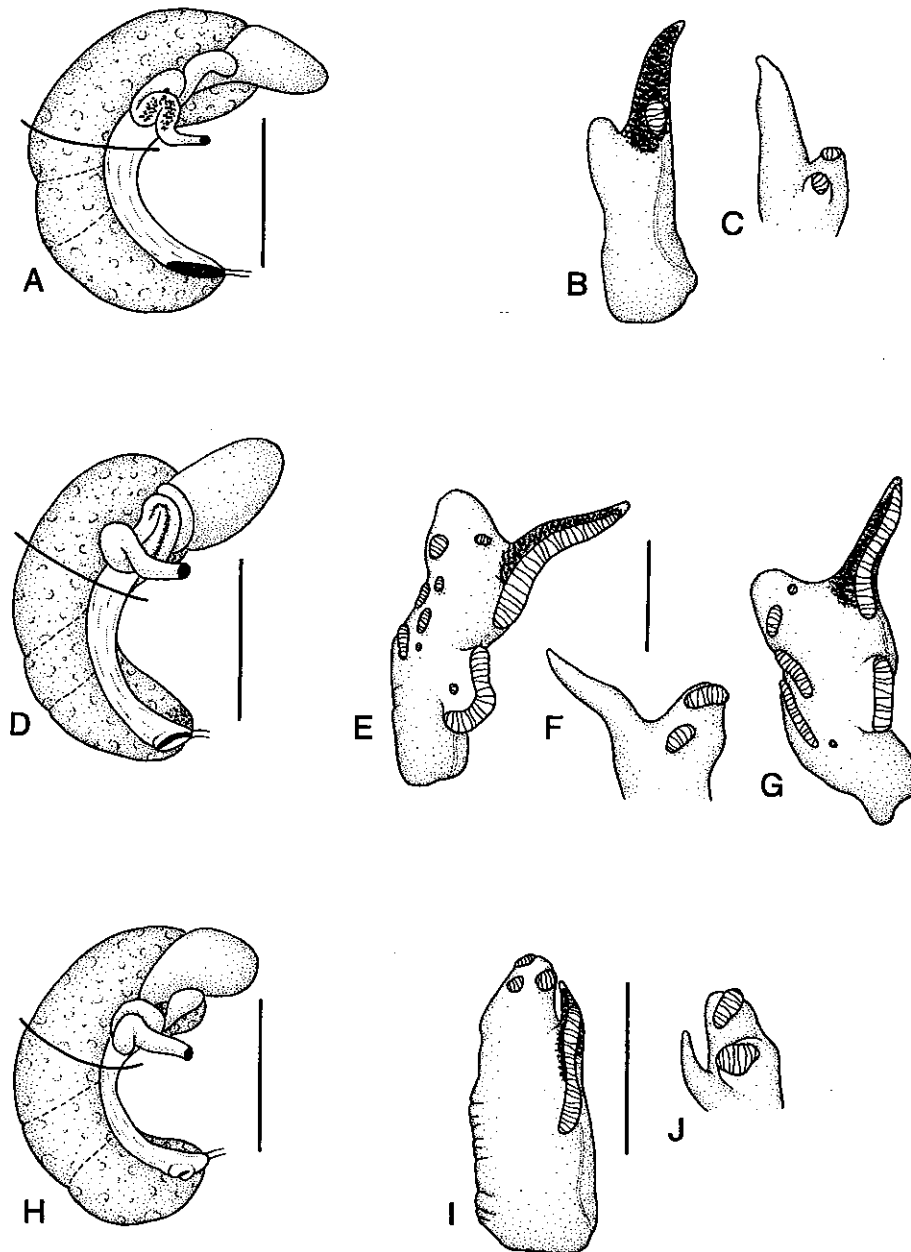


Figure 47

Genitalia of *Pyrgulopsis* species (A, *P. fusca*, USNM 860728; B, *P. fusca*, USNM 883484; D–G, *P. chamberlini*, USNM 860729; H–J, *P. inopinata*, USNM 860730). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the dorsal penis (E, G) are shown for *P. chamberlini*.

to medium grey. Opercular lobe dark along inner edge, sometimes along outer edge as well. Neck unpigmented except for scattered grey granules. Pallial roof, visceral coil near uniform black (pigment slightly lighter on genital ducts). Penial filament darkly pigmented internally for most of length.

Ctenidial filaments, 15, weakly pleated; ctenidium connected to pericardium by short efferent vein. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive

gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43A. Albumen gland having medium (up to 33%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, mounted on weak papilla, having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by weak to well-developed posterior twist. Bursa copulatrix medium length and width, ovate, longitudinal, slightly less than 33% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa; short (up to 50% of bursa length), medium width. Seminal receptacle small, sometimes minute, pouchlike or sub-globular, overlapping anteriormost section of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, sub-globular, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight or having weak undulation. Penis (Figure 43B, C) small to medium-sized; base rectangular, weakly folded; filament 66% length of base, medium width, tapering to point, longitudinal or slightly oblique; lobe slightly shorter to as long as filament, clublike, longitudinal or slightly oblique. Terminal gland medium-sized, ovate or circular, rarely bifurcate, variably oriented, ventral. Penial duct straight, near outer edge.

Type locality: Springs, 0.5 km east of White Rock Cabin Springs, Hamlin Valley, Beaver County, Utah, T. 30 S, R. 20 W, SE ¼ section 2 (Figure 55). Holotype, USNM 883215 (Figure 22K), collected by R. Hershler and P. Hovingh, 9 May 1993; paratypes, USNM 860695. The type locality is a small, high elevation rheocrene slightly impacted by cattle (Figure 5D).

Remarks: This species is contrasted with *P. montana* above.

Material examined: UTAH. *Beaver County:* Springs, 0.5 km east of White Rock Cabin Springs (Figure 5D), USNM 860695, USNM 883215.

Pyrgulopsis peculiaris Hershler, sp. nov.

Bifid duct pyrg

(Figures 9J, 23A–G, 43D–I)

Etymology: From *peculiaris* (Latin), singular; referring to the unique configuration of the female bursal duct in this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis large; filament and lobe medium length. Penial ornament a medium-large, fragmented terminal gland;

small penial gland, large Dg1, large Dg2, large Dg3, additional four to seven dorsal glands, and two large ventral glands.

Description: Shell (Figures 9J, 23A–G) ovate to narrow conic, width/height, 62–89%; height, 1.7–3.0 mm; width, 1.3–2.1 mm; whorls, 3.5–5.0. Protoconch 1.25–1.5 whorls, diameter 0.34 mm, initial 0.5–1.0 whorl finely wrinkled, later portion smooth. Teleoconch whorls highly convex, shoulders weak to well developed; body whorl often slightly disjunct behind the aperture and having sub-sutural ramp bordered below by pronounced angulation. Aperture ovate, usually disjunct. Inner lip slightly thickened; columellar shelf very narrow to broad. Outer lip thin or slightly thickened, slightly prosocline, without sinuation. Umbilicus narrowly perforate. Periostracum light tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick, sometimes broadly so, all around.

Radula 720 × 100 μm, with 57 rows of teeth. Central tooth 32 μm wide, with slightly indented dorsal edge; lateral cusps, 4; central cusp medium width, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-3; neck weakly flexed; outer wing 130% of cutting edge length. Inner marginal teeth with 18–20 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 27% of length of tooth. Stomach larger than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot light to medium brown. Opercular lobe dark along inner edge, often all around. Neck unpigmented except for scattered dark granules to light brown. Pallial roof, visceral coil uniform dark brown to black. Penial filament darkly pigmented along most of length; adjacent portion of base similarly pigmented.

Ctenidial filaments, 16, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white, slightly raised. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43D. Albumen gland having very short pallial component. Capsule gland longer, but narrower than albumen gland, broadly ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique to almost circular loop; proximal arm sometimes kinked, usually darkly pigmented. Oviduct and bursal ducts joining a little behind pallial wall. Bursa

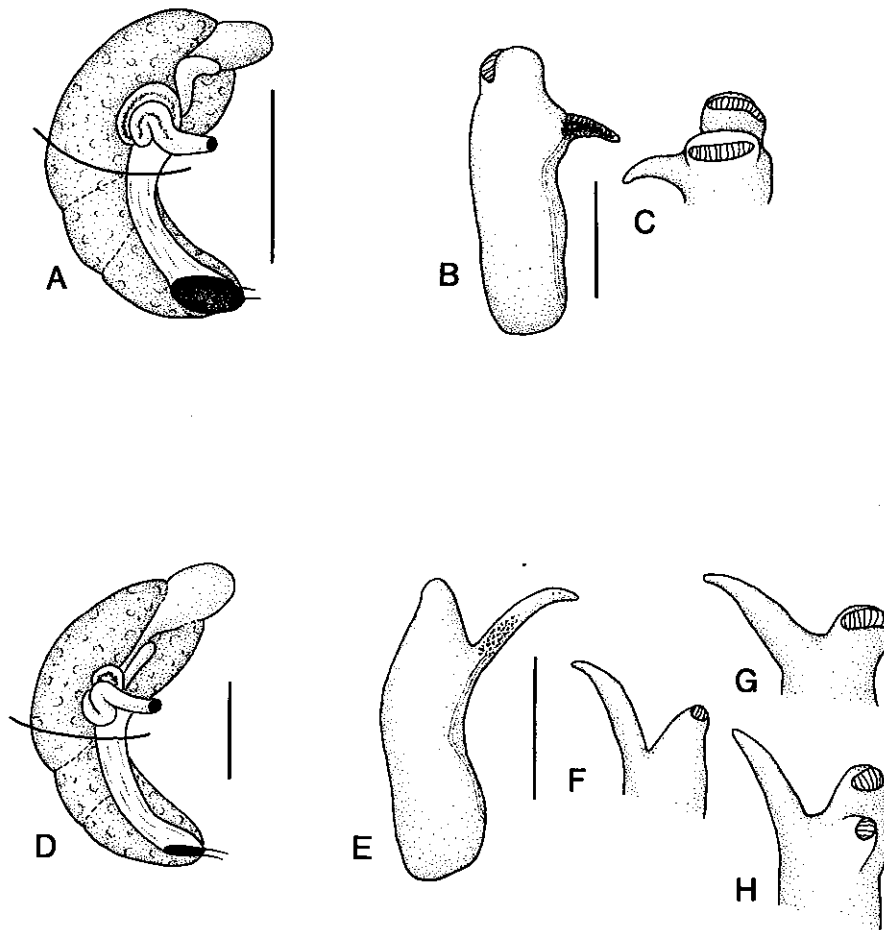


Figure 48

Genitalia of *Pyrgulopsis* species (A–C, *P. nonaria*, USNM 860731; D–F, *P. transversa*, USNM 860732; G, H, *P. transversa*, USNM 883422). A–C. Bars = 0.5 mm. D. Bar = 0.25 mm. E–H. Bar = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Three examples of the ventral penis (F–H) are illustrated for *P. transversa*.

copulatrix medium length, but as wide as albumen gland, pyriform, longitudinal, with almost entire length posterior to gland. Bursal duct bifid (Figure 43E), consisting of duct originating from anterior edge at or near mid-line, medium length, narrow; and much narrower duct (of same length) originating from anterior edge near ventral margin; ducts share common opening to oviduct. Seminal receptacle a small, narrow pouch folded into an inverted U-shape, overlapping middle of bursa copulatrix.

Testis 1.0–1.25 whorls, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 43F–I) large; base rectangular, expanded distally, with pronounced swelling along inner edge, inner edge folded; filament medium length, narrow,

tapering to point, usually oblique; lobe as long as filament, triangular, longitudinal. Terminal gland consisting of three short, ovate-circular units along edge of lobe (mostly ventral) unit along outer edge often fused with distal unit, occasionally all three units fused. Penial gland small, narrow, positioned near base of filament. Dg1 large (rarely reduced), positioned medially, usually transverse, sometimes fused with either Dg3 or outermost of additional longitudinal glands. Dg2 large, distal, borne on expanded edge of lobe. Dg3 large, extending to near base of filament (abutting or fusing with Dg1), sometimes curving across lobe, portion on lobe raised. Dorsal penis also bearing four to seven additional units (typically elongate, longitudinal, sometimes small, circular or dotlike) positioned between penial gland, Dg1 and Dg2; innermost units often fused distally. Ventral glands, two, large, distal gland narrow (sometimes accompanied distally by

raised, dotlike unit), borne on large swelling, traversing most of width of penis near base of filament; proximal gland shorter, broader, borne on prominent swelling, transverse, positioned near base of penis. Penial duct straight, near outer edge.

Type locality: Spring, Maple Grove, Round Valley, Millard County, Utah, T. 21 S, R. 2 1/2 W, NW ¼ section 1. Holotype, USNM 883933 (Figure 23A), collected by R. Hershler and P. Hovingh, 11 May 1995; paratypes, USNM 860703. The type locality is a small, montane rheocene slightly disturbed by recreational activities.

Remarks: The penis of this snail somewhat resembles those of the group of species having a full complement of glands, but differs in that the penial gland is very small. Additionally, the terminal gland is weaker than in many members of this group, and a pronounced distal swelling is present along the inner edge of the penis base, a feature absent in the above species but similar to that of *P. limaria*, from northwest Lahontan Basin. This species is also unique among *Pyrgulopsis* in having a bifid bursal duct, a condition apparently paralleling that seen in *Cincinnatia integra* (see Hershler & Thompson, 1996). The distribution of this species is shown in Figure 55.

Material examined: NEVADA. *White Pine County:* Springs, Big Springs Creek, Snake Valley, T. 10 N, R. 70 E, SW ¼ section 22, USNM 874683.—Turnley Spring, Spring Valley, T. 16 N, R. 68 E, SW ¼ section 16, USNM 874319, USNM 874666. UTAH. *Millard County:* Spring, Maple Grove, USNM 860703, USNM 883602, USNM 883933.—Church Spring, Pahvant Valley, T Spring, T. 19 S, R. 4 W, NE ¼ section 14, USNM 892053.—South Fork Chalk Creek, Pahvant Valley, T. 22 S, R. 3 W, NW ¼ section 6, USNM 883603.—Big Spring, Oak Creek, Sevier River drainage, T. 17 S, R. 4 W, NW ¼ section 12, USNM 883622.—Spring, above Swasey Spring, Whirlwind Valley, T. 16 S, R. 13 W, SW ¼ section 23, USNM 883222.—Antelope Spring, House Range, Sevier Desert drainage, T. 16 S, R. 13 W, NE ¼ section 34, USNM 883227.

Pyrgulopsis anguina Hershler, sp. nov.

Longitudinal gland pyrg

(Figures 9K, 23H–J, 44A–E)

Etymology: From *anguinus* (Latin), of snakes; referring to endemism of this species in Snake Valley, Nevada-Utah.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe short. Penial ornament a medium-sized terminal gland, large penial gland, medium-large Dg1, large Dg2, medium-large Dg3, additional dorsal gland, and large ventral gland.

Description: Shell (Figures 9K, 23H–J) sub-globose to

ovate-conic, apex often eroded; width/height, 70–95%; height, 2.0–3.5 mm; width, 1.7–2.4 mm; whorls, 3.0–5.0. Protoconch 1.25 whorls, diameter 0.30 mm, weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium to highly convex, shoulders narrow or absent, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture pyriform, adnate or disjunct. Inner lip slightly thickened in larger specimens, often forming narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus shallowly perforate. Periostracum tan-green.

Operculum ovate, amber, nuclear region slightly reddish; nucleus eccentric; dorsal surface frilled. Attachment scar often thick all around.

Radula 820 × 120 μm, with 62 rows of teeth. Central tooth 26 μm wide, with medium-highly indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded; basal cusps large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4(5); neck medium flexed; outer wing 195% of cutting edge length. Inner marginal teeth with 27–34 cusps (basal enlarged, separated); cutting edge occupying 43% of length of tooth. Outer marginal teeth with 32–40 cusps; cutting edge occupying 26% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium brown. Snout, foot light to medium brown. Opercular lobe dark along inner edge, sometimes also along sides. Neck unpigmented except for scattered granules to medium brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along almost entire length; black granules sometimes scattered on remainder of penis.

Ctenidial filaments, 18, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening thick, white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44A. Albumen gland having large (ca. 40%) pallial component. Capsule gland shorter, narrower than albumen gland, sub-globular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes mounted on weak papilla, having short anterior extension. Coiled oviduct of two overlapping posterior-oblique loops; posterior loop often overlapping bursa copulatrix. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, with most or all of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line and close to oviduct;

very short (20%), narrow. Seminal receptacle very small, pouchlike, overlapping anterior half of bursa.

Testis 1.25–1.5 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very large, elongate bean-shaped, pallial portion large (almost 50%), ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 44B–E) large; base rectangular, sometimes slightly expanded distally, weakly folded; filament short, medium width, tapering to point, longitudinal or slightly oblique; lobe as long as filament, triangular, longitudinal. Terminal gland medium-sized, narrow, longitudinal, largely or entirely ventral. Penial gland filling most of length of filament and slightly overlapping base, slightly narrower than filament. Dg1 medium-large, narrow, slightly or prominently raised, sometimes slightly curved, longitudinal or slightly oblique, positioned near mid-length at or near outer edge. Dg2 large, sometimes bifurcate, slightly raised or crestlike, positioned along inner edge. Dg3 medium-large, narrow, positioned near outer edge of lobe. Dorsal penis also bearing long gland (rarely bifurcate) near inner edge distally (extending distal to Dg2 and slightly overlapping lobe), often fused with Dg3 to form U-shaped loop. Small, circular glands sometimes found alongside Dg1 and Dg2, just proximal to edge of Dg3. Ventral gland large, usually narrow (rarely small, circular), borne on prominent swelling, usually straight and transverse, but sometimes curved; positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Big Springs, Snake Valley, White Pine County, Nevada, T. 10 N, R. 70 E, NE ¼ section 33. Holotype, USNM 874678 (Figure 23H), collected by R. Hershler and P. Hovingh, 23 June 1992; paratypes, USNM 860725. The type locality is a shallow, 4 m wide rheocene moderately disturbed by livestock.

Remarks: Among the group of species having a full complement of penial ornament, *P. anguina* most closely resembles *P. chamberlini* (described below), from Sevier River drainage, but differs in its broader shell, larger penial lobe, longitudinal orientation of terminal gland, and stronger Dg3 and ventral gland. The distribution of *P. anguina* is shown in Figure 55.

Material examined: NEVADA. *White Pine County:* Big Springs, Snake Valley, USNM 860725, USNM 874678. UTAH. *Millard County:* Clay Spring, Snake Valley, T. 22 S, R. 19 W, NW ¼ section 33, USNM 883205.

Pyrgulopsis saxatilis Hershler, sp. nov.

Sub-globose Snake pyrg

(Figures 9L, 11H, 16A–C, 23K, L, 44F–H)

Etymology: From *saxatilis* (Latin), found among rocks; referring to the habitat of species.

Diagnosis: Small, with sub-globose shell. Penis large, filament and lobe short. Penial ornament a small terminal gland, small Dg1, and large ventral gland.

Description: Shell (Figures 9L, 23K, L) sub-globose, apex usually eroded in adult specimens; width/height, 90–106%; height, 1.0–1.4 mm; width, 1.0–1.4 mm; whorls, 3.5–4.0. Protoconch (Figure 11H) 1.25 whorls, diameter 0.28 mm; initial 0.75 whorl finely wrinkled. Teleoconch whorls medium convexity; shoulders well developed, final 0.25 whorl sometimes having pronounced sub-sutural angulation. Aperture ovate-pyriform, adnate. Inner lip slightly thickened, columellar shelf medium width. Outer lip thin, prosocline, weakly sinuate. Umbilicus narrowly rimate to shallowly perforate. Periostracum eroded or absent.

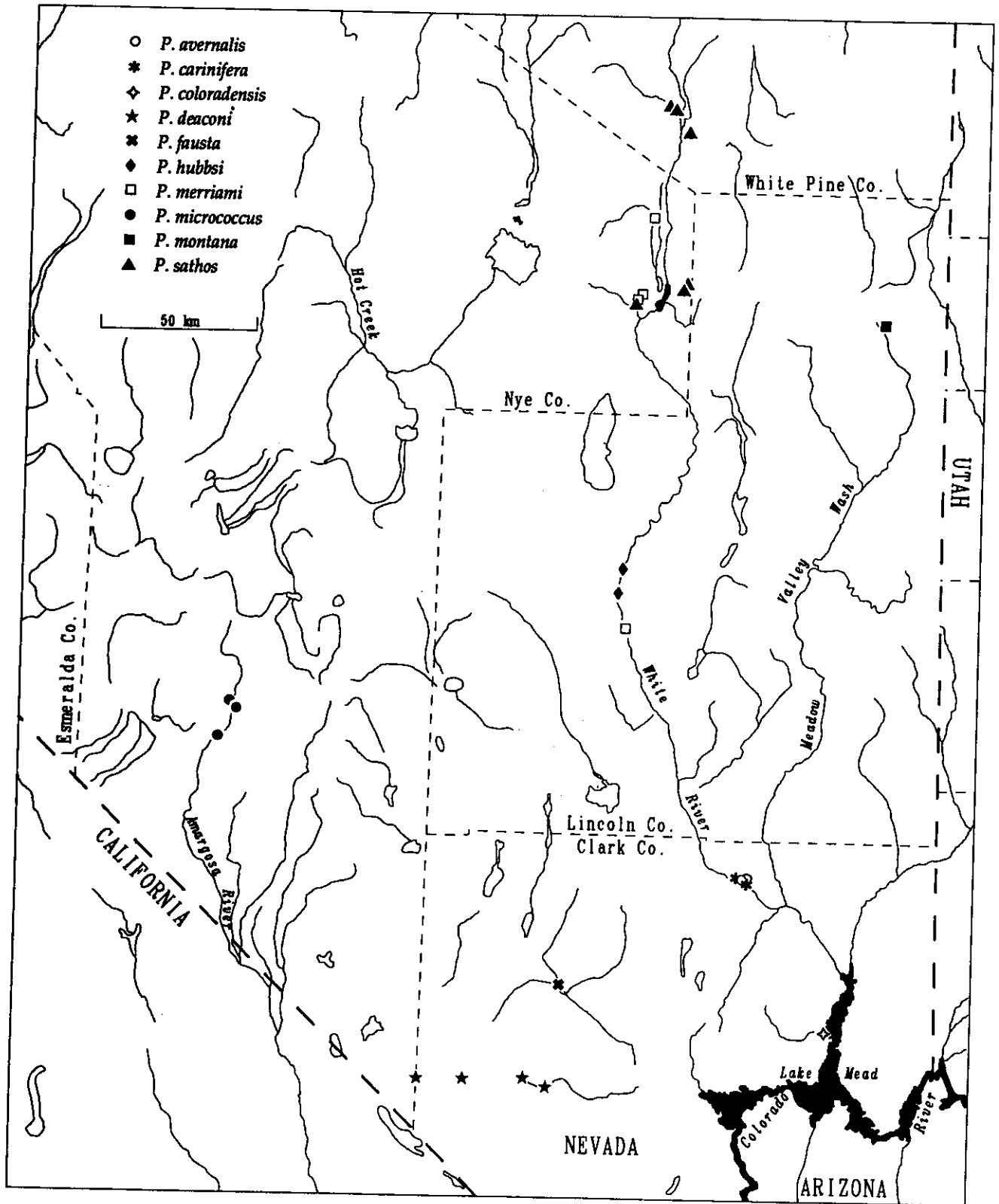
Operculum ovate, amber, slightly darker in nuclear region; dorsal surface smooth or weakly frilled; outer margin sometimes having very faint rim. Attachment scar thick along inner edge and between inner edge and nucleus.

Radula (Figure 16A–C) 480 × 65 μm, with 60 rows of teeth. Central tooth 15 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp long, daggerlike; basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 22–25 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 24–27 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; stomach chambers poorly distinguished externally, but anterior chamber slightly larger; stomach caecum very small.

Cephalic tentacles, foot light to medium brown. Snout medium to dark brown. Opercular lobe unpigmented or diffuse light brown. Neck light to medium grey-brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along most of length; base also containing scattered black granules.

Ctenidial filaments, 12, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44F. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit mounted on weak papilla, anterior extension short. Coiled oviduct a small circular loop, usually preceded by well-developed posterior twist. Oviduct and bursal duct joining a little behind



pallial wall. Bursa copulatrix short, narrow, globular-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at midline, long, narrow to medium width. Seminal receptacle small to medium-sized, pouchlike, overlapping proximal to medial portion of bursal duct, often overlapped by albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens with well-developed loop. Penis (Figure 44G, H) large; base elongate-rectangular, smooth or weakly folded along inner edge; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe as long as filament, clublike, but narrowing distally, longitudinal. Terminal gland small, circular to ovate (usually transverse), ventral. Dg1 small, ovate, longitudinal or slightly oblique, positioned just proximal to base of filament. Ventral gland large, narrow, slightly raised, angling across penis to base of lobe at inner edge. Dorsal and ventral penis also frequently having one to six minute, variably positioned, glandular dots. Penial duct slightly undulating near outer edge distally.

Type locality: Warm Springs, Snake Valley, Millard County, Utah, T. 16 S, R. 19 W, SW ¼ section 31 (Figure 55). Holotype, USNM 883237 (Figure 23K), collected by R. Hershler and P. Hovingh, 10 May 1993; paratypes, USNM 860726. The type locality is a series of large, thermal (26.9°C) rheocrenes issuing from the side of a hill.

Remarks: This thermal endemic is contrasted above with *P. lata*, from White River Valley. *Pyrgulopsis saxatilis* also resembles widespread *P. kolobensis*, but differs in its minute, globose shell, narrower central cusps on the central radular teeth, more elongate outer wing on the lateral radular teeth, smaller penial lobe and filament, and weakly developed terminal gland.

Material examined: UTAH. Millard County: Warm Springs, USNM 860726, USNM 883237.

Pyrgulopsis variegata Hershler, sp. nov.

Northwest Bonneville pyrg
(Figures 10A, 24A–D, 45A–F)

Etymology: From *variegatus* (Latin), of different sorts; referring to the substantial variation in penial glands among populations assigned to this species.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis small to large, filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (often absent), and small ventral gland (often absent).

Description: Shell (Figures 10A, 24A–D) ovate- to narrow-conic, width/height, 63–75%; height, 2.2–3.0 mm; width, 1.5–2.4 mm; whorls, 4.25–5.0. Protoconch 1.4–1.5 whorls, diameter 0.33 mm; smooth except for weak spiral striae along outer edge of whorl. Teleoconch whorls medium to highly convex, shoulders weak or absent; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip slightly thickened in largest specimens, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum light or reddish-brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; outer margin having weak rim. Attachment scar thick all around.

Radula 665 × 105 μm, with 62 rows of teeth. Central tooth 26 μm wide, with medium indented dorsal edge; lateral cusps, 5–7, central cusp medium width, rounded; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 185% of cutting edge length. Inner marginal teeth with 25–31 cusps (basal cusp enlarged); cutting edge occupying 35% of length of tooth. Outer marginal teeth with 31–36 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small or very small.

Cephalic tentacles unpigmented or having proximal light grey patch. Snout, foot light to medium grey. Opercular lobe black along inner edge. Neck unpigmented except for scattered black granules to medium grey. Pallial roof, visceral coil medium grey to black, pigment non-uniform. Penial filament darkly pigmented; pigment granules scattered on base.

Ctenidium medium width; filaments, 17, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum straight, broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45A.

←

Figure 49

Map showing distributions of *Pyrgulopsis* species of southern Nevada. Previously known records for *P. micrococcus*, *P. avernalis*, *P. carinifera*, and *P. merriami* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

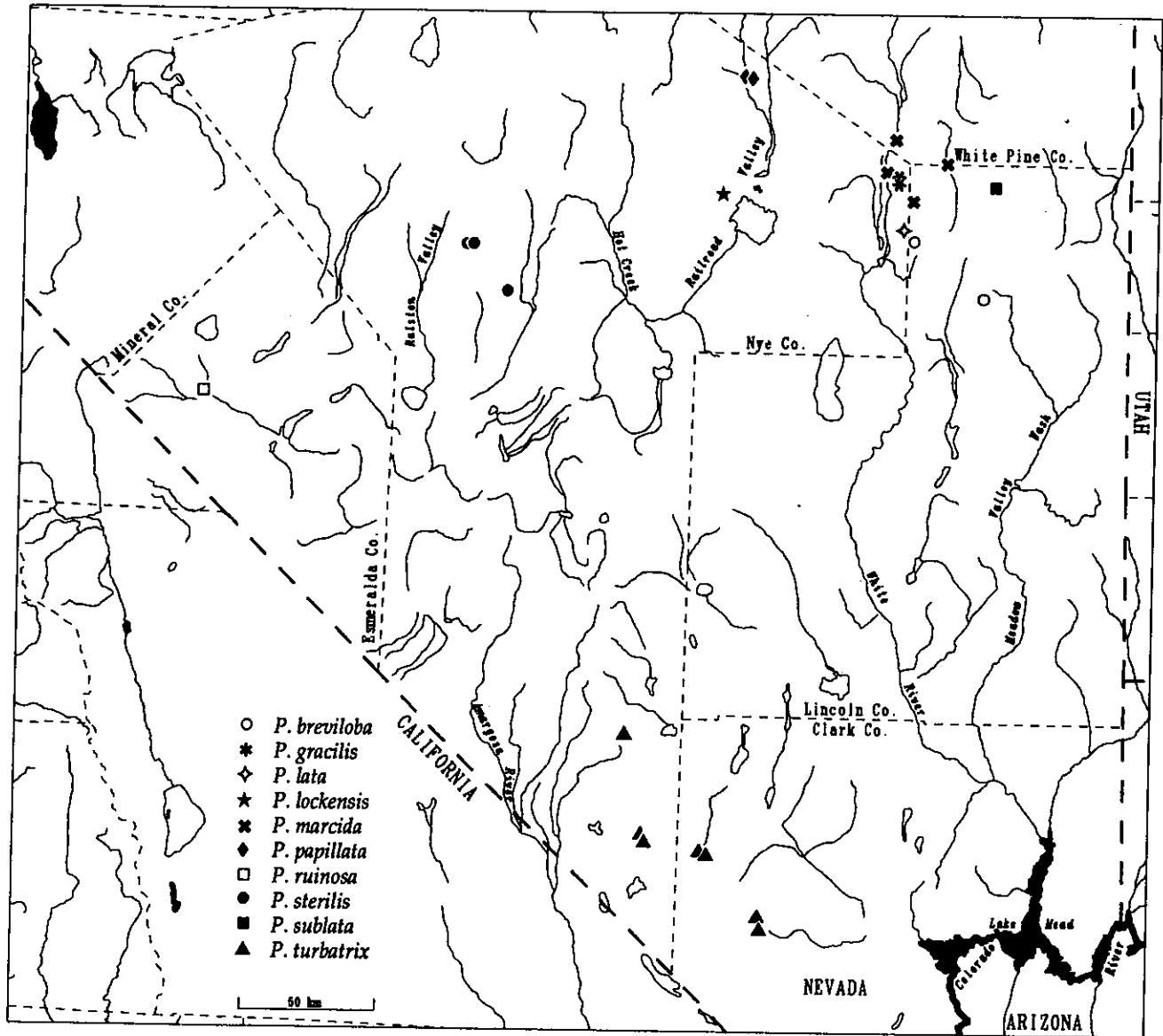


Figure 50

Map showing distributions of *Pyrgulopsis* species of the Colorado River drainage basin and isolated basins of Nevada. In cases where congeners are sympatric, symbols are slightly offset.

Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore often mounted on weak papilla; anterior extension short. Coiled oviduct a posterior-oblique loop often preceded by weak posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, medium width, pyriform, often having silvery sheen, longitudinal, with 50% or more of length usually posterior to gland, dorsal

edge sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle small, pouchlike, overlapping or slightly ventral to proximal portion of bursal duct.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and portion of anterior stomach chamber. Prostate gland small, subglobular, entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 45B-F) small to large; base

rectangular, sometimes elongate, folds along inner edge weak to well developed; filament 50% to almost as long as base, medium width, tapering to point, longitudinal or slightly oblique; lobe shorter than filament, slightly narrower than base, knoblike, longitudinal. Terminal gland small, rarely dotlike, narrow, circular-ovate, usually transverse (rarely longitudinal), entirely ventral or partly overlapping dorsal surface. Penial gland very small (often absent), narrow, positioned near base of filament. Ventral gland small (often absent), ovate-narrow, often slightly raised, longitudinal, distal. Penial duct straight, near outer edge.

Type locality: Spring, ca. 2.5 km south of South Patterson Spring, Pilot Valley, Box Elder County, Utah, T. 4 N, R. 19 W, SW ¼ section 1. Holotype, USNM 883627 (Figure 24A), collected by R. Hershler and P. Hovingh, 9 July 1993; paratypes, USNM 860723. The type locality is a small, minimally disturbed basin floor rheocrene.

Remarks: This species differs from similar *P. kolobensis* in having a smaller penial lobe and reduced (sometimes absent) glands on the penis. Populations of this species from the south and west have relatively well developed penial and terminal glands, and a weak or absent ventral glands; while those to the north and east (e.g., Grouse Creek, Park Valleys) have weak terminal gland, often lack a penial gland, and have stronger ventral glands. However, intergradation between these two conditions is evident in some populations, in which the penis has a well-developed penial gland, but weak terminal and ventral glands. The distribution of this species is shown in Figure 55.

Material examined: NEVADA. *Elko County:* Parson Springs, Pilot Creek Valley, T. 38 N, R. 70 E, NE ¼ section 28, USNM 874713.—McCuition Springs, Pilot Creek Valley, T. 37 N, R. 70 E, NE ¼ section 30, USNM 874723, USNM 883888.—Spring, lower Jay Creek, Goose Creek drainage, T. 47N, R. 69E, SW ¼ section 23, USNM 874721. UTAH. *Box Elder County:* Spring, ca. 2.5 km south of South Patterson Spring, USNM 860723, USNM 883627.—Spring, Halls Meadow, T. 3 N, R. 19 W, section 22, USNM 873431.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, SE ¼ section 29, USNM 883636.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, section 32, UCM 34042.—Spring brook, tributary to Etna Reservoir, Grouse Creek Valley (Figure 5E), T. 11 N, R. 18 W, NW ¼ section 6, USNM 883614.—North Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, NW ¼ section 32, USNM 883624.—South Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, SE ¼ section 31, USNM 883583.—Spring, Left Hand Fork, Dove Creek, Park Valley (Figure 3C), T. 13 N, R. 16 W, NE ¼ section 26, USNM 883599. *Tooele County:* Spring, ca. 4.8 km south of Donner Spring, Pilot

Valley, T. 3 N, R. 19 W, center section 14, USNM 883608.

Pyrgulopsis hovinghi Hershler, sp. nov.

Upper Thousand Spring pyrg

(Figures 10B, 111, 16D–F, 24E, 45G–I)

Etymology: Named after Peter Hovingh, in recognition of his extensive support and encouragement throughout this study.

Diagnosis: Medium-sized, with sub-globose to ovate-conic shell. Penis small to medium-sized; filament and lobe medium length. Penial ornament a large penial gland.

Description: Shell (Figures 10B, 24E) sub-globose to ovate-conic, apex and early teleoconch often eroded; width/height, 67–80%; height, 2.2–2.8 mm; width, 1.7–2.0 mm; whorls, 4.0–4.75. Protoconch (Figure 111) 1.2 whorls, 0.32 mm, initial 0.75 whorl finely (sometimes strongly) wrinkled, later portion near smooth. Teleoconch whorls highly convex, shoulders well developed, sculpture including well-developed spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip slightly thickened, sometimes forming narrow columellar shelf. Outer lip thin, orthocline to slightly prosocline, sinuate. Umbilicus rimate or shallowly perforate. Periostracum dark tan or brown.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula (Figure 16D–F) 675 × 110 μm, with 50 rows of teeth. Central tooth 26 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp long, narrow, daggerlike; basal cusps medium-large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4; neck weak; outer wing 180% of cutting edge length. Inner marginal teeth with 27–32 cusps (basal cusp enlarged); cutting edge occupying 34% of length of tooth. Outer marginal teeth with 30–37 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium brown. Snout medium to dark brown or black. Foot medium to dark brown. Opercular lobe black along inner edge, elsewhere unpigmented to medium grey-black. Neck unpigmented except for scattered black granules to almost uniform black. Pallial roof, visceral coil black, pigment slightly lighter on genital ducts. Penial filament darkly pigmented; pigment granules sometimes also scattered on base.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal

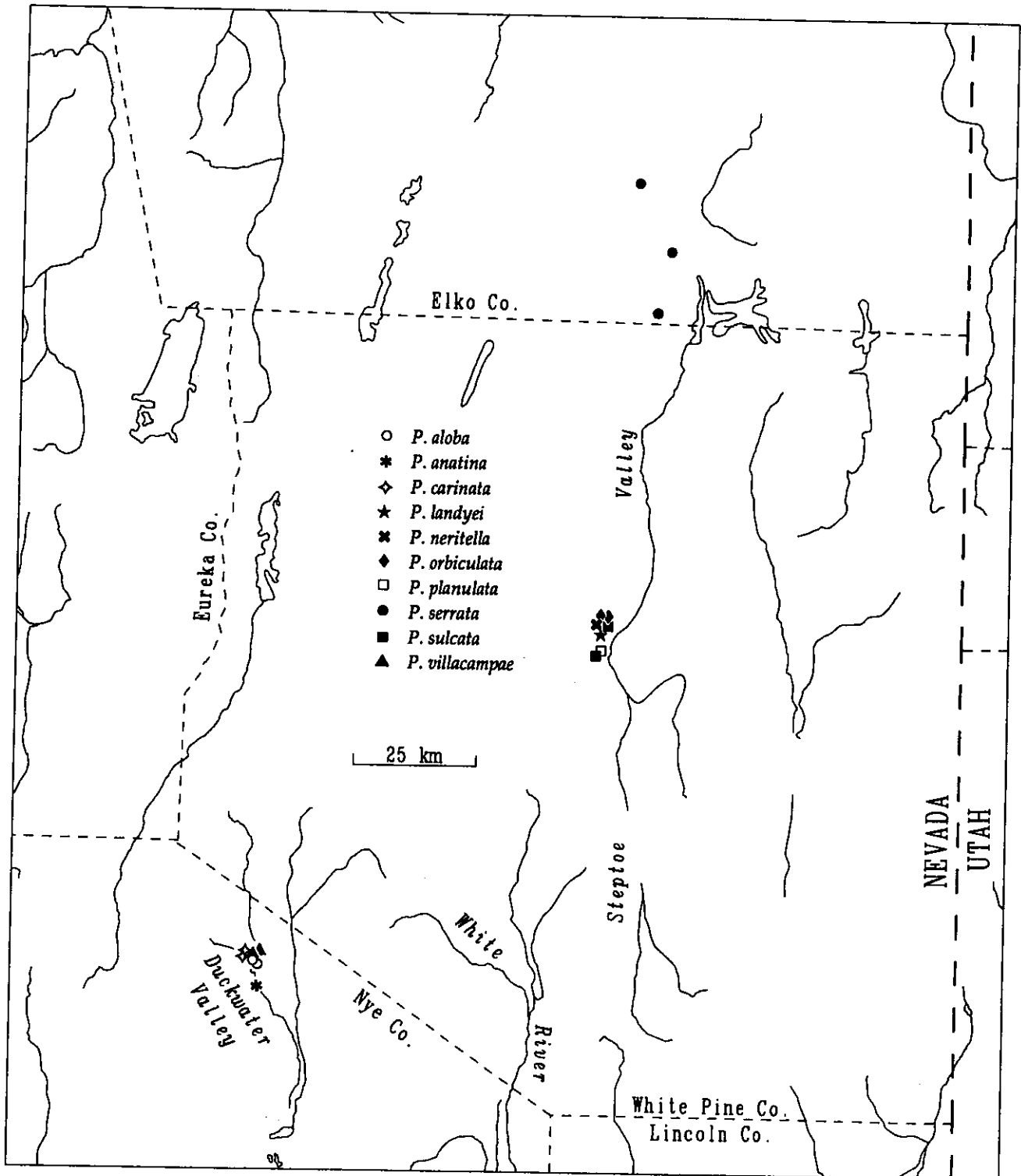


Figure 51

Map showing distributions of locally endemic *Pyrgulopsis* species of Duckwater and Steptoe Valleys, Nevada. In cases where congeners are sympatric, symbols are slightly offset.

gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45G. Albumen gland having short pallial component. Capsule gland sub-equal to albumen gland in length and width, sub-globular in section, rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore having short anterior extension. Coiled oviduct a small, posterior-oblique loop preceded and overlapped by weak twist (sometimes forming a similar posterior-oblique loop). Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, almost as wide as albumen gland, sub-globular to ovate, longitudinal, with 33–50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66% of bursa length, medium width. Seminal receptacle small, pouchlike, lateral to proximal portion of bursal duct, positioned near ventral edge of albumen gland.

Testis 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, often reflexed loop, duct broad. Penis (Figure 45H, I) small to medium-sized; base rectangular, often expanded distally, weakly folded; filament medium length, narrow, often curved, tapering to point, longitudinal; lobe slightly shorter to as long as filament, clublike to hemispherical, longitudinal or slightly oblique. Penial gland large, narrow, slightly raised, positioned along outer edge of proximal filament and distal base. Penial duct straight, near outer edge.

Type locality: Prather Springs, Thousand Springs Valley, Elko County, Nevada, T. 40 N, R. 64 E, SE ¼ section 21 (Figure 56). Holotype, USNM 874075 (Figure 24E), collected by P. Hovingh, 18 September 1990; paratypes, USNM 860720. The type locality is a small rheocrene moderately impacted by cattle.

Remarks: While *P. hovinghi* is similar to the other two species endemic to the Thousand Springs drainage (described below) in some respects, particularly the configuration of the distal female genitalia, these snails are heterogeneous in penial and other features and probably do not compose a clade. *Pyrgulopsis hovinghi* differs from the above in having narrower central cusps on the central radular teeth, and is distinguished from these as well as all other congeners by its unique penial ornament, consisting solely of an elongate Dg1 positioned just behind the penial filament.

Material examined: NEVADA. *Elko County:* Prather Springs, USNM 860720, USNM 874075, USNM 874715.

Pyrgulopsis millenaria Hershler, sp. nov.

Twentyone Mile pyrg

(Figures 10C, 24F, 46A, B)

Etymology: From *millenarius* (Latin), of a thousand; referring to the endemism of this snail in the Thousand Springs Creek drainage, Nevada.

Diagnosis: Medium-sized, with ovate-conic shell. Penis small; filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 10C, 24F) ovate-conic, width/height, 67–78%; height, 2.4–3.1 mm; width, 1.8–2.3 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.27 mm, smooth except for very small, finely wrinkled area at apex. Teleoconch whorls medium convexity, weakly shouldered; sculpture including faint spiral striae. Aperture ovate, broadly adnate to very slightly disjunct. Inner lip thin, columellar shelf absent or very narrow. Outer lip thin, orthocline, without sinuation. Umbilicus rimate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula 780 × 135 μm, with 47 rows of teeth. Central tooth 36 μm wide, with weakly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, considerably longer than laterals, daggerlike or rounded; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-2(3, 4); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–31 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having light brown patch proximally. Snout light to dark brown. Foot unpigmented or light brown. Opercular lobe medium to dark brown along sides; small central zone unpigmented. Neck unpigmented or having scattered grey-brown granules. Pallial roof, visceral coil medium brown-black; pigment not uniform. Penial filament darkly pigmented internally.

Ctenidial filaments, 19; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46A. Albumen gland having short or no pallial component. Capsule gland as long and slightly narrower than albumen gland, ovate in section; rectal furrow very weak. Ventral

channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by posterior-oblique twist, coil sometimes kinked or twisted at mid-line. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, positioned along ventral margin of gland, sub-globose to ovate, usually having silvery sheen, longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66–100% length of bursa, medium width. Seminal receptacle small, narrow pouchlike, overlapping or ventral to anterior half of bursa, sometimes partly overlapped by albumen gland.

Testis 1.5–1.75 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, sub-globose, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 46B) small; base rectangular, strongly folded along inner edge; filament medium length, broad, muscular, tapering, longitudinal; lobe absent, distal edge of penis blunt; glands absent. Penial duct straight, near outer edge.

Type locality: Springs, below Twentyone Mile Dam, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 67 E, SW $\frac{1}{4}$ section 14 (Figure 56). Holotype, USNM 874720 (Figure 24F), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860721. The type locality is a small rheocrene (Figure 5F).

Remarks: *Pyrgulopsis millenaria* differs from other species locally endemic in Thousand Springs drainage in having a much smoother protoconch and bursa copulatrix positioned near the ventral margin of the albumen gland. It is further distinguished from these and other species in the region in consistently lacking both a penial lobe and penial glands. This snail does not closely resemble other Great Basin species that have a simple penis.

Material examined: NEVADA. *Elko County:* Springs, below Twentyone Mile Dam (Figure 5F), USNM 860721, USNM 873329, USNM 874720.

Pyrgulopsis lentiglans Hershler, sp. nov.

Crittenden pyrg

(Figures 10D, 24G, H, 46C–E)

Etymology: From *lentis* (Latin), lentil-shaped; and *glans*, gland; referring to the dotlike terminal gland on the penis of this species.

Diagnosis: Small, with ovate-conic to pupiform shell. Penis large, filament medium length, lobe short or absent. Penial ornament a very small terminal gland (often absent).

Description: Shell (Figures 10D, 24G, H) ovate-conic to pupiform, width/height, 58–71%; height, 1.4–1.8 mm;

width, 0.9–1.2 mm; whorls, 4.25–4.75. Protoconch 1.2 whorls, diameter 0.27 mm, initial 0.75 whorl finely wrinkled, otherwise smooth. Teleoconch whorls low to medium convexity, without shoulders, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline, sometimes weakly sinuate. Umbilicus rimate to shallowly perforate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface strongly frilled; outer margin sometimes having weak rim. Attachment scar strongly thickened between nucleus and inner edge, slightly thickened along inner edge.

Radula $440 \times 70 \mu\text{m}$, with 60 rows of teeth. Central tooth $15 \mu\text{m}$ wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp medium width, spoon-shaped; basal cusps medium-large, sometimes accompanied by weak thickenings to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3–1–4; neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–26 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–32 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout light to dark brown. Foot light brown. Opercular lobe nearly unpigmented or having light, diffuse, grey pigment all around. Neck unpigmented except for scattered granules to light brown. Pallial roof, visceral coil medium to dark brown, sometimes uniformly pigmented. Penial filament darkly pigmented for almost entire length; base having scattered black granules.

Ctenidial filaments, 15, pleated; ctenidium connected to pericardium by short efferent vein. Osphradium 33% of ctenidium length, narrow, positioned posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46C. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore sometimes expanded or mounted on weak papilla; anterior extension absent. Coiled oviduct a posterior-oblique loop, often kinked at mid-length and/or preceded by small posterior twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, sub-globular to ovate, often having silvery sheen, longitudinal or slightly oblique (anterior end dorsal), with 50–80% of length posterior to gland. Bursal duct originating from

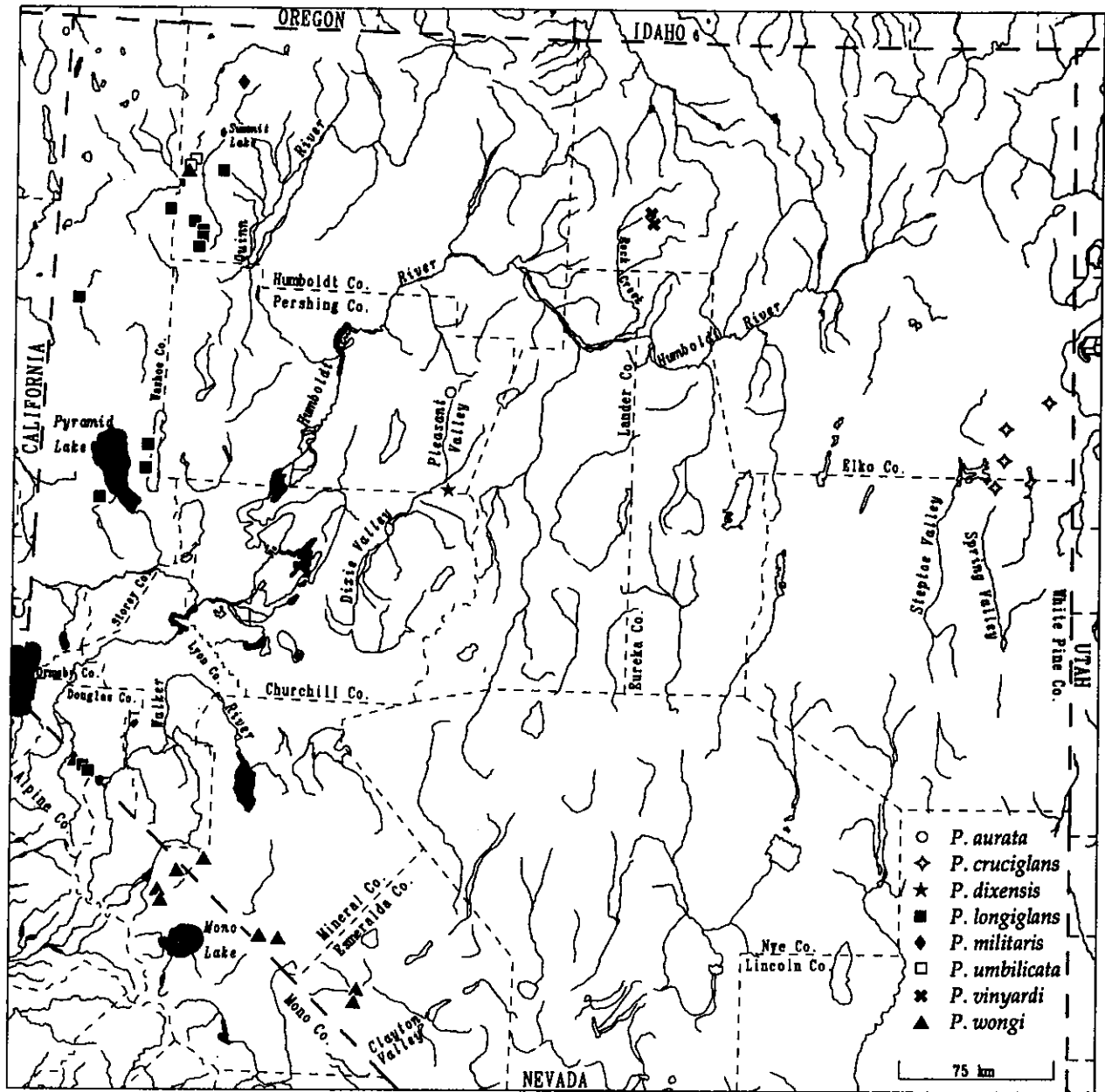


Figure 52

Map showing distributions of *Pyrgulopsis* species of isolated basins of Nevada and the Lahontan Basin. Previously known records for *P. wongi* are not shown. The distributions of *P. limaria* and *P. notidicola*, locally endemic species dwelling in very close proximity to *P. umbilicata* (in Mud Meadows), are not shown.

anterior edge at or near mid-line, slightly shorter to as long as bursa, medium width. Seminal receptacle small, pouchlike, overlapping or lateral to anteriormost bursa or proximal bursal duct.

Testis 1.25-1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and

part of anterior stomach chamber. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens nearly straight or having a weak loop. Penis (Figure 46D, E) large; base rectangular, weakly folded or smooth; filament medium length and width, muscular, tapering to point; lobe short,

pointed, slightly oblique; sometimes nearly absent, with distal edge of penis rounded and slightly bulging. Terminal gland very small (often absent), dotlike, ventral. Penial duct straight, near outer edge.

Type locality: Crittenden Springs, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 69 E, NE ¼ section 8 (Figure 56). Holotype, USNM 874724 (Figure 24G), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860722. The type locality is a shallow, broad (30 m) rheocene flowing down a steep mountainside.

Remarks: *Pyrgulopsis lentiglans* differs from other endemic species of Thousand Springs drainage in its smaller size and strongly frilled operculum. This snail differs from these and other congeners of the region in having a small penial lobe bearing a very reduced (often absent) terminal gland.

Material examined: NEVADA. *Elko County:* Crittenden Springs, USNM 854639, USNM 860722, USNM 873327, USNM 874724.—Spring, southwest corner of Crittenden Reservoir, Thousand Springs Creek, T. 42 N, R. 69 E, SW ¼ section 17, USNM 854540.

Pyrgulopsis plicata Hershler, sp. nov.

Black Canyon pyrg

(Figures 10E, 13F, 24I, J, 46F, G)

Etymology: From *plicatus* (Latin), folded; referring to the basally folded penis characterizing this species.

Diagnosis: Medium-sized, with broadly to ovate conic shell. Penis medium-large; filament medium length, lobe short. Penial ornament a large Dg1.

Description: Shell (Figures 10E, 24I, J) broadly to ovate conic; width/height, 72–85%; height, 2.3–2.9 mm; width, 1.8–2.2 mm; whorls, 4.0–4.5. Protoconch 1.5 whorls, diameter 0.38 mm; initial 0.5–0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity; shoulders absent to medium developed; body whorl often slightly disjunct and strongly translated behind the aperture. Aperture large, ovate, usually disjunct. Inner lip thick, without columellar shelf. Outer lip slightly thickened, orthocone or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum (Figure 13F) ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled. Attachment scar thick all around.

Radula 740 × 100 μm, with 60 rows of teeth. Central tooth 26 μm wide, with medium to highly indented dorsal edge; lateral cusps, 4–7; central cusp broad, daggerlike; basal cusps medium-sized, sometimes accompanied by weak swelling to outside. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-

3(4); neck weakly flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 19–25 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 24–30 cusps; cutting edge occupying 30% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark grey-brown or black. Snout light to dark grey-brown. Foot light to medium grey-brown. Opercular lobe black along outer edge; inner edge medium to dark grey-brown. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Almost entire length of penial filament and distal penis, particularly portion near outer edge, medium to darkly pigmented.

Ctenidial filaments, 17; without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 46F. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal pore, slightly raised, having short anterior extension. Coiled oviduct a tight, posterior-oblique loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% or less of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, 50% of length of bursa, narrow to almost as wide as bursa, duct sometimes shallowly embedded in albumen gland. Seminal receptacle small, overlapping or adjacent to anterior portion of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having large, well-developed loop, sometimes weakly reflexed. Penis (Figure 46G) medium-large; base elongate-rectangular, proximal portion folded under remaining penis; inner edge folded; filament medium length, narrow or medium width, tapering to point, slightly oblique; lobe short, hemispherical, longitudinal. Dg1 large, narrow, raised; longitudinal (although proximal portion curves slightly across width of penis), borne along outer edge proximally. Penial duct straight, very close to outer edge.

Type locality: Spring, Black Canyon, East Fork Sevier River, Garfield County, Utah, T. 32 S, R. 2 W, NW ¼ section 11 (Figure 56). Holotype, USNM 883594 (Figure

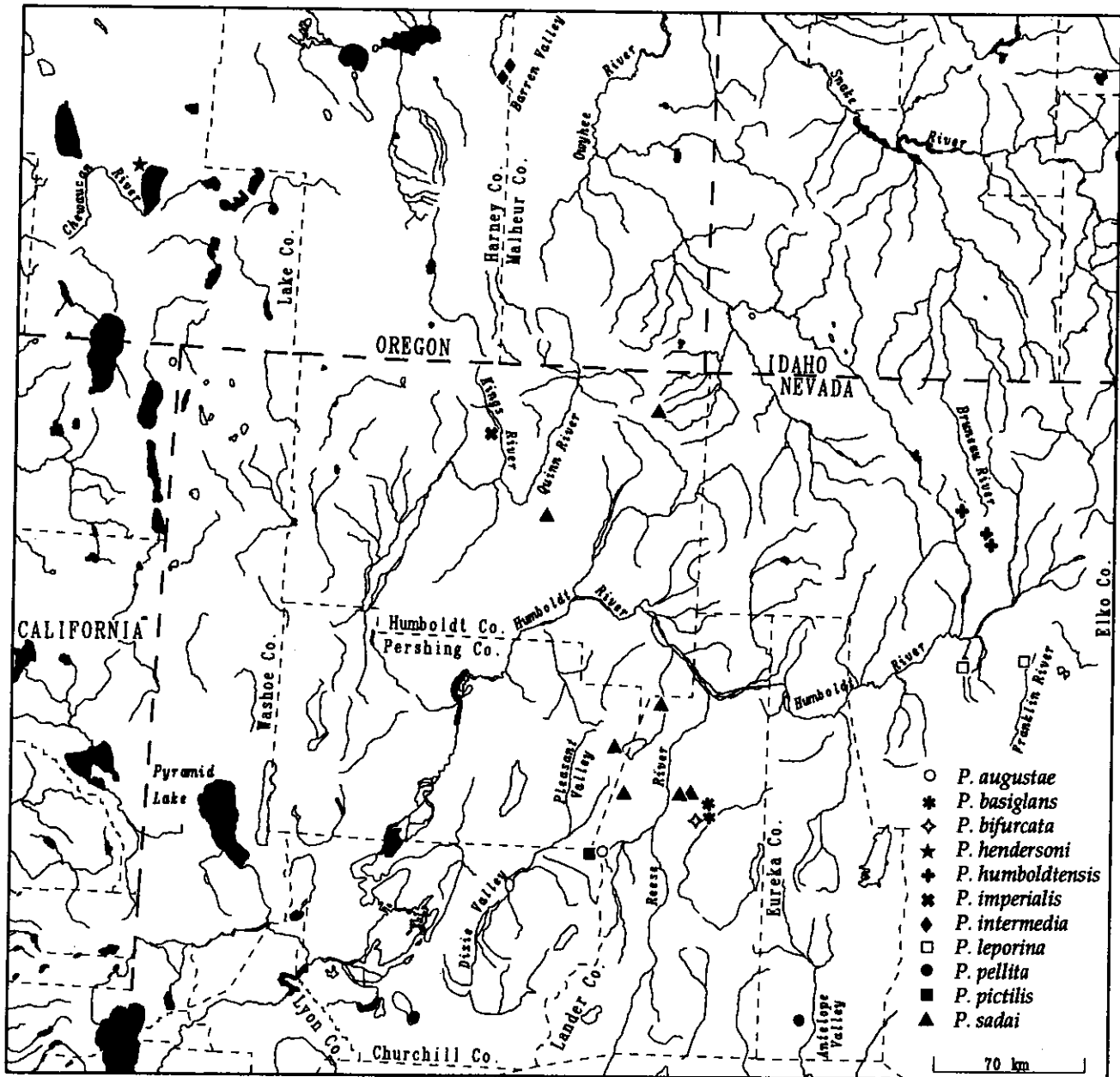


Figure 53

Map showing distributions of *Pyrgulopsis* species of the Lahontan Basin and the Oregon lakes region. Previously known records for *P. hendersoni* and *P. intermedia* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

241), collected by R. Hershler and P. Hovingh, 14 July 1993; paratypes, USNM 860727. The type locality is a series of small rheocrenes emerging from a steep hillside and feeding a reservoir.

Remarks: *Pyrgulopsis plicata* differs from other species of the Sevier River drainage in penial ornament, which

consists solely of an elongate Dg1. *Pyrgulopsis cruciglans*, from eastern Nevada, has a similar pattern of ornament, although the gland is much larger and transverse positioned in this species.

Material examined: UTAH. *Garfield County:* Spring, Black Canyon, USNM 860727, USNM 883594.

Pyrgulopsis fusca Hershler, sp. nov.

Otter Creek pyrg

(Figures 10F, 24K-M, 47A-C)

Etymology: From *fuscus* (Latin), dark, swarthy; referring to the black body pigmentation characterizing this snail.

Diagnosis: Medium-sized, with ovate- to elongate-conic shell. Penis medium-sized; filament medium length; lobe short. Penial ornament of small terminal, penial, and ventral glands.

Description: Shell (Figures 10F, 24K-M) ovate- to elongate-conic, width/height, 61-73%; height, 2.5-4.4 mm; width, 1.6-2.9 mm; whorls, 4.25-5.25. Protoconch 1.5 whorls, diameter 0.40 mm; initial 0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity, shoulders narrow to broad, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, adnate or slightly disjunct. Inner lip thin, sometimes having very narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum dark tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened along inner edge and between nucleus and inner edge.

Radula 650 × 100 μm, with 50 rows of teeth. Central tooth 24 μm wide, with highly indented dorsal edge; lateral cusps, 3-8; central cusp medium width, spoonlike; basal cusps small, sometimes accompanied by slight thickenings to outside. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4, 5); neck weakly flexed; outer wing 220% of cutting edge length. Inner marginal teeth with 21-28 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 27-33 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles dark brown or black, with narrow unpigmented streak centrally. Snout, foot medium brown or black. Opercular lobe sometimes dark along inner edge and/or along outer edge. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Penial filament darkly pigmented internally.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 1.0-1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure

47A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct usually of two overlapping posterior-oblique loops; proximal loop lightly pigmented internally. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% to almost as long as bursa, medium width. Seminal receptacle medium-sized, pouch-like, curved or folded, overlapping anteriormost portion of bursa.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland broad bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 47B, C) medium sized; base elongate-rectangular, inner edge weakly folded or smooth; filament medium length, broad, tapering to point, longitudinal or slightly oblique; lobe short, truncate, longitudinal. Terminal gland small, sub-circular, distal, ventral. Penial gland small (sometimes reduced or absent), narrower than filament, positioned on filament near base. Ventral gland small, sub-circular or ovate (transverse), borne on low swelling, positioned near base of filament. Penial duct straight, near outer edge.

Type locality: Spring brook, Otter Creek, ca. 1.6 km above The Narrows, Piute County, Utah, T. 28 S, R. 1 W, SW ¼ section 17. Holotype, USNM 883439 (Figure 24K), collected by R. Hershler and P. Hovingh, 1 October 1993; paratypes, USNM 860728. The type locality is a small brook (2 cm deep, 1 m wide), fed by numerous small springs, which enters Otter Creek.

Remarks: This snail differs from similar *P. kolobensis* in its much narrower penis, with very reduced lobe, and weakly developed glands; and smaller, narrower bursa copulatrix. The distribution of this snail is shown in Figure 56.

Material examined: UTAH, *Piute County:* Spring brook, Otter Creek, USNM 860728, USNM 883439, USNM 883484. *Sevier County:* Burr Creek, Otter Creek drainage, T. 25 S, R. 1 W, SW ¼ section 26, USNM 883573, USNM 892028.—Spring, Little Lost Creek, Sevier River drainage, T. 24 S, R. 1 E, center section 18, USNM 883430, USNM 883442.

Pyrgulopsis chamberlini Hershler, sp. nov.

Smooth Glenwood pyrg

(Figures 10G, 25A-C, 47D-G)

Etymology: Named after the late Ralph V. Chamberlin, in recognition of his extensive fieldwork and taxonomic

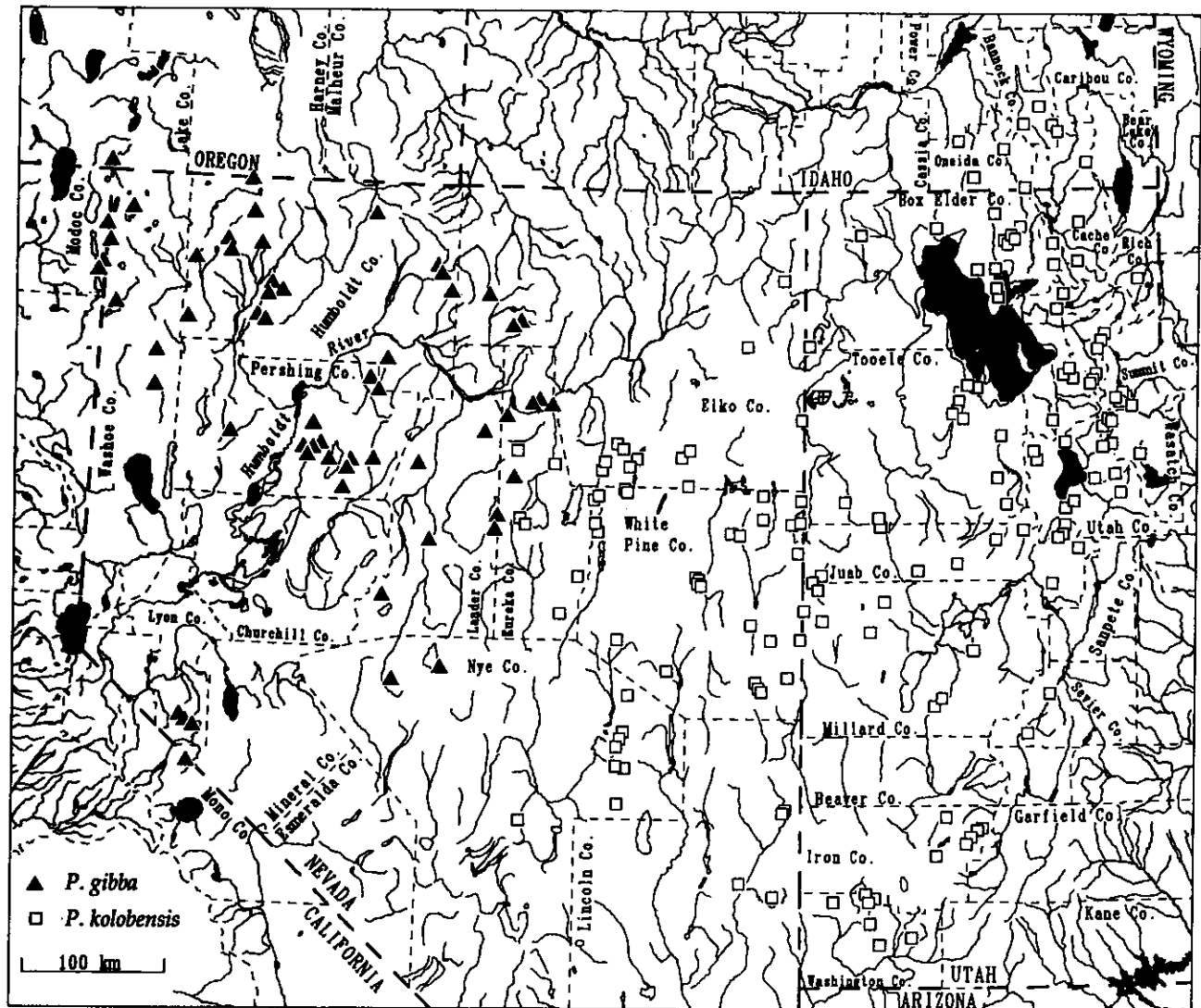


Figure 54

Map showing distributions of *P. gibba* and *P. kolobensis*. Previously known records for *P. gibba* are not shown.

studies pertaining to aquatic mollusks of the eastern Great Basin.

Diagnosis: Medium-sized to large, with ovate-conic shell. Penis large, filament medium length, lobe short. Penial ornament a medium-sized terminal gland, large penial gland, large Dg1, small Dg2, small Dg3 (sometimes absent), one to six additional dorsal glands, and small ventral gland.

Description: Shell (Figures 10G, 25A–C) ovate-conic, width/height, 64–78%; height, 2.3–4.3 mm; width, 1.8–3.1 mm; whorls, 4.5–6.0. Protoconch 1.25 whorls, diameter 0.33 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity,

shoulders well developed, often having with broad shelf; body whorl often slightly disjunct behind the aperture. Aperture ovate, slightly disjunct in largest specimens. Inner lip slightly thickened, columellar shelf medium width. Outer lip usually thin, but slightly thickened in largest specimens, prosocline, without situation. Umbilicus absent or narrowly rimate. Periostracum light green.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around, broadly so between nucleus and inner edge.

Radula $710 \times 100 \mu\text{m}$, with 62 rows of teeth. Central tooth $28 \mu\text{m}$ wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow (sometimes long),

daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 26-30 cusps; cutting edge occupying 40% of length of tooth. Outer marginal teeth with 32-34 cusps; cutting edge occupying 25% of length of tooth. Stomach as long a style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light brown; proximal section unpigmented. Snout light to dark grey-brown. Foot light brown. Opercular lobe light grey along inner edge, sometimes all around. Neck very light grey. Pallial roof, visceral coil dark brown or black, sometimes uniformly pigmented. Penial filament darkly pigmented along almost entire length; distal base often similarly pigmented.

Ctenidial filaments, 18, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75-1.0 whorl, filling 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47D. Albumen gland having medium-large (33% or more) pallial component. Capsule gland shorter, narrower than albumen gland, having distinct pigment patch alongside genital aperture, sub-globose in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore mounted on small papilla, having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique loops, distal loop having dark pigmented streak. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix long, medium width, lying along ventral margin of gland, ovate, longitudinal, 50-75% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of length of bursa, medium width. Seminal receptacle small, elongate pouch, rarely folded, overlapping anteriormost portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figures 47E-G) large; base rectangular, often elongate, smooth or weakly folded along inner edge, usually constricted proximally; filament medium length, narrow, gently tapering, oblique; lobe short, broadly rounded, longitudinal or slightly oblique. Terminal gland medium-sized, ovate, rarely bifurcate, usually transverse, ventral. Penial gland filling most of length of filament and small portion of base, almost as wide as filament. Dg1 large, narrow, raised on low pedicel, longitudinal (although proximal portion sometimes oblique), borne along outer

edge proximally, rarely abutting the penial gland, sometimes accompanied along inner side by small, circular, raised gland. Dg2 small, ovate, distal. Dg3 small, ovate-elongate (sometimes dotlike or absent), slightly raised. Dorsal surface having one to six additional longitudinal glands proximal to Dg2, units usually dotlike or ovate, but also often including one to two elongate glands near inner edge. Ventral gland small, ovate, transverse, borne on low swelling, positioned near base of lobe; sometimes accompanied by dotlike or small, circular gland proximally. Penial duct straight, near outer edge.

Type locality: Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW ¼ section 36 (Figure 56). Holotype, USNM 883576 (Figure 25A), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860729. Two springs are found in a small drainage at Glenwood. An upper spring flows alongside HWY 119, while in a deeply entrenched area below, a second, more mineralized rheocene emerges amongst a thicket of downed trees. The type locality is the lower spring, which was highly impacted by recreational activities. Note that this species also occurs in the upper spring and that *P. inopinata*, described next, also is present in both springs.

Remarks: This species is contrasted above with *P. anguina*, from Snake Valley.

Material examined: UTAH. *Sevier County:* Spring (lower), Glenwood, USNM 854786, USNM 860729, USNM 883576, USNM 883944.—Glenwood, FMNH 178389.—Spring (upper), Glenwood, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 36, USNM 854784.

Pyrgulopsis inopinata Hershler, sp. nov.

Carinate Glenwood pyrg

(Figures 10H, 25D-F, 47H-J)

Etymology: From *inopinatus* (Latin), unexpected; referring to the investigator's surprise at discovering a carinate *Pyrgulopsis* along the Wasatch Front.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament short, lobe medium length. Penial ornament a medium-sized terminal gland, large Dg1, small Dg2 (often absent), small Dg3, and medium-sized ventral gland.

Description: Shell (Figures 10H, 25D-F) ovate- to narrow-conic, width/height, 55-63%; height, 2.9-3.5 mm; width, 1.4-2.1 mm; whorls, 5.0-5.75. Protoconch 1.25 whorls, diameter 0.34 whorls, smooth or very weakly wrinkled at apex. Teleoconch whorls flat to medium convexity, without shoulders, sutures shallow; final 2.0 whorls usually having weak to well-developed peripheral angulation or narrow keel, sculpture sometimes weaker on body whorl; body whorl often slightly disjunct behind

the aperture. Aperture ovate, usually slightly disjunct. Inner lip thickened in larger specimens, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus absent or rimate. Periostracum tan.

Operculum ovate, amber, slightly darker in nuclear region; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar strongly thickened all around.

Radula $610 \times 105 \mu\text{m}$, with 55 rows of teeth. Central tooth $29 \mu\text{m}$ wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded or daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5); neck weakly to medium flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 23–27 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 28–33 cusps; cutting edge occupying 27% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles medium grey to black, unpigmented around eyes. Snout medium grey to black. Foot light grey to black. Opercular lobe diffuse black along inner edge. Neck light grey. Pallial roof, visceral coil medium grey to black, pigment lighter along genital ducts. Penial filament black along almost entire length; pigment often extending onto distal penis.

Ctenidial filaments, 24, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal, kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47H. Albumen gland having short pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold small. Genital aperture a terminal pore mounted on a slightly muscular papilla, having short anterior extension. Coiled oviduct of two small, posterior-oblique loops; proximal portion sometimes only weakly kinked. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of bursa length, medium width, often shallowly embedded in albumen gland. Seminal receptacle small, pouch-like, overlapping or lateral (ventral) to anterior portion of bursa.

Testis 1.5–2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal

pallial vas deferens having well-developed, weakly reflexed loop. Penis (Figure 47I, J) medium-sized; base elongate-rectangular, folded; filament short, narrow, tapering to point, longitudinal; lobe longer (sometimes considerably so) than filament, rectangular, longitudinal. Terminal gland medium-sized, ovate, transverse, largely ventral. Dg1 elongate, extending from middle of penis base near outer edge onto proximal half of filament, almost as wide as filament, slightly raised; longitudinal, but with proximal-most portion slightly oblique. Dg2 small, circular, absent in about 50% of specimens, positioned near inner edge of lobe. Dg3 small, ovate, positioned along outer edge of lobe. Ventral gland medium-sized, ovate, borne on low swelling, transverse-oblique, positioned near base of lobe. Penial duct straight, near outer edge.

Type locality: Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW $\frac{1}{4}$ section 36 (Figure 56). Holotype, USNM 883943 (Figure 25D), collected by R. Hershler and P. Hovingh, 10 May 1995; paratypes, USNM 860730. The type locality is the upper spring at Glenwood (see above), which flows out of a pipe and forms a shallow brook.

Remarks. Recent carinate species of *Pyrgulopsis* have previously been recorded only in the western Lahontan and Klamath Lake basins (*P. nevadensis*, *P. archimedis* Berry, 1947, respectively; Taylor, 1960:fig. 1). The penial ornament of *Pyrgulopsis inopinata* is substantially different than that shared by the above species (see Hershler, 1994), as well as that of *P. carinata* from southeastern Nevada (described above), and instead suggests affinity with the group of snails having an elongate, distal Dg1. Among members of this group, *P. inopinata* most closely resembles species from Snake River drainage (*P. robusta*) and Oregon Lakes (*P. hendersoni*), but differs in its smaller size and carinate shell.

At a second, nearby site south of Sigurd, the typical narrow-carinate form of this species is found along with a smooth, ovate-shelled snail. The nature of this variation is as yet unclear—one possibility is that this species may be hybridizing with *P. kolobensis*, which occurs in a typical form in a spring only 3 km to the north.

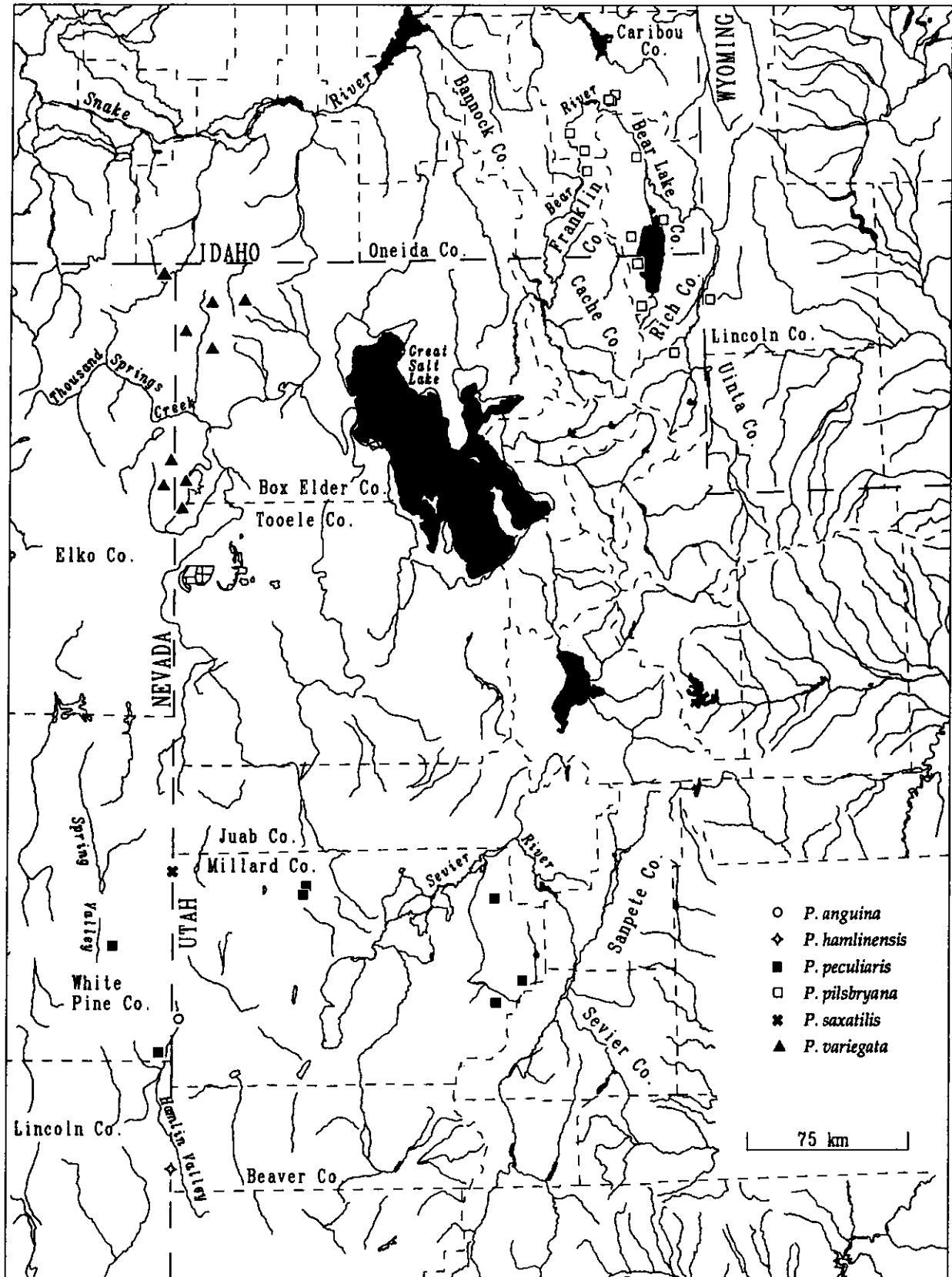
Material examined: UTAH. *Sevier County:* Spring (upper), Glenwood, USNM 854783, USNM 860730, USNM 883943.—Spring (lower), Glenwood, USNM 854785, USNM 883886.—Spring, 5.4 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, SW $\frac{1}{4}$ section 14, USNM 883942, USNM 892032, USNM 892033.

Pyrgulopsis nonaria Hershler, sp. nov.

Ninemile pyrg

(Figures 10I, 25G, 48A–C)

Etymology: From *nonarius* (Latin), of the ninth; referring to endemism of this species in the vicinity of Nine-mile Reservoir, Utah.



Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis large, filament and lobe short. Penial ornament of large terminal and ventral glands.

Description: Shell (Figure 10I, 25G) ovate- to narrow-conic; width/height, 60–71%; height, 2.5–2.9 mm; width, 1.6–1.9 mm; whorls, 4.5–5.0. Protoconch 1.25–1.3 whorls, diameter 0.35 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity, shoulders medium development; body whorl often slightly disjunct behind the aperture. Aperture ovate; usually disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline. Umbilicus shallowly perforate. Periostracum tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar thick all around.

Radula $750 \times 120 \mu\text{m}$, with 57 rows of teeth. Central tooth $32 \mu\text{m}$ wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp broad, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 23–33 cusps; cutting edge occupying 39% of length of tooth. Outer marginal teeth with 29–39 cusps; cutting edge occupying 29% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to dark brown. Snout light to medium brown. Foot unpigmented to light brown. Opercular lobe usually dark brown-black all around. Neck pigmented with scattered grey-brown granules. Pallial roof, visceral coil dark brown-black, pigment often uniform. Penial filament darkly pigmented along most of length.

Ctenidial filaments, 16, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, subglobose in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a broad, terminal slit having short anterior extension. Coiled oviduct a pos-

terior-oblique loop sometimes preceded by weak twist or (overlapping) small posterior-oblique coil; coiled portion usually having narrow, light pigment band. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate or sub-globular, longitudinal, with 33–60% of length posterior to gland; anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, medium length and width. Seminal receptacle medium-sized, pouchlike, overlapping anterior half of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed loop. Penis (Figure 48B, C) large; base elongate-rectangular, smooth; filament short, narrow, tapering to point, usually oblique; lobe as long as filament, broad, clublike, longitudinal. Terminal gland large, narrow, slightly curved, transverse, largely ventral. Distal penis bearing two glandular dots (conforming to Dg2) in single specimen. Ventral gland large, narrow, transverse, borne on prominent swelling, positioned near base of lobe, sometimes accompanied distally by small, circular unit (also borne on swelling). Penial duct straight, near outer edge.

Type locality: Spring, east side of Ninemile Reservoir, Sanpete Valley, San Pete County, Utah, T. 19 S, R. 2 E, NW $\frac{1}{4}$ section 9 (Figure 56). Holotype, USNM 883566 (Figure 25G), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860731. The type locality is a shallow, broad, mineralized (1213 micromhos/cm) rheocrene emptying into Ninemile Reservoir.

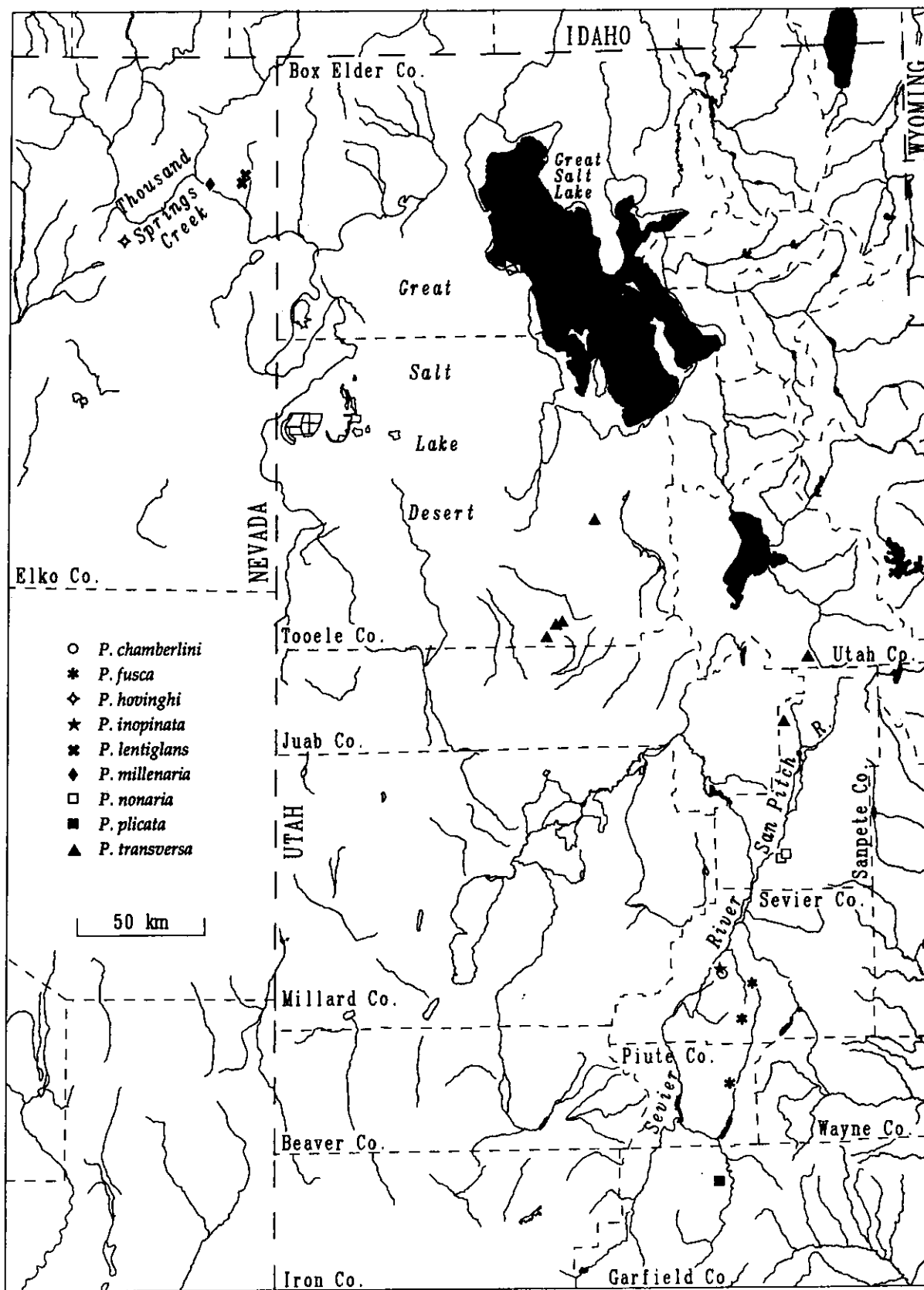
Remarks: This species is similar to *P. kolobensis* in many details, but differs in consistently lacking a penial gland. Among the group of species having penial ornament consisting solely of terminal and ventral glands, *Pyrgulopsis nonaria* and *P. transversa* (described below), which occurs in the northern portion of SanPete Valley, are distinctive in sharing a relatively narrow shell. These species differ in that *P. nonaria* has a shorter penial filament, larger ventral gland, and a more posteriorly positioned seminal receptacle.

Material examined: UTAH. *San Pete County:* Spring, east side of Ninemile Reservoir, USNM 860731, USNM 874376, USNM 883566.—Spring, northeast of Ninemile Reservoir, T. 19 S, R. 2 E, center section 4, USNM 874377.

←

Figure 55

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. Previously known records for *P. pilsbryana* are not shown.



Pyrgulopsis transversa Hershler, sp. nov.

Southern Bonneville pyrg

(Figures 10J, 16G-I, 25H-K, 48D-H)

Etymology: From *transversus* (Latin), crosswise; referring to the east-west distribution of this species, which cuts across several southern drainages in the Bonneville Basin.

Diagnosis: Medium-sized, with ovate- to narrow-conic shell. Penis medium-large, filament and lobe medium length. Penial ornament a small-medium terminal gland and small ventral gland (often absent).

Description: Shell (Figures 10J, 25H-K) ovate- to narrow-conic, width/height, 58–78%; height, 2.0–3.1 mm; width, 1.3–2.2 mm; whorls, 4.25–5.25. Protoconch 1.4–1.5 whorls, diameter 0.35 mm; weakly wrinkled along inner edge of initial 0.5 whorl, otherwise smooth. Teleoconch whorls low to medium convexity, shoulders weak to medium; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thick, with narrow to medium columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum tan or light brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled; outer margin sometimes having very weak rim. Attachment scar sometimes slightly thickened along inner edge and between inner edge and nucleus.

Radula (Figure 16G-I) 650 × 110 μm, with 53 rows of teeth. Central tooth 26 μm wide, with highly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3; neck straight or weakly flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 20–22 cusps; cutting edge occupying 37% of length of tooth. Outer marginal teeth with 28–34 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to light grey-brown. Snout unpigmented to medium grey-brown. Foot light to medium grey-brown. Opercular lobe black along inner edge, sometimes all around. Neck having scattered black granules. Pallial roof, visceral coil black, often uniformly pigmented. Penial filament usually lightly pigmented on proximal half; penis occasionally unpigmented.

Ctenidial filaments, 17, weakly pleated; ctenidium

overlapping pericardium posteriorly. Osphradium small, narrow, positioned posteriorly. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48D. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes weakly raised, having short anterior extension. Coiled oviduct usually of two small, overlapping posterior-oblique loops (proximal portion sometimes only twisted or kinked); distal loop usually having narrow band of light epithelial pigment. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate-elongate, longitudinal, with 67–80% of length posterior to gland, anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at or slightly lateral to midline, medium length and width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct.

Testis 1.5–2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland very small, bean-shaped, entirely visceral, narrowly ovate in section. Proximal pallial vas deferens having well-developed bend. Penis (Figure 48E-H) large; base rectangular, smooth; filament medium length and width, gently tapering to point, slightly oblique; lobe medium length, slightly narrower than base, clublike, longitudinal. Terminal gland small-medium, circular-narrow, longitudinal-transverse, ventral. Glandular smear seen on base of filament in single specimen. Similar smear conforming to distal Dg2 seen in single specimen. Ventral gland small, circular-ovate, often absent, borne near base of lobe on low swelling. Penial duct straight, near outer edge.

Type locality: Sixmile Springs, Simpson Mountains, Old River Bed, Tooele County, Utah, T. 10 S, R. 8 W, NW ¼ section 33. Holotype, USNM 883221 (Figure 25H), collected by R. Hershler and P. Hovingh, 12 May 1993; paratypes, USNM 860732. The type locality is a series of small, mineralized (1126 micromhos/cm) springs at about 1778 m elevation. The spring sampled is a small "rheocrene" issuing out of a pipe (Figure 3D).

Remarks: This species is contrasted with *P. nonaria*

←

Figure 56

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. In cases where congeners are sympatric, symbols are slightly offset.

above. The distribution of this species is shown in Figure 56.

Material examined: UTAH. *Sanpete County*: Spring, west-northwest of Fountain Green, San Pete Valley, T. 14 S, R. 2 E, NW ¼ section 2, USNM 873333, USNM 883597. *Tooele County*: Sixmile Springs, Old River Bed (Figure 3D), USNM 860732, USNM 883221.—Indian Springs, Simpson Mountains, Old River Bed, T. 10 S, R. 8 W, NE ¼ section 3, USNM 883422.—Spring, Lee Creek, Government Creek drainage, Dugway Valley, T. 9 S, R. 8 W, SW ¼ section 36, USNM 883481.—Springs, Clove Creek, Rush Valley, T. 5 S, R. 6 W, NW ¼ section 32, USNM 883210. *Utah County*: Spring, Thistle Creek, Utah Lake drainage, T. 11 S, R. 3 E, SW ¼ section 12, USNM 883572.

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LITERATURE CITED

- ANTHONY, J. G. 1840. Descriptions of three new species of shells. *Boston Journal of Natural History* 3:278-279 + plate III [in part].
- BAILY, J. L. & R. I. BAILY. 1951-1952. Further observations on the Mollusca of the relict lakes in the Great Basin. *The Nautilus* 65:46-53, 85-93.
- BAILY, J. L. & R. I. BAILY. 1952. *Ammicola pilsbryana*, new name. *The Nautilus* 65:144.
- BERRY, E. G. 1931. Mollusca of Lamb's Canyon, Utah. *The Nautilus* 44:113-114.
- BERRY, E. G. 1948 ("1947"). Snails collected for the schistosomiasis investigations. *United States National Institute of Health Bulletin* 189:55-69.
- BERRY, S. S. 1947. A new *Pyrgulopsis* from Oregon. *The Nautilus* 60:76-78.
- BOUCHARD, R. W. 1978. Taxonomy, distribution, and general ecology of the genera of North American crayfishes. *Fisheries* 3:11-19.
- BROWN, W. J. & M. R. ROSEN. 1995. Was there a Pliocene-Pleistocene fluvial-lacustrine connection between Death Valley and the Colorado River? *Quaternary Research*, 43:286-296.
- BRUES, C. T. 1928. Studies on the fauna of hot springs in the western United States and the biology of thermophilous animals. *Proceedings of the American Academy of Arts and Sciences* 63:139-228 + plates 1-6.
- BRUES, C. T. 1932. Further studies on the fauna of North American hot springs. *Proceedings of the American Academy of Arts and Sciences* 67:185-303.
- CALL, R. E. 1884. On the Quaternary and Recent Mollusca of the Great Basin with descriptions of new forms. Introduced by a sketch of the Quaternary lakes of the Great Basin by G. K. Gilbert. *United States Geological Survey Bulletin* 11: 66 pp. + plates I-VI.
- CALL, R. E. & H. A. PILSBRY. 1886. On *Pyrgulopsis*, a new genus of Rissoid mollusk, with descriptions of two new forms. *Proceedings of the Davenport Academy of Natural Sciences* 5:9-14.
- CHAMBERLIN, R. V. & D. T. JONES. 1929. A descriptive catalog of the Mollusca of Utah. *Bulletin of the University of Utah* 19:IX + map + 203 pp.
- CHAMBERLIN, R. V. & E. J. ROSCOE. 1948. Check list of Recent Utah Mollusca. *Bulletin of the University of Utah* 39:1-16.
- COVICH, A. P. 1978 ("1977"). How do crayfish respond to plants and Mollusca as alternate food resources? *Freshwater Crayfish* 3:165-179. [In O. V. Lindqvist (ed.), *Papers from the Third International Symposium on Freshwater Crayfish at the University of Kuopio, Finland, August 5-8, 1976*]
- CURREY, D. R., G. ATWOOD & D. R. MABEY. 1983. Major levels of Great Salt Lake and Lake Bonneville. *Utah Geological and Mineral Survey Map* 73. [map with text]
- D'AZEVEDO, W. L. 1986. Introduction. Pp. 1-14 in W. L. D'Azavedo (ed.), *Great Basin*. Smithsonian Institution: Washington, D.C. [W. C. Sturtevant (general ed.), *Handbook of North American Indians*; Volume 11]
- DEACON, J. E. & W. L. MINCKLEY. 1974. Desert fishes. Pp. 385-487 in G. W. Brown, Jr. (ed.), *Desert Biology*. Special Topics

- on the Physical and Biological Aspects of Arid Regions. Volume II. Academic Press: New York.
- DEACON, J. E., T. B. HARDY, J. POLLARD, W. TAYLOR, J. LANDYE, J. WILLIAMS, C. WILLIAMS, P. GREGER & M. CONRAD. 1980. Environmental analysis of four aquatic habitats in east-central Nevada June–September 1980. 123 pp. + appendices. [Unpublished report prepared by Environmental Consultants, Inc. for HDR Sciences under contract No. HDR/RPA15 Ext.]
- GARSDIE, L. J. & J. H. SCHILLING. 1979. Thermal waters of Nevada. Nevada Bureau of Mines and Géology Bulletin 91: 163 pp. + plate 1.
- GOULD, A. A. 1855. New species of land and freshwater shells from western (N.) America. Proceedings of the Boston Society of Natural History 5:127–130.
- GREGG, W. O. & D. W. TAYLOR. 1965. *Fontelicella* (Prosobranchia: Hydrobiidae), a new genus of west American freshwater snails. Malacologia 3:103–110.
- HANNIBAL, H. 1912a. The aquatic mollusks of southern California and adjacent regions, a transition fauna. Bulletin of the Southern California Academy of Sciences 11:18–46.
- HANNIBAL, H. 1912b. A synopsis of the Recent and Tertiary freshwater mollusks of the Californian Province, based upon an ontogenetic classification. Proceedings of the Malacological Society of London 10:112–166, 167–211.
- HENDERSON, J. 1924. Mollusca of Colorado, Utah, Montana, Idaho and Wyoming. University of Colorado Studies 13:65–223.
- HENDERSON, J. 1936. Mollusca of Colorado, Utah, Montana, Idaho and Wyoming—Supplement. University of Colorado Studies 23:81–145.
- HENDERSON, J. & L. E. DANIELS. 1916. Hunting Mollusca in Utah and Idaho. Proceedings of the Academy of Natural Sciences of Philadelphia 68:315–339 + plates XV–XVIII.
- HENDERSON, J. & L. E. DANIELS. 1917. Hunting Mollusca in Utah and Idaho in 1916. Proceedings of the Academy of Natural Sciences of Philadelphia 69:48–81.
- HERSHLER, R. 1989. Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa River (exclusive of Ash Meadows) drainages, Death Valley system, California–Nevada. Proceedings of the Biological Society of Washington 102:176–248.
- HERSHLER, R. 1994. A review of the North American freshwater snail genus *Pyrgulopsis* (Hydrobiidae). Smithsonian Contributions to Zoology 554:115 pp.
- HERSHLER, R. 1995. New freshwater snails of the genus *Pyrgulopsis* (Rissooidea: Hydrobiidae) from California. The Veliger 38:343–373.
- HERSHLER, R. & J. J. LANDYE. 1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). Smithsonian Contributions to Zoology 459:63 pp.
- HERSHLER, R. & W. L. PRATT. 1990. A new *Pyrgulopsis* (Gastropoda: Hydrobiidae) from southeastern California, with a model for historical development of the Death Valley Hydrographic System. Proceedings of the Biological Society of Washington 103:279–299.
- HERSHLER, R. & D. W. SADA. 1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, Amargosa Basin, California–Nevada. Proceedings of the Biological Society of Washington 100:776–843.
- HERSHLER, R. & F. G. THOMPSON. 1987. North American Hydrobiidae (Gastropoda: Rissoacea): redescription and systematic relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886. The Nautilus 101:25–32.
- HERSHLER, R. & F. G. THOMPSON. 1996. Redescription of *Paludina integra* Say, 1821, Type species of genus *Cincinnatia* (Gastropoda: Hydrobiidae). Journal of Molluscan Studies 62:33–55.
- HOLSINGER, J. R. 1974. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States. Smithsonian Contributions to Zoology 160:63 pp.
- HOLSINGER, J. R. & G. LONGLEY. 1980. The subterranean amphipod crustacean fauna of an artesian well in Texas. Smithsonian Contributions to Zoology 308:62 pp.
- HUBBS, C. L. & R. R. MILLER. 1948. II. The zoological evidence. Correlation between fish distribution and hydrographic history in the desert basins of western United States. Bulletin of the University of Utah 38 (Biological Series 10):17–191. [in The Great Basin, With Emphasis on Glacial and Post-glacial Times]
- JOHNSON, J. E. 1986. Inventory of Utah crayfish with notes on current distribution. Great Basin Naturalist 46:625–631.
- JONES, D. T. 1935. Mollusks from Weber Canyon, Utah. Proceedings of the Utah Academy of Sciences, Arts and Letters 12:227–228.
- JONES, D. T. 1940a. Recent collections of Utah Mollusca, with extralimital records from certain Utah cabinets. Proceedings of the Utah Academy of Sciences, Arts and Letters 17:33–45.
- JONES, D. T. 1940b. Mollusks of the Oquirrh and Stansbury Mountains in Utah. The Nautilus 54:27–29.
- KING, G. O. 1982. Morphometry of Great Basin playas. [unpublished] Doctoral Dissertation, University of Utah, Salt Lake City. xi + 137 pp.
- MIFFLIN, M. D. 1988. Region 5, Great Basin. Pp. 69–83 + plate 3 in W. Back, J. S. Rosenshein & P. R. Seaber (eds.), Hydrogeology. Geological Society of America: Boulder. [The Geology of North America, volume O-2]
- MIFFLIN, M. D. & M. M. WHEAT. 1979. Pluvial lakes and estimated pluvial climates of Nevada. Nevada Bureau of Mines and Geology, Bulletin 94:57 pp. + plate 1.
- MINCKLEY, W. L. & J. E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species." Science 159: 1424–1432.
- MLADENKA, G. C. 1992. The ecological life history of the Bruneau Hot Springs Snail (*Pyrgulopsis bruneauensis*). Unpublished report prepared for the United States Fish and Wildlife Service. 116 pp.
- MÜLLER, O. F. 1774. Vermium terrestrium et fluviatilium, seu animalium Infusorium, Helminthicorum et Testaceorum, non marinorum, succincta historia. Volume 2 (Testacea). Heineck et Faber: Havniae et Lipsiae: 214 pp. + index.
- MUNDORFF, J. J. 1971. Nonthermal springs of Utah. Utah Geological and Mineralogical Survey, Water-Resources Bulletin 16:70 pp.
- MURRAY, H. D. 1970. Discussion of Dr. Taylor's paper. Malacologia 10:33–34. [in A. H. Clarke (ed.), Papers on the Rare and Endangered Mollusks of North America]
- NELSON, R. A. 1992. Handbook of Rocky Mountain Plants. Revised by R. L. Williams. Roberts Rinehart: Niwot (Colorado). 444 pp.
- NOEL, M. S. 1954. Animal ecology of a New Mexico springbrook. Hydrobiologia 6:120–135.
- NYQUIST, D. 1963. The ecology of *Eremichthys acros*, an endemic thermal species of cyprinid fish from northwestern Nevada. [unpublished] Master of Science Dissertation, University of Nevada, Reno. xii + 247 pp., 27 plates, 2 maps.

- PENNAK, R. W. 1958. Some problems of freshwater invertebrate distribution in the western states. Pp. 223-230 in C. L. Hubbs (ed.), Zoogeography. A Symposium Presented on August 26-27, 1957, at the Stanford University Joint Meeting of the American Institute of Biological Sciences and the Pacific Division of the American Association for the Advancement of Science and a Symposium Presented on December 28, 1957, at the Indianapolis Meeting of the American Association for the Advancement of Science. American Association for the Advancement of Science: Washington, D.C. [Publication 51]
- PILSBRY, H. A. 1892. Preliminary notices of new forms of freshwater mollusks. The Nautilus 5:142-143.
- PILSBRY, H. A. 1899. Catalogue of the Amnicolidae of the western United States. The Nautilus 12:121-127.
- PILSBRY, H. A. 1933. Amnicolidae from Wyoming and Oregon. The Nautilus 47:9-12 + plate 2.
- PILSBRY, H. A. 1935. Western and southwestern Amnicolidae and a new *Humboldtiana*. The Nautilus 48:91-94.
- PRATT, W. L. 1977. Hydrobiid snails of the Moapa warm spring complex, Nevada. Western Society of Malacologists, Annual Report 10:7 [abstract].
- RUSSELL, R. H. 1971. Mollusca of Fish Springs, Juab County, Utah: rediscovery of *Stagnicola pilsbryi* (Hemphill, 1890). Great Basin Naturalist 31:223-236.
- SMITH, G. R. 1981. Late Cenozoic freshwater fishes of North America. Annual Review of Ecology and Systematics 12:163-193.
- SOLTZ, D. L. & R. J. NAIMAN. 1978. The natural history of native fishes in the Death Valley system. Natural History Museum of Los Angeles, Science Series 30:76 pp.
- STEARNS, R. E. C. 1883. Description of a new hydrobiinoid gastropod from the mountain lakes of the Sierra Nevada, with remarks on allied species and the physiographical features of said region. Proceedings of the Academy of Natural Sciences of Philadelphia 35:171-176.
- STEARNS, R. E. C. 1893. Report on the land and fresh-water shells collected in California and Nevada by the Death Valley Expedition, including a few additional species obtained by Dr. C. Hart Merriam and assistants in parts of the southwestern United States. North American Fauna 7:269-283.
- TAYLOR, D. W. 1960. Distribution of the freshwater clam *Pisidium ultramontanum*; a zoogeographic inquiry. American Journal of Science (Bradley Volume) 258-A:325-334.
- TAYLOR, D. W. 1966a. Summary of North American Blancan nonmarine mollusks. Malacologia 4:172 pp.
- TAYLOR, D. W. 1966b. A remarkable snail fauna from Coahuila, México. The Veliger 9:152-228.
- TAYLOR, D. W. 1975. Index and bibliography of Late Cenozoic freshwater Mollusca of western North America. University of Michigan Museum of Paleontology, Papers on Paleontology 10:384 pp. + errata (March, 1976). [Claude W. Hibbard Memorial Volume 1]
- TAYLOR, D. W. 1983. Late Tertiary mollusks from the Lower Colorado River Valley. University of Michigan Museum of Paleontology, Contributions 26:289-298.
- TAYLOR, D. W. 1985. Evolution of freshwater drainages and mollusks in western North America. Pp. 265-321 in C. J. Smiley & A. J. Leviton (eds.), Late Cenozoic History of the Pacific Northwest. American Association for the Advancement of Science: San Francisco.
- TAYLOR, D. W. 1987. Fresh-water molluscs from New Mexico and vicinity. New Mexico Bureau of Mines & Mineral Resources, Bulletin 116:50 pp.
- TAYLOR, D. W. & R. C. BRIGHT. 1987. Drainage history of the Bonneville Basin. Pp. 239-256 in R. S. Koop & R. E. Cohenour (eds.), Cenozoic Geology of Western Utah: Sites for Precious Metal and Hydrocarbon Accumulations. Utah Geological Association Publication 16.
- TAYLOR, D. W. & G. R. SMITH. 1981. Pliocene mollusks and fishes from northeastern California and northwestern Nevada. University of Michigan Museum of Zoology, Contributions 25:339-413.
- THOMPSON, F. G. 1995. A new freshwater snail from the Coosa River, Alabama (Gastropoda: Prosobranchia: Hydrobiidae). Proceedings of the Biological Society of Washington 108:502-507.
- TODD, D. K. 1980. Groundwater Hydrology. 2nd ed. John Wiley & Sons: New York. 535 pp.
- TROSCHEL, F. H. 1856-1863. Das gebiss der shnecken zur begründung einer natürlichen classification. Volume 1. Nicolaische Verlagsbuchhandlung: Berlin. 252 pp.
- TRYON, G. W. 1865. Descriptions of new species of *Amnicola*, *Pomatiopsis*, *Somatogyrus*, *Gabbia*, *Hydrobia* and *Rissoa*. American Journal of Conchology 1:219-222 + plate 22.
- UNITED STATES DEPARTMENT OF THE INTERIOR [USDI]. 1994. Endangered and threatened wildlife and plants; animal candidate review for listing as endangered or threatened species. Federal Register 59:58982-59028.
- UNITED STATES DEPARTMENT OF THE INTERIOR [USDI]. 1996. Endangered and threatened wildlife and plants; review of plant and animal taxa that are candidates for listing as endangered or threatened species. Federal Register 61:7596-7613.
- VERMEI, G. J. & A. P. COVICH. 1978. Co-evolution of freshwater gastropods and their predators. American Naturalist 112:833-843.
- WALKER, B. 1906. New and little known species of Amnicolidae. The Nautilus 19:114-117.
- WILKINSON, L. 1986. Systat: the system for statistics. Systat, Inc: Evanston (Illinois). 519 pp.
- WILLIAMS, J. E., D. B. BOWMAN, J. E. BROOKS, A. A. ECHELLE, R. J. EDWARDS, D. A. HENDRICKSON, & J. J. LANDYE. 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. Journal of the Arizona-Nevada Academy of Science 20:1-62.
- WILLIAMS, T. R. & M. S. BEDINGER. 1984. Selected geologic and hydrologic characteristics of the Basin and Range Province, Western United States. Pleistocene lakes and marshes. United States Geological Survey, Miscellaneous Investigations Series Map I-1522-D. [map + text]
- WOOLSTENHULME, J. P. 1942a. New records of Mollusca. Bulletin of the University of Utah 32:1-14.
- WOOLSTENHULME, J. P. 1942b. Uinta Mountain mollusks. The Nautilus 56:50-55.