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

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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 microscopic 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. (Pernak, 1958:224)

INTRODUCTION

Pernak'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 (Neal, 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 habitats 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 (Mittfitt, 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 localities. Field coverage has been extremely uneven as, for instance, the Great

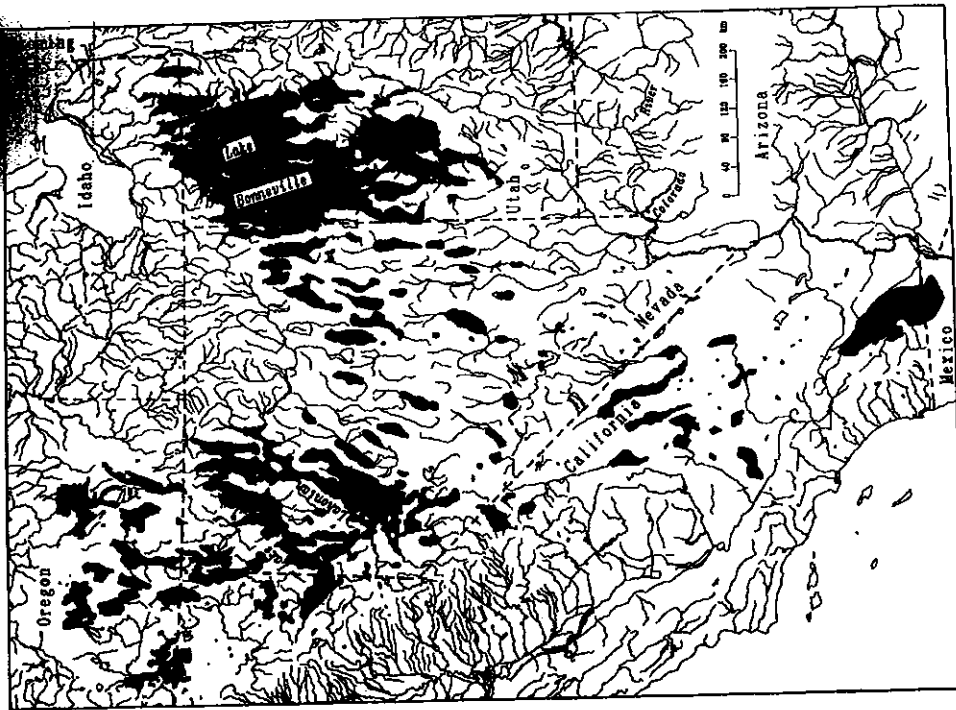


Figure 1
Map showing pluvial lakes (black) of the Great Basin superimposed on modern drainage (line distribution from Mifflin & Wheat, 1979; King, 1962; Curry et al., 1963; Williams & Bodinger, 1964).

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 & Suda, 1987; Hershler, 1989; Hershler & Fruit, 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 biogeographic Great Basin 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. 21) 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 tabbed 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 Steppe 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. gibber* Hershler, 1995, and *P. kotobensis* (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-

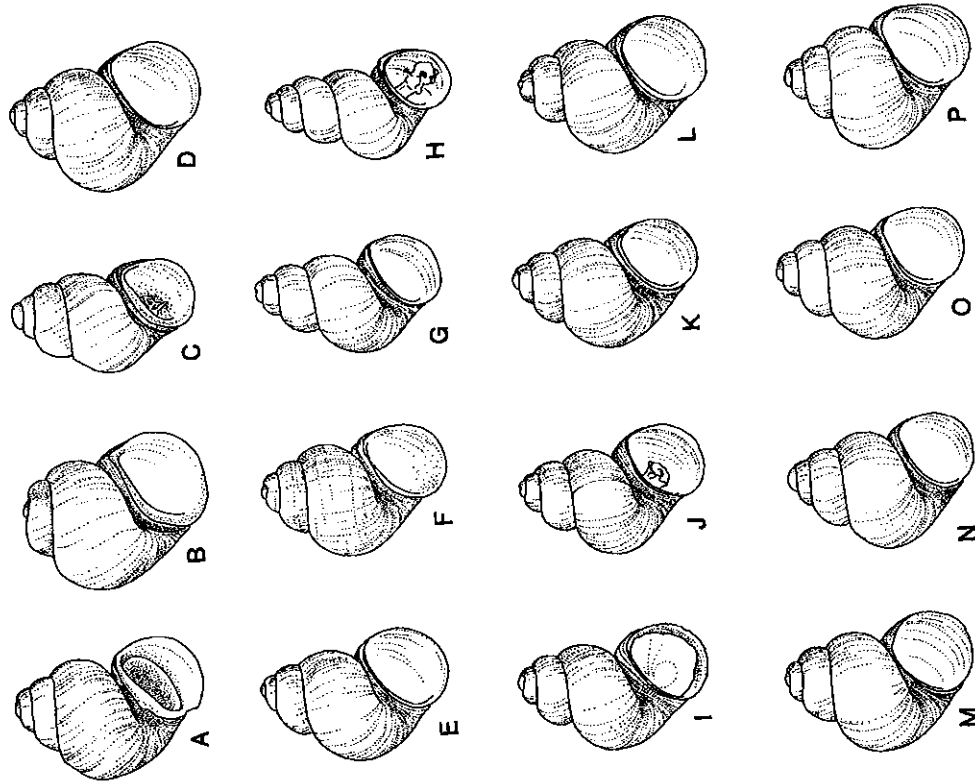


Figure 18

Shells of *Pyrgulopsis* species: A. *P. lens*, holotype, USNM 874667 (shell height, 1.9 mm). B. *P. gracilis*, holotype, USNM 873158 (2.0 mm). C. *P. aculeata*, USNM 863885 (2.1 mm). D. *P. macrida*, holotype, USNM 873154 (3.3 mm). E. *P. macrida*, USNM 874682 (3.9 mm). F. *P. macrida*, USNM 873170 (2.5 mm). G. *P. turbinata*, holotype, USNM 883978 (2.9 mm). H. *P. turbinata*, USNM 854738 (3.4 mm). I. *P. turbinata*, USNM 874485 (2.5 mm). J. *P. turbinata*, USNM 874775 (3.1 mm). K. *P. strobilis*, holotype, USNM 874876 (3.1 mm). L. *P. strobilis*, USNM 874769 (2.6 mm). M. *P. ruficauda*, holotype, USNM 873407 (2.6 mm). N. *P. strobilis*, holotype, USNM 874681 (2.9 mm). O. *P. P. sublinea*, USNM 860724 (2.2 mm). 2.4 mm, respectively.

Operculum (Figure 12B) ovate, dark amber, nuclear region reddish, nucleus eccentric; dorsal surface smooth; outer margin having weak rim. Attachment scar margin thick between nucleus and inner edge.

Racula 630 x 108 µm, with 55 rows of teeth. Central tooth 23 µm wide, with medium indented dorsal edge; lateral cusps, 6-7; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(5); neck medium flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 27-30 cusps; cutting edge occupying 33% of tooth length. Outer marginal teeth with 30-31 cusps; cutting edge occupying 24% of tooth length. Stomach slightly longer than style sac; stomach chambers equal in size; stomach caecum very small.

Cephalic tentacles, snout, neck light to dark grey-brown. Foot light to dark grey, pigment heaviest along anterior and posterior margins. Opercular lobe medium to dark grey; pigment heaviest along inner edge and sides. Pallial roof, visceral coil near uniform medium to dark brown-grey or black. Dark internal pigment filling most of penial filament and portion of proximal penis; lobe also sometimes having scattered black pigment.

Ctenidial filaments, 17, pleated; ctenidium slightly overlapping, pericardium posteriorly. Ophiurae small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal-slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, abutting prostate gland.

Ovary 0.5-0.75 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Distal female gametia shown in Figure 27C. Albumen gland having medium pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel moderately overlapping capsule gland; longitudinal fold moderately developed. Ctenial aperture a terminal slit having short anterior extension. Coelot oviduct a tight circular loop usually preceded by weak twist. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatory medium length and width, narrow-ovate, often having silvery appearance, longitudinal or oblique, positioned along postero-ventral edge of albumen gland, with small portion extending posterior to gland. Bursal duct originating from anterior edge at mid-line, long, me-

dium width, broadening distally. Seminal receptacle small, pouchlike, overlapping or abutting proximal portion of bursal duct close to ventral edge of albumen gland.

Testis 1.25-1.5 whorls, filling 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland small, broadly ovate, entirely visceral or having short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight or with weak undulation. Penis (Figure 27D, E) small; base rectangular to near square, strongly folded; filament slightly shorter than base, broad, tapering to sharp point, longitudinal; lobe short, knoblike, longitudinal. Terminal gland short, narrow-circular, sometimes longitudinal, ventral. Penial duct straight, near outer edge.

Type locality: Spring, upper Camp Valley, Lincoln County, Nevada, T. S. N. R. 69 E, center section 8 (Figure 49). Holotype, USNM 874686 (Figure 17E), collected by R. Hershler and P. Hovingh, 24 June 1992, paratypes, USNM 860694. The type locality is a small thicket heavily impacted by cattle.

Remarks: This species closely resembles *P. hamifera* (described below), which occurs to the east in the Bonneville Basin, as both species share a smooth protoconch and relatively simple penis ornamented solely by a terminal gland. *Pyrgulopsis montana* differs from this species in its slightly broader shell with simple whorl outline, and weaker operculum attachment scar.

Material examined: NEVADA, Lincoln County, Spring, upper Camp Valley, USNM 860694, USNM 874686.

Pyrgulopsis hubbsi Hershler, sp. nov.
Hubbs pyrg

(Figures 6E, 14A-C, 17F, G, 27F-H)

Etymology: Named after the late Carl Hubbs, in recognition of his extensive contributions to the study of fishes and drainage history of the Great Basin.

Diagnosis: Medium-sized to large, with globose to low-conical shell. Penis medium-sized, filament long, lobe short. Penial ornament a dotlike terminal gland.

Description: Shell (Figures 6E, 17F, G) globose to low-conical, apex usually eroded, width/height, 82-93%;

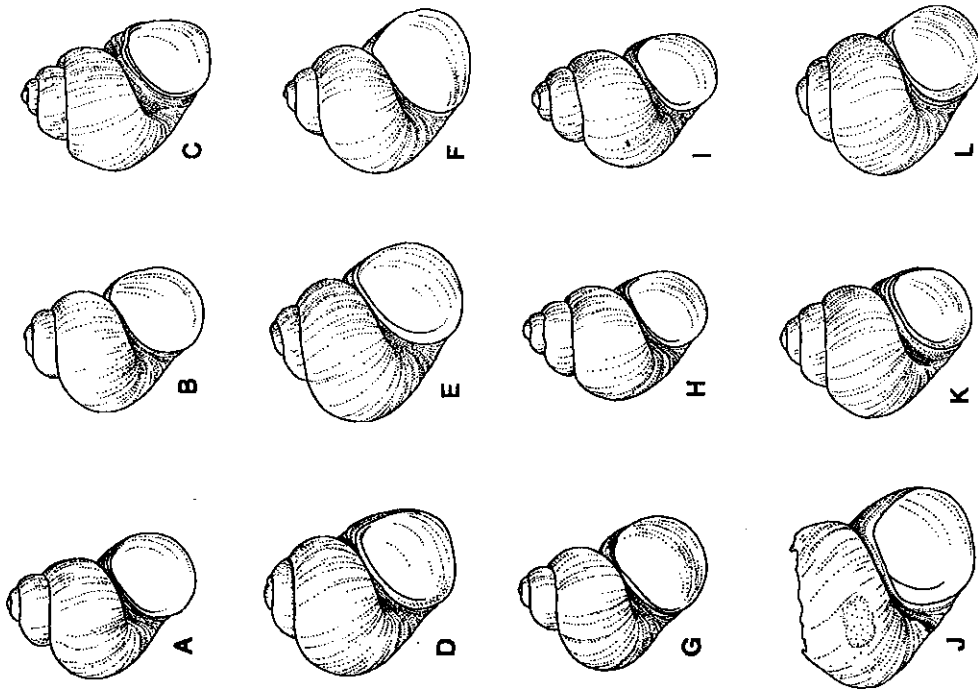


Figure 19

Shells of *Pyrgulopsis* species. A. *P. beckeri*, holotype, USNM 874779 (shell height, 2.0 mm). B. *P. papillata*, holotype, USNM 873185 (2.1 mm). C. *P. carinata*, holotype, USNM 863975 (2.2 mm). D. *P. atoea*, holotype, USNM 863847 (1.1 mm). E. *P. alba*, holotype, USNM 873187 (1.5 mm). F. *P. vitaceae*, holotype, USNM 873191 (2.5 mm). G. *P. vitaceae*, USNM 863938 (3.6 mm). H. *P. arctica*, holotype, USNM 863948 (2.8 mm). I. *P. arctica*, USNM 860710 (2.5 mm). J. *P. pennsylvanica*, holotype, USNM 892023 (1.2 mm). K. *P. salsicola*, holotype, USNM 874626 (1.6 mm). L. *P. orbicularis*, holotype, USNM 873196 (1.3 mm).

height, 2.5–3.8 mm; width, 2.2–3.4 mm; whorls, 3.25–3.75; protoconch 1.3 whorls, diameter 0.33 mm, initial 0.25 whorl finely wrinkled, later portion near smooth. Teleoconch whorls moderately convex, shoulders absent to well developed. Apertures broad, crescentlike, often strongly angled above; anasae or, less commonly, slightly distinct. Inner lip thick, with medium width columellar shelf. Outer lip thick in larger specimens, prosocline, weakly sinuate. Umbilicus absent or rimate; umbilical region often weakly excavated with slight adaxial ridge. Periostracum light brown, thick.

Operculum ovate, amber; nuclear region reddish; nucleus eccentric; dorsal surface weakly filled, outer margin having weak rim. Attachment seta slightly thickened between nucleus and inner edge.

Radula (Figure 14A–C) 1.19 × 140 μm, with 78 rows of teeth. Central tooth 40 μm wide, with slightly indented dorsal edge; lateral cusps, 4–6; central cusp long, median width, daggerlike; basal cusps small. Basal tongue broad, nearly U-shaped, considerably shorter than lateral margins; basal sockets medium depth. Lateral tooth formula 2(3)–1–3(4); neck medium flexed; outer wing broad, 110% of cutting edge length. Inner marginal teeth with 21–24 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 30–31 cusps; cutting edge occupying 50% of length of tooth. Stomach and style sac equal-sized; anterior and posterior stomach chambers equal-sized; stomach caecum absent or very small.

Cephalic tentacles light to dark brown, usually lighter centrally and around eyespots. Snout light to dark brown, usually darker than tentacles. Foot light to dark brown. Opercular lobe unsegmented to dark along inner edge and sides. Neck light to medium brown. Pallial roof, visceral coil nearly uniform dark brown-black. Pallial filament darkly pigmented internally for entire length except distalmost portion; pigment extending into distal portion of base.

Ctenidial filaments, 30, pleated, ctenidium overlapping postcardium posteriorly. Oesophradium small, narrowly ovate, centrally positioned. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

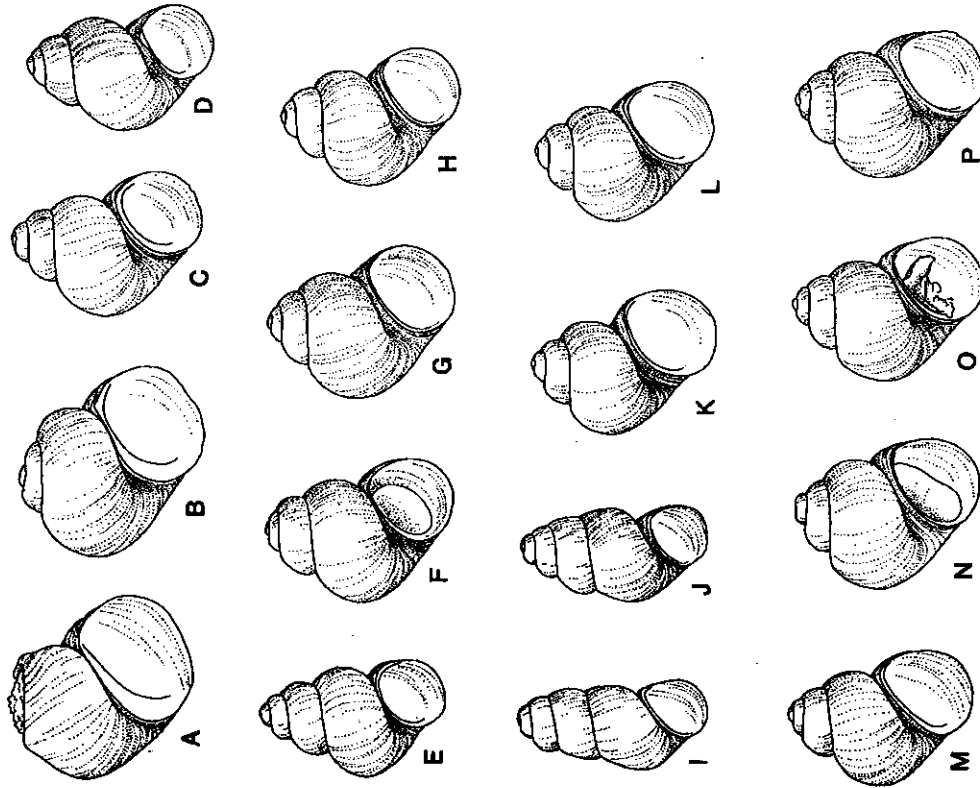
Ovary 0.75–1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and an-

terior stomach and extending to edge of albumen gland. Distal female genitalia shown in Figure 27F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, subcircular in section; renal furrow well developed. Ventral channel slightly overlapping capsule gland, longitudinal fold weakly developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct a tight circular loop preceded and overlapped by posterior arched kink or twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, medium width, sub-globular to broadly ovate, longitudinal, with 50–75% of length posterior to gland, anteriormost portion usually embedded in gland. Bursal duct originating from anterior edge at mid-line, long, narrow, embedded in albumen gland except for distalmost portion. Seminal receptacle small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 1.0 whorl, filling almost all of digestive gland behind stomach, overlapping anterior and posterior stomach chambers and extending to edge of prostate gland. Prostate gland very small, broadly ovate, entirely visceral or with short pallial component, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 27G, H) medium-sized; base rectangular, weakly folded along inner edge; filament is long or slightly longer than base, broad, tapering, longitudinal, lobe very short, bud-like, longitudinal. Terminal gland dotlike, circular, sometimes divided into two units, ventral. Penial duct weakly undulating in base, straight in filament, near outer edge.

Type locality: Hiko Spring, Pahramagat Valley, Lincoln County, Nevada, T. 4 S. R. 60 E. SE ¼ section 14. Holotype, USNM 873415 (Figure 17F), collected by R. Hershler, 9 July 1986; paratypes, USNM 860690. The type locality is a large, thermal (27°C), rheocrene.

Remarks: *Pyrgulopsis beckeri* resembles *P. anthers* (described next), from White River Valley, in having weak protoconch sculpture; short, broad lateral wings on the lateral marginal teeth; ovate bursa copulatrix with long duct; very small, anteriorly positioned seminal receptacle; and penis with enlarged filament, very small penial lobe, and small terminal gland. *Pyrgulopsis beckeri* differs from this species in having a squatter shell, and lacking a ven-



tral gland on the penis. Distribution of *P. hazbetti* is shown in Figure 49.

Material examined: NEVADA. Lincoln County: Hiko Spring, USNM 860690, USNM 873166, USNM 873399, USNM 873415, USNM 874776.—Cystal Spring, Pah-rangas Valley, T. S. R. 60 E. NE ¼ section 10, USNM 873173, USNM 873404, USNM 873405, USNM 874081, USNM 874770.

Pygulopsis saithos Hershler, sp. nov.

White River Valley FVF

(Figures 6E, 12C, 17H-K, 28A-C)

Etymology: From *saithos* (Greek), one with large penis; referring to the enlarged penial filament characterizing this species.

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

Description: Shell (Figures 6E, 17H-K) ovate to narrow-conic, width/height, 67-91%; height, 1.4-4.6 mm; width, 1.2-3.5 mm; whorls, 3.25-5.25. Protoconch 1.25 whorls, diameter 0.33 mm, weakly wrinkled along inner edge at apex, otherwise smooth. Teleoconch whorls medium to highly convex; shoulders absent or narrow. Aperture ovate, narrow adaxial or slightly separated from body whorl. Inner lip slightly thickened, sometimes having very narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan-brown.

Operculum (Figure 12C) ovate, reddish; nucleus slightly eccentric; dorsal surface weakly filled; outer margin having well-developed rim. Attachment scar thick almost all around (except for section along outer edge).

Rostrum 890 × 150 µm, with 36 rows of teeth. Central tooth 39 µm wide, with slightly indented dorsal edge; lateral cusps, 4-5, central cusp medium width, dagger-like; basal cusps medium-sized, sometimes accompanied by vestige of second, outer cusp. Basal tongue broad V-shaped, shorter than lateral margins, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck median filled; outer wing 150-170% of cutting edge length, broad. Inner marginal teeth with 21-26 cusps; cutting

edge occupying 36% of length of tooth. Outer marginal teeth with 31-35 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles unpigmented to dark brown. Snout foot light to dark brown. Opercular lobe usually dark along sides and inner edge. Neck unpigmented to medium brown. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally along almost entire length.

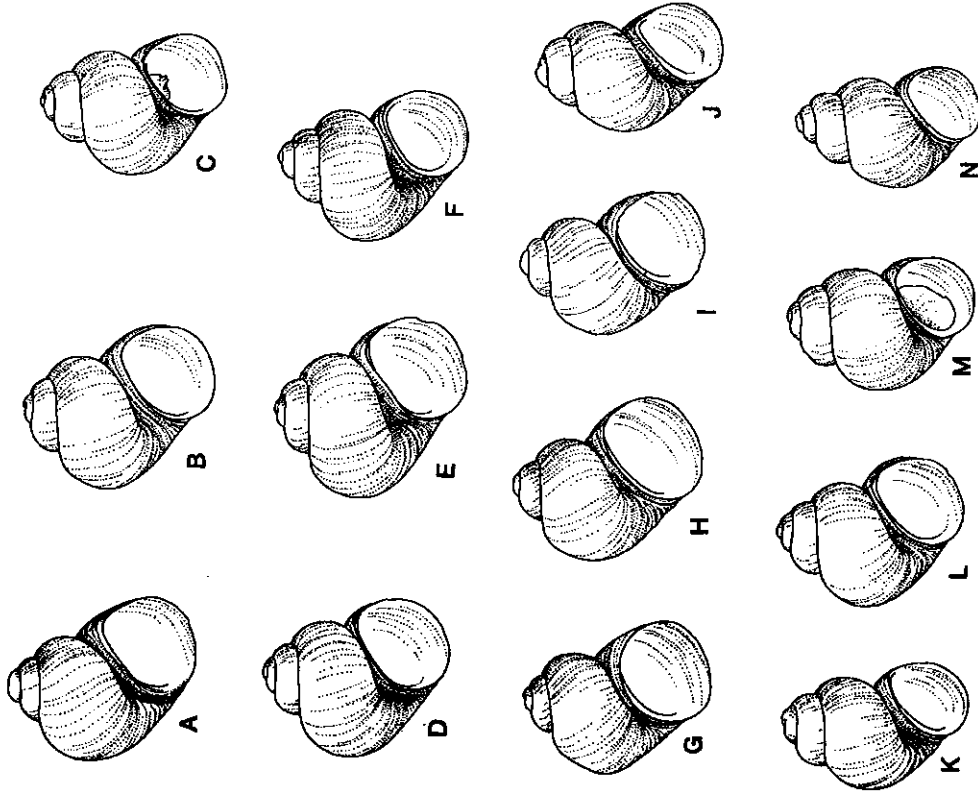
Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Ophiostadium small, narrow, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening grey-white. Rescum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, abutting or very slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 28A. Albumen gland having short pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Ctenial aperture a terminal slit, sometimes slightly raised and papillate, with short anterior extension. Coiled oviduct of two small, overlapping posterior loops. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copularis short, slightly narrower than albumen gland, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge of bursa at mid-line, as long or slightly shorter than bursa, ventral edge sometimes embedded in albumen gland. Seminal receptacle very small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, with short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 28B, C) medium-sized; base rectangular, sometimes weakly folded along inner edge basally; filament as long or longer than base, broad, tapering to point, slightly oblique; lobe short, knoblike (sometimes quite narrow), oblique. Terminal gland short, sub-circular, transverse, ventral. Ventral

Figure 20

Shells of *Pygulopsis* species. A. *P. verticilla*, holotype, USNM 883932 (shell height, 1.3 mm). B. *P. lanofjel*, holotype, USNM 892014 (1.4 mm). C. *P. serrata*, holotype, USNM 874314 (2.2 mm). D. *P. serrata*, USNM 874318 (2.5 mm). E. *P. ...* USNM 874112 (3.5 mm). F. *P. ...* USNM 874331 (2.2 mm). I. *P. ...* USNM 874391 (1.8 mm). J. *P. ...* USNM 860688 (1.8 mm). K. *P. ...* USNM 874393 (2.7 mm). L. *P. ...* USNM 866096 (2.4 mm). M. *P. ...* USNM 873409 (2.3 mm). N. *P. ...* USNM 883461 (1.4 mm). O. *P. ...* USNM 883436 (2.1 mm). P. *P. ...* USNM 874293 (2.0 mm).



gland similarly small and circular; borne on swelling, sometimes pronounced so that distal lobe has forklike appearance; positioned near outer edge distally. Penial duct straight, positioned very close to outer edge.

Type locality: Flag Springs, White River Valley, Nye County, Nevada, T. 7 N., R. 62 E., NE ¼ section 33. Holotype, USNM 874664 (Figure 17H), collected by R. Hershler and P. Hovingh, 23 June 1992, paratypes, USNM 860691. The type locality, the northernmost spring of the Flag Spring complex, is a large rheocrene (Figure 4A). Snails were collected on hard substrate in the pool just below the spring source.

Remarks: This species is compared with *P. hubbsi* above. The distribution of *P. sethosi* is shown in Figure 49.

Material examined: NEVADA, Nye County: Flag Springs (north) (Figure 4A), USNM 860691, USNM 873165, USNM 874664, USNM 883856.—Flag Springs (middle), White River Valley, T. 7 N., R. 62 E., NW ¼ section 33, USNM 873179. Lincoln County: Camp Spring, White River Valley, T. 6 N., R. 60 E., NW ¼ section 36, USNM 874380, USNM 874663. White Pine County: Spring Lund, White River Valley, T. 11 N., R. 62 E., NE ¼ section 4, USNM 874019, USNM 883591, USNM 883852.—Arnoldson Springs, White River Valley, T. 12 N., R. 61 E., SE ¼ section 12, USNM 874687.—Preston Big Spring, White River Valley, T. 12 N., R. 61 E., NE ¼ section 2, USNM 873198, USNM 874022, USNM 874673.

Pygulopsis breviflaba Hershler, sp. nov.

Flag pyrB

(Figures 6G, 11C, 14D–F, 17L, M, 28D–F)

Etymology: From *brevis* (Latin), short, and *lobus*, projection, referring to the short penial lobe characterizing this species.

Diagnosis: Small, with low-trochoid shell. Penis large; filament medium length, distally bifid; lobe very short. Penial ornament a very small terminal gland.

Description: Shell (Figures 6G, 17L, M) low-trochoid,

apex usually eroded; width/height, 77–105%; height, 1.2–2.2 mm; width, 1.0–2.0 mm; whorls 2.75–3.75. Protoconch (Figure 11C) 1.25 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex (sculpture sometimes coalescing to form weak spiral elements), otherwise smooth. Teleoconch whorls medium convexity; strongly shouldered, sometimes strongly angulate near aperture. Aperture crescent-shaped, usually distinct. Inner lip usually thick, having medium width columellar shelf. Outer lip slightly thickened, strongly proscelate, without sinuation. Umbilicus minute or perianth; umbilical region sometimes well excavated with edaxial ridge. Periostracum light brown, thick.

Operculum narrowly ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth or weakly filled near inner edge; outer margin sometimes having weak rim. Attachment seat narrowly thickened between nucleus and inner edge.

Radula (Figure 14D–F) 667 × 110 µm, with 67 rows of teeth. Central tooth 21 µm wide, with highly indented dorsal edge; lateral cusps, 5–6, sometimes partly fused dorsally; central cusp broad, spoonlike; basal cusps small, sometimes flanked on inner side by weakly developed second cusp. Basal tongue broad V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3-1-4; neck weakly flexed; outer wing 370% of cutting edge length. Inner marginal teeth with 33–34 cusps; cutting edge, 33% of length of tooth. Outer marginal teeth with 29–32 cusps; cutting edge 27% of length of tooth. Stomach and style sac equal in length; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark brown. Snout dark brown. Foot medium to dark brown, pigment usually heavier along anterior edge. Opercular lobe dark along inner edge, sometimes all around. Neck nearly unprojected to dark. Pallial roof, visceral coil uniformly dark brown-black. Distal half of penis densely pigmented with internal grey granules.

Cerata 17, pleated; ctenidium short or slightly overlapping pericardium posteriorly. Oesophagus small, narrow-ovate, centrally positioned. Renal gland longitudinal-oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Figure 21

Shells of *Pygulopsis* species: A. *P. milliana*, holotype, USNM 873203 (shell height, 1.4 mm). B. *P. milliana*, USNM 883821 (1.6 mm). C. *P. amblicosta*, holotype, USNM 873208 (2.0 mm). D. *P. amblicosta*, USNM 873202 (2.0 mm). E. *P. R.*, holotype, USNM 873226 (1.7 mm). F. *P. R.*, holotype, USNM 874281 (2.0 mm). G. *P. amblicosta*, holotype, USNM 873215 (2.0 mm). H. *P. amblicosta*, USNM 874286 (1.7 mm). I. *P. longicauda*, holotype, USNM 874240 (2.4 mm). J. *P. longicauda*, holotype, USNM 874207 (1.8 mm). K. *P. imperialis*, USNM 874211 (1.6 mm). L. *P. sethosi*, holotype, USNM 874397 (2.5 mm). M. *P. sethosi*, USNM 865900 (2.9 mm). N. *P. sethosi*, USNM 883851 (3.0 mm).

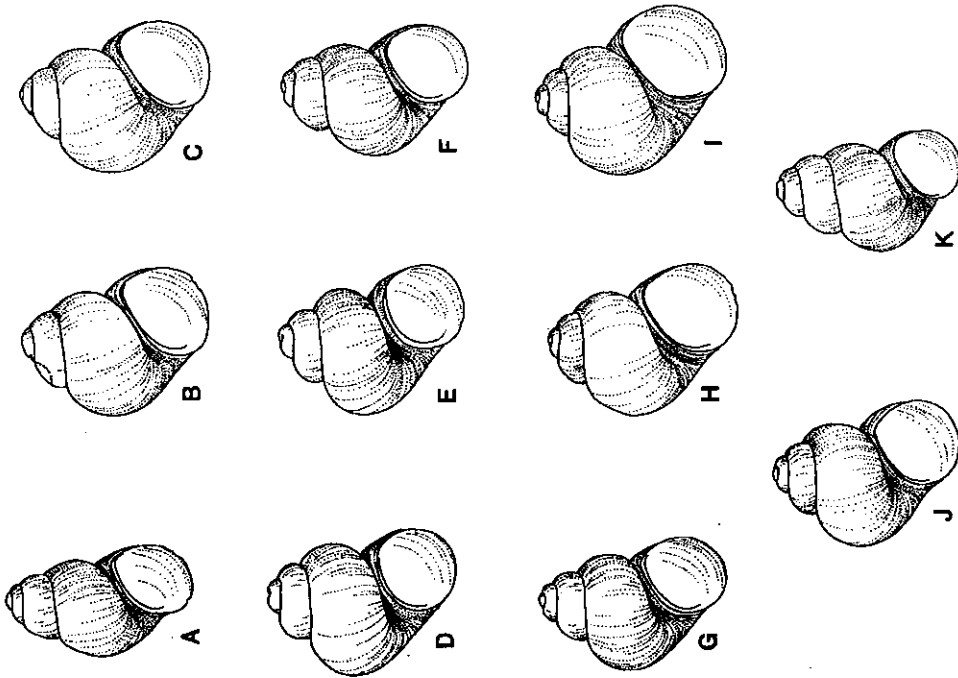


Figure 22

Shells of *Pyrgulopsis* species. A. *P. angustata*, holotype, USNM 874402 (shell height, 2.3 mm). B. *P. plicatilis*, holotype, USNM 874401 (2.6 mm). C. *P. plicatilis*, USNM 860713 (2.4 mm). D. *P. acroplicata*, holotype, USNM 874280 (1.5 mm). E. *P. affinis*, holotype, USNM 874306 (1.3 mm). F. *P. pallida*, holotype, USNM 883850 (2.2 mm). G. *P. laportiana*, holotype, USNM 874336 (2.9 mm). H. *P. kumboldensis*, holotype, USNM 874722 (2.2 mm). I. *P. kumboldensis*, USNM 874725 (2.5 mm). J. *P. kumboldensis*, USNM 874719 (2.5 mm). K. *P. kumboldensis*, holotype, USNM 883215 (2.0 mm).

Ovary a little more than 1.0 whorl, filling most of digestive gland behind stomach, overlapping posterior and part of anterior chambers anteriorly. Distal female genitalia shown in Figure 28D. Albumen gland having small-medium (16-30%) pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section, rectal furrow pronounced. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Colled oviduct a broad circular loop preceded by a proximal twist. Oviduct and bursa duct joining a little behind pallial wall. Bursa copulatory: medium length and width, narrow or clublike, longitudinal, extending to edge of albumen gland. Bursa duct originating from anterior edge as mid-line, abutting oviduct; up to 50% length of bursa, medium width. Seminal receptacle small, narrow, overlapping anterior bursa along ventral edge, well anterior to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly and abutting edge of prostates gland. Prostate broadly ovate, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens having sharp bend. Penis (Figure 28E, F) large; elongate-rectangular, base weakly folded along inner edge; filament medium length, rectangular, as wide as base, distally bifid; lobe extremely short, tapered, longitudinal. Terminal gland very small, circular, borne on ventral surface of lobe. Penial duct straight, near outer edge.

Type locality: Flag Springs, White River Valley, Nye County, Nevada, T. 7 N., R. 62 E., NE ¼ section 32. Holotype, USNM 873174 (Figure 17L), collected by J. J. Landye, 1 September 1973; paratypes, USNM 860689. Flag Springs comprises three springs draining to Sunny-side Creek, located within the Wayne Kirch Wildlife Management Area. The type locality, the middle of the three, nearly north-south trending springs; is a narrow rheocrene having a relatively large discharge.

Remarks: This snail and two other species from White River Valley, *P. lata* and *P. gracilis* (described next), share unusual features of strongly shouldered shell whorls, angular aperture, and well-developed columellar shelf. These species, which occur in closely adjacent

spring complexes, are also closely similar in shape of central and lateral radular teeth, and configuration of distal female genitalia, but their penes are dissimilar, and that of *P. brevifluka* is unique in its combination of elongate shape; very small lobe bearing weak terminal gland; and broadly rectangular, distally bifurcate filament. *Pyrgulopsis bifurcata* (described below), from Carico Lake Basin, also has a bifurcate penial filament, but has a completely different pattern of penial ornament than *P. brevifluka* and also differs in various other features. The distribution of *P. brevifluka* is shown in Figure 50.

Material examined: NEVADA, Lincoln County: Malcoy Spring, Dry Lake Valley, T. 5 N., R. 65 E., NE ¼ section 32, USNM 874671, Nye County: Flag Springs (middle), USNM 860689, USNM 873174, USNM 883846.—Flag Springs (north), T. 7 N., R. 62 E., NE ¼ section 30, USNM 873188, USNM 874029, USNM 874031, USNM 883874.

Pyrgulopsis lata Herschler, sp. nov.

Butterfield p.775

(Figures 6H, 12D, 18A, 29A-E)

Etymology: From *latus* (Latin), broad or wide; referring to the prominent columellar shelf characterizing shells of this species.

Diagnosis: Small, with ovate to narrow-conic shell. Penis large, filament short, lobe short. Penial ornament a small, fragmented terminal gland; very small Dgl, and small ventral gland.

Description: Shell (Figures 6H, 18A) ovate to narrow-conic, apex usually eroded, width/height, 66-84%; height, 1.6-2.1 mm; width, 1.2-1.6 mm; whorls, 3.75-4.25. Protoconch 1.25 whorls, diameter 0.28 mm, early portion wrinkled along inner edge, otherwise smooth. Teleoconch whorls moderately convex, strongly shouldered; adapical region strongly angulate or keel-like; body whorl often, slightly distinct behind the aperture. Aperture ovate, angled above, usually distinct, sometimes broadly so. Inner lip slightly thickened, having broad, well-developed columellar shelf. Outer lip slightly thickened, prosocline, without sinuation. Umbilicus perforate to broadly open. Periostracum light brown.

Operculum (Figure 12D) ovate, light amber, inner edge

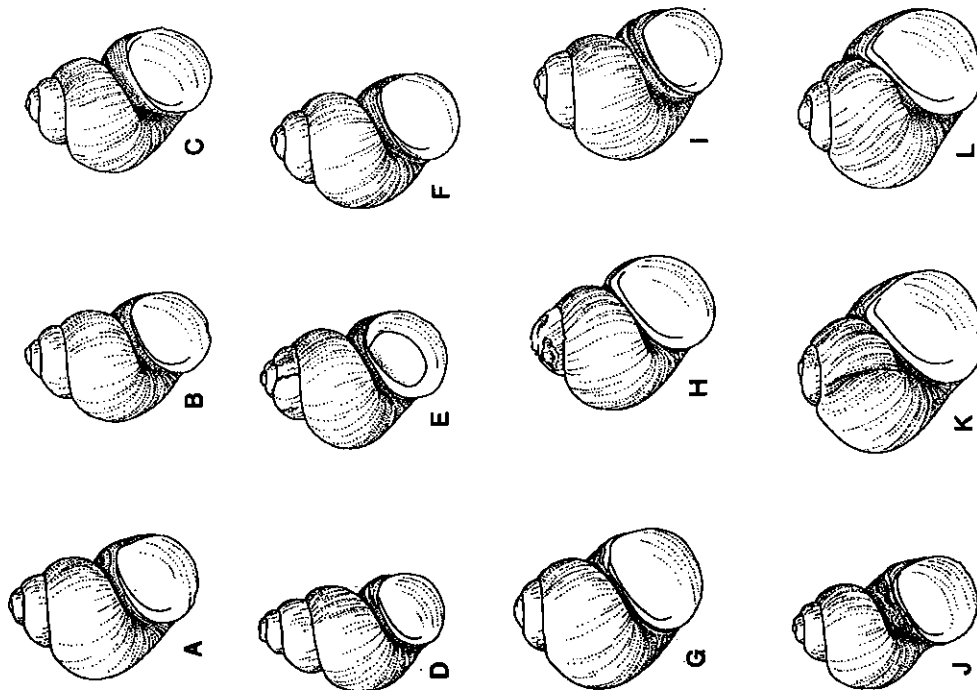


Figure 23

Shells of *Pyrgulopsis* species. A. *P. pseudalis*, holotype, USNM 883933 (shell height 2.2 mm). B. *P. pseudalis*, USNM 883622 (2.8 mm). C. *P. pseudalis*, USNM 883609 (2.5 mm). D. *P. pseudalis*, USNM 874683 (2.7 mm). E. *P. pseudalis*, USNM 874319 (2.5 mm). F. *P. pseudalis*, USNM 883227 (2.2 mm). G. *P. pseudalis*, USNM 883222 (1.9 mm). H. *P. esquivae*, holotype, USNM 874678 (2.3 mm). I. *P. esquivae*, USNM 883225 (2.7 mm, 2.6 mm, respectively). K. *P. saxatilis*, holotype, USNM 883237 (1.5 mm). L. *P. saxatilis*, USNM 886728 (1.1 mm).

straight, nucleus eccentric; dorsal surface smooth. Attachment scar slightly thickened between nucleus and inner edge.

Rachula 575 × 85 μm, with 74 rows of teeth. Central tooth 17 μm wide, with highly indented dorsal edge; lateral cusps, 6-7 (often fused dorsally), central cusp medium width to broad, spoonlike; basal cusps medium sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula, 3(4)-1-5; neck weakly flexed; outer wing 277% of cutting edge length. Inner marginal teeth with 34-36 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 31-34 cusps; cutting edge occupying 24% of length of tooth. Stomach longer than style sac, anterior chamber larger than posterior chamber; stomach caecum very small to nearly absent.

Cephalic tentacles light to dark grey-brown, sometimes lighter around eyespots and along narrow central zone. Snout medium to dark grey-brown. Foot, neck light to dark grey-brown. Opercular lobe dark along inner edge and sides, light-dark elsewhere. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length.

Caudal filaments, 15, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Ophradium small, narrow, positioned centrally. Renal gland slightly oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary 1.0-1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 29A. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; renal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Cephalic aperture a short, terminal slit often mounted on small raised swelling or papilla; anterior extension short. Coiled oviduct a circular loop usually preceded by small anterior twist or bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix considerably narrower and shorter than albumen gland, ovate, longitudinal or slightly oblique, less than 33% of length posterior to gland. Bursal duct originating from anterior edge near midline, median length and width, slightly broader distally. Seminal receptacle small, pouchlike, overlapping or abutting ven-

tral edge of anterior portion of bursa (a little dorsal to ventral edge of albumen gland).

Testis 1.0-1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Prostate gland bean-shaped, pallial portion short, narrow ovate in section. Proximal pallial ves deferens with undulation. Penis (Figure 29B-E) large, base rectangular, often elongate and expanded distally, weakly folded along inner edge; filament short, medium width, tapering to pointed tip, longitudinal or slightly oblique; lobes short to near absent, hemispherical, slightly oblique. Terminal gland small, usually divided into two to six small dotlike units along edge of lobe. Dg1 very small, rarely including a second, dotlike unit, bursa on low swelling, near outer edge just proximal to filament. Ventral gland small, narrow, borne on low swelling, often curved into U-shape and extending near or onto edge of lobe, positioned near outer edge distally. Penial duct straight, near outer edge.

Type locality: Butterfield Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 28 (Figure 50). Holotype, USNM 874667 (Figure 18A), collected by R. Hershler and P. Hovingh, 28 June 1992; paratypes, USNM 860697. The type locality is a small rheocrene.

Remarks: *Pyrgulopsis lata* differs from similarly shelled White River Valley species (see above) in having a very weak penial lobe; small, distal Dg1 (absent in the above); and large ventral gland (smaller in *P. brevifolia*, absent in *P. gracilis*). *Pyrgulopsis lata* resembles *P. saxatilis* (described below), from western Bonnerville Basin, in penial form and ornament, but is readily distinguished by its narrower shell, fragmented terminal gland, larger bursa copulatrix with shorter duct, and more posteriorly positioned seminal receptacle.

Material examined: NEVADA, Nye County: Butterfield Springs, USNM 860697, USNM 873167, USNM 874667.

Pyrgulopsis gracilis Hershler, sp. nov.

Emigrant type

(Figures 6I, 11D, 18B, C, 29F-H)

Etymology: From *gracilis* (Latin), slender; referring to the narrow penial filament characterizing this species.

Diagnosis: Small, with broad- to narrow-conic shell. Penis medium-sized, filament long, lobe short or absent. Penial ornament a terminal gland and large penial gland.

Description: Shell (Figures 61, 18B, C) narrow conic, but apex usually highly eroded, producing a broadly conical shape; width/height, 81–92%; height, 1.6–1.9 mm; width, 1.3–1.6 mm; up to 4.0 whorls remaining. Protoconch (Figure 11D) 1.24 whorls, diameter 0.28 mm, initial 0.75 whorl finely wrinkled, later portion near smooth. Telioconch often moderately convex, shoulders well developed, often forming a pronounced subventral angulation on penultimate two whorls. Aperture ovate, well angled above, broadly adaxial to slightly distal; inner lip thick, with narrow columellar shelf. Outer lip thin-thick, pro-socline, weakly sinuate. Umbilicus absent or rimate. Periconcave tan, brown, or reddish.

Operculum ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth. Attachment scar margin slightly thickened between nucleus and inner edge, and along inner edge.

Radula 490 × 80 µm, with 60 rows of teeth. Central tooth 18 µm wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp medium width, spoonlike; basal cusps medium-sized. Basal process V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flared; outer wing 21.5% of cutting edge length. Inner marginal teeth with 30–31 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles light to medium brown, often unpigmented around clypeus and along narrow central region. Snout medium to dark brown. Foot light to dark brown-black, especially dark along anterior edge. Opercular lobe usually medium brown, often slightly darker along sides. Neck nearly unpigmented to medium brown, often much lighter than rest of head. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments 19, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Oosphradium small, narrow, positioned alongside posterior half of cte-

nidium. Renal gland oblique, sometimes strongly so; kidney opening grey-white. Rectum broadly overlapping pallial oviduct and slightly overlapping prostate gland.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, partly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 29F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; recal narrow weak or absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short terminal slit without anterior extension. Coiled oviduct a tight sub-circular coil preceded by weak posterior bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copularia medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge near mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle short, narrow, overlapping or abutting proximal bursal duct, sometimes slightly overlapped by albumen gland.

Testis 1.25 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial section short, ovate in section. Proximal pallial vas deferens having weak undulation, almost straight. Penis (Figure 29C, H) medium-sized; base rectangular, folded along inner edge; filament as long as base, narrow, gently tapering, longitudinal; lobe short to almost absent, knoblike, longitudinal. Terminal gland small, sometimes very reduced, circular, sometimes divided into two to three dotlike units, usually ventral. Penial gland filling 50% of filament length, narrow, centrally positioned, usually bulging below inner edge of filament. Filament also sometimes bearing small, dotlike gland near base. Penial duct straight, near outer edge.

Type locality: Emigrant Springs, White River Valley, Nye County, Nevada, T. 9 N. R. 62 E. NE ¼ section 19 (Figure 50). Holotype, USNM 873158 (Figure 18B), collected by J. J. Landye, 2 September 1973; paratypes, USNM 860698. Emigrant Springs comprises a spring complex alongside Nevada State HWY 318. The type locality, the northernmost spring in this complex, is a small rheocrene.

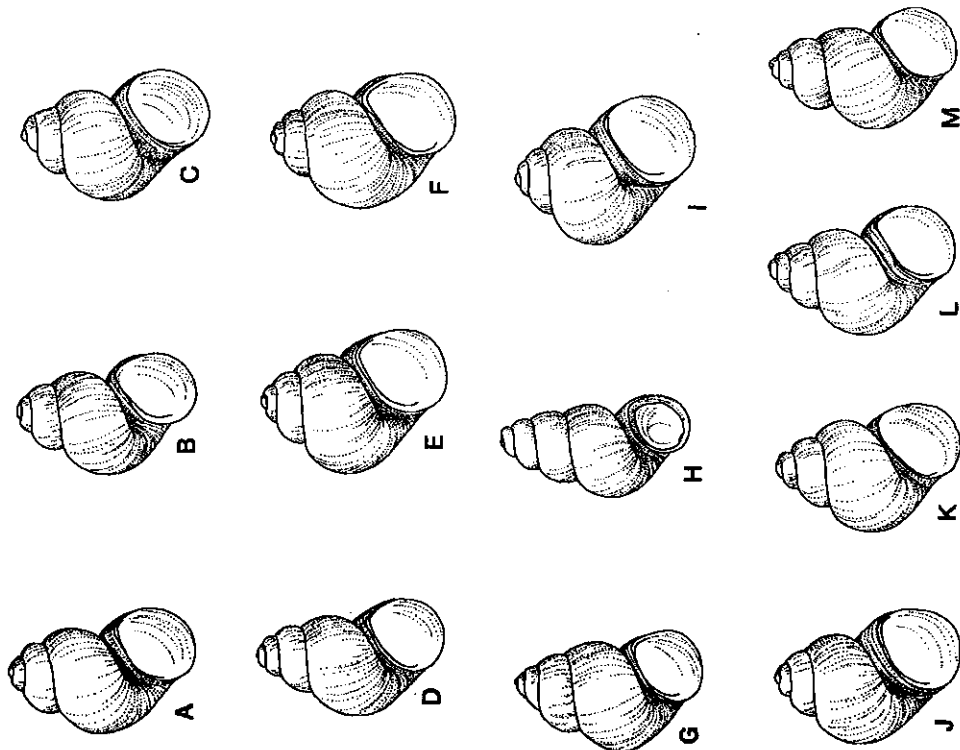


Figure 24

Shells of *Pyralogastri* species. A, *P. wrightae*, holotype, USNM 883427 (shell height, 2.7 mm). B, *P. wrightae*, USNM 883488 (2.5 mm). C, *P. wrightae*, USNM 874713 (2.7 mm). D, *P. wrightae*, USNM 883499 (3.1 mm). E, *P. wrightae*, holotype, USNM 874675 (2.5 mm). F, *P. wrightae*, holotype, USNM 874720 (2.5 mm). G, *P. wrightae*, holotype, USNM 874724 (1.8 mm). H, *P. wrightae*, USNM 854546 (2.2 mm). I, *P. wrightae*, holotype, USNM 883394 (2.5 mm). J, *P. wrightae*, USNM 860727 (2.7 mm). K, *P. wrightae*, holotype, USNM 883439 (2.7 mm). L, *P. wrightae*, USNM 883573 (3.3 mm). M, *P. wrightae*, USNM 883442 (2.9 mm).

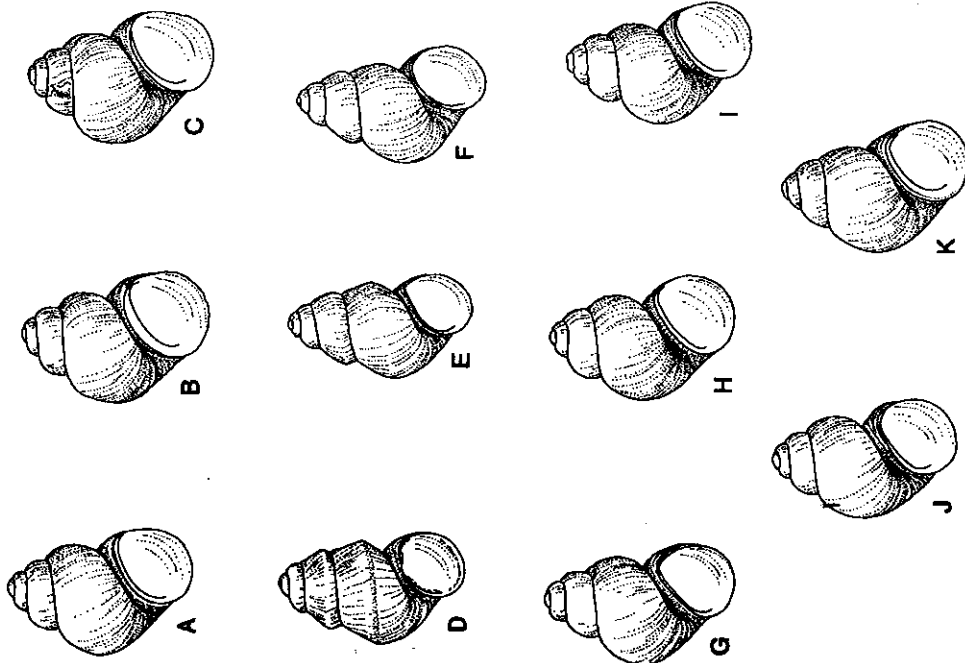


Figure 25

Shells of *Pygulopsis* species. A. *P. chanderident*, holotype, USNM 883576 (2.8 mm). B. *P. chanderident*, USNM 883944 (2.9 mm, 3.8 mm, respectively). D. *P. jagdipura*, holotype, USNM 883943 (2.9 mm). E. *P. jagdipura*, USNM 860730 (2.9 mm, 2.8 mm, respectively). G. *P. manaburu*, holotype, USNM 883566 (2.5 mm). H. *P. transverata*, holotype, USNM 883221 (2.3 mm). I. *P. transverata*, USNM 860732 (2.3 mm). J. *P. transverata*, USNM 883597 (3.0 mm, 2.4 mm). K. *P. transverata*, USNM 883597 (3.0 mm).

Remarks: This species has a unique penial morphology featuring a very slender filament with an elongate penial gland along its inner edge. Although *P. gracilis* otherwise resembles two other species found in White River Valley (see above), this small is further distinguished by stronger protoconch microsculpture, unfused cusps on the central nodular teeth, and the more posteriorly positioned bursa copulatrix.

Material examined: NEVADA, Nye County: Emigrant Springs (north), USNM 860698, USNM 873158, USNM 874382, USNM 883942.—Emigrant Springs (south), White River Valley (Figure 4B), T. 9 N, R. 62 E, NE ¼ section 30, USNM 883885.

Pygulopsis maredae Hershler, sp. nov.

Hardy pyrg

(Figures 61, 18D-F, 30A-C)

Etyymology: From *maredae* (Latin), withdrawn or wasted; referring to the reduced penial glands of this species.

Diagnosis: Small to medium-sized, with ovate- to elongate-conic shell. Penis medium-large; filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (sometimes absent), and occasional small gland on ventral surface of lobe.

Description: Shell (Figures 61, 18D-F) ovate- to elongate conic, width/height, 66-86%; height, 1.6-3.9 mm; width, 1.2-3.0 mm; whorls, 3.5-4.75. Protoconch 1.25 whorls, diameter 0.35 mm, smooth. Teleconch whorls moderately convex, shouldered, often having deep sutures; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate to slightly disjunct. Inner lip thin, without columellar shelf. Outer lip usually thin, orthocone or slightly prosocline, without sinuation. Umbilicus narrow-perforate. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface filled; outer margin having weak rim. Attachment scar thick (especially so along inner edge) all around.

Rachis 687 × 119 µm, with 57 rows of teeth. Central tooth 28 µm wide, with medium indented dorsal edge; lateral cusps, 7-8; central cusp medium width, rounded; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4-1-5; neck well

flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 31-34 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 37-39 cusps; cutting edge occupying 24% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles very light grey-brown. Snout light to medium grey. Foot light to medium grey, darkest along anterior edge. Opercular lobe medium grey to black along anterior edge and sides, sometimes all around (central region lighter). Neck light to medium grey-brown. Pallial roof and visceral coil uniformly dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments, 21, pleated; ctenidium slightly overlapping pericardium posteriorly. Oosphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland 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, abutting or slightly overlapping posterior stomach chamber anteriorly. Dorsal female genitalia shown in Figure 30A. Albumen gland having short pallial component. Capsule gland as wide and slightly shorter to as long as albumen gland, sub-circular in section, receding row deep. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two short, overlapping tight coils, usually posterior-oblique in coelomation. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, usually longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge near mid-line, shorter than bursa, medium width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct near ventral edge of albumen gland, often shallowly embedded in gland.

Testis 1.75-2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and small portion of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having sharp, reflected bend. Penis (Figure 30B, C) medium-large; base rectangular, sometimes weakly folded along inner edge; filament slightly shorter than base, medium width, tapering to point, near longitudinal to strongly oblique; lobe short,

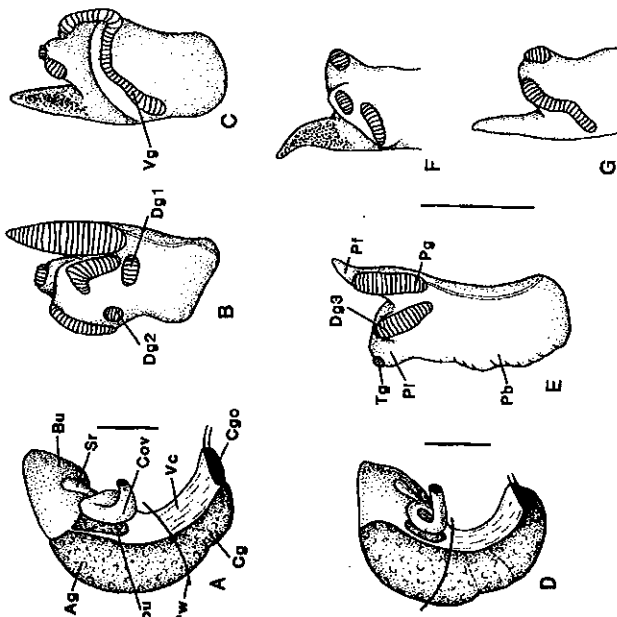


Figure 26

Genitalia of *Pygospio* species (A-C, *P. fusca*, USNM 873175; D-G, *P. decorei*, USNM 873355). A. Female glandular oviduct and associated structures, NE = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Ventral aspect of penis, scale as in A. D. Female glandular oviduct and associated structures, bar = 0.25 mm. E. Dorsal aspect of penis, bar = 0.5 mm. F. G. Ventral aspect of distal penis, scale as in E. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsular gland, Cgo = opening of capsular gland, Cov = coiled oviduct, Dgo = duct from bursa copulatrix, Dg1 = proximal filament on penis, Dg2 = dorsal gland near inner distal edge of penis, Dg3 = dorsal gland near outer edge of penis lobe, Pb = base of penis, Pw = penial filament, Pg = gland on penial filament, Pl = lobe of penis, Pw = penial wall, Sr = seminal receptacle, Vc = ventral channel of capsular gland, Vg = gland on ventral surface of penis.

sometimes near absent, knoblike, near longitudinal to oblique. Terminal gland small, narrow, variably oriented or reduced to two to three denticles units, usually ventral. Penial gland very small, ovate, positioned near base of filament, often absent. Denticle Dg2 rarely present along inner edge distally. Ventral lobe sometimes bearing small, often slightly raised gland proximally (adjacent to terminal gland) but many represent a reduced ventral gland. Penial duct straight, near outer edge.

Type locality: Hardy Springs, White River Valley, Nye County, Nevada, T. 9 N. R. 61 E. SW ¼ section 13, Ho-

loype, USNM 873154 (Figure 18D), collected by J. J. Landye, 3 September 1973; paratypes, USNM 860711. The type locality is a small rheocrene.

Remarks: This species resembles *P. amabilis* (described below), from Duckwater Valley, but differs in having a reflexed pallial vis. deferens, squarer penis with shorter, broader lobe and filament; occasional presence of gland on ventral penis; smaller penial gland; narrower oviduct coil with two well-developed loops; and smaller seminal receptacle. Shells from Cave Valley have considerably lighter

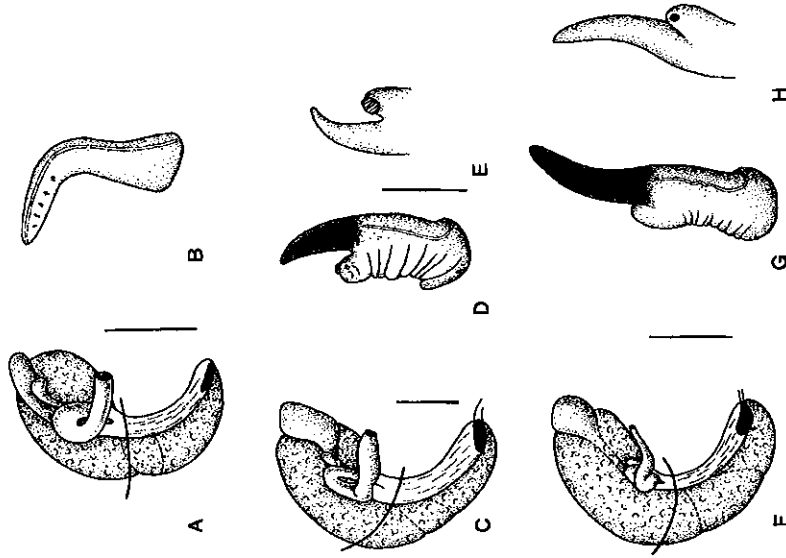


Figure 27

Genitalia of *Pygospio* species (A, B, *P. coloradensis*, USNM 873360, bar = 0.25 mm; C-E, *P. nevada*, USNM 860894; F-H, *P. hubbsi*, USNM 871166). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Female glandular oviduct and associated structures, bar = 0.25 mm. D. Dorsal aspect of penis, bar = 0.25 mm. E. Ventral aspect of distal penis, scale as in D. F. Female glandular oviduct and associated structures, bar = 0.5 mm. G. Dorsal aspect of penis, scale as in F. H. Ventral aspect of distal penis, scale as in G.

body pigmentation that those from White River Valley. The USNM 874688.—Emigrant Springs (north), White River Valley, T. 9 N. R. 62 E. NE ¼ section 19, USNM 873170, USNM 833843.—Butterfield Springs, White River Valley, T. 7 N. R. 62 E. NE ¼ section 28, USNM 874378, USNM 874662.—Emigrant Springs (south), White River

Valley (Figure 4B), T. 9 N. R. 62 E. NE ¼ section 30, USNM 874688.—Emigrant Springs (north), White River Valley, T. 9 N. R. 62 E. NE ¼ section 19, USNM 873170, USNM 833843.—Butterfield Springs, White River Valley, T. 7 N. R. 62 E. NE ¼ section 28, USNM 874378, USNM 874662.—Emigrant Springs (south), White River

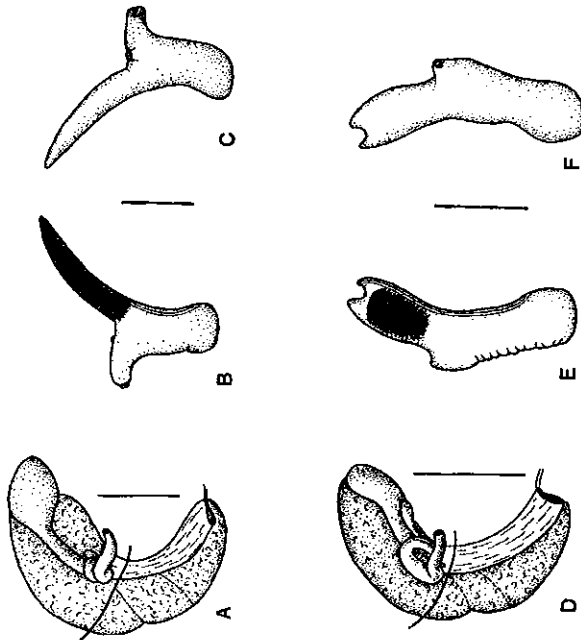


Figure 28

Genitalia of *Pyrgulopsis* species (A-C, *P. acutus*, USNM 860689; D-E, *P. brevis*, USNM 860689). Bars = 0.5 mm. Drawings show (from left to right) female glandular evider and associated structures, dorsal aspect of penis, ventral aspect of penis.

883972, USNM 883973. Lincoln County: Silver Springs, White River Valley, T. 8 N, R. 62 E, SW $\frac{1}{4}$ section 14, USNM 874672.—Springs, Preker Station, Cave Valley, T. 9 N, R. 64 E, NW $\frac{1}{4}$ section 6, USNM 874682. White Pine County: Rappes Boghole, White River Valley, T. 10 N, R. 62 E, SE $\frac{1}{4}$ section 7, USNM 874685.

Species from Isolated Basins in Nevada

Pyrgulopsis turbatrix Herschler, sp. nov.

Southeast Nevada pyrg

(Figures 6K, 18G-I, 30D-F)

Pyrgulopsis micrococcus (Fishery, 1893). Herschler, 1989: 183 [not Fishery, 1893, in part; Frenchman Flat].—Herschler & Pratt, 1990:285, 286 [in part, northern Spring Mountains].

Etymology: *Turbatrix* (Latin), disturber, trouble-maker;

referring to the difficulty encountered in separating this species from *P. micrococcus*.

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

Description: Shell (Figures 6K, 18G-I) narrow-conic to turritiform, width/height, 56-76%; height, 2.1-3.6 mm; width, 1.5-2.2 mm; whorls, 4.25-5.5. Protoconch 1.4-1.5 whorls, diameter 0.36 mm; surface smooth except for very weak wrinkling at apex. Telioconch whorls medium to highly convex, shoulders absent to well developed (often having weak sub-apical angulation); body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin or slightly thickened, columellar shelf absent or narrow. Outer lip thin, orthocone or slightly protocone,

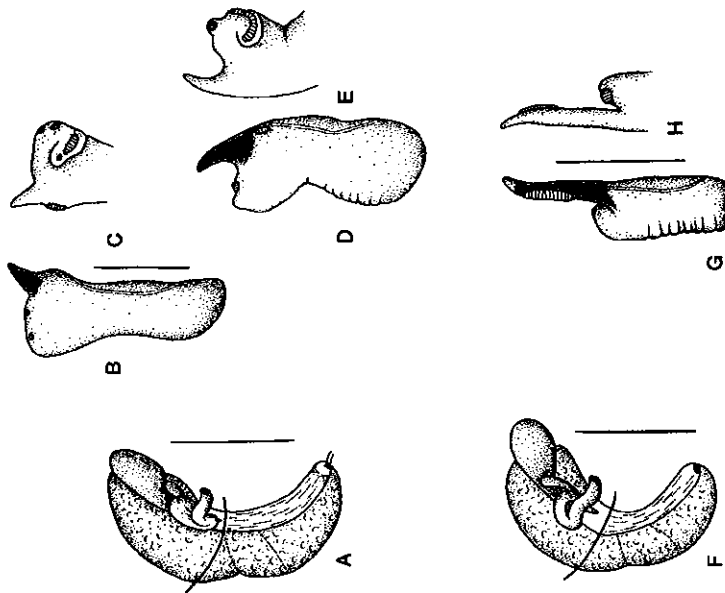


Figure 29

Genitalia of *Pyrgulopsis* species (A, D, E, *P. laus*, USNM 873167; B, C, *P. laus*, USNM 860697; F, H, *P. gracilis*, USNM 860698). A, Female glandular evider and associated structures, bar = 0.5 mm. B, Dorsal aspect of penis, bar = 0.5 mm. C, Ventral aspect of distal penis, scale as in B. D, Dorsal aspect of penis, scale as in B. E, Ventral aspect of distal penis, scale as in B. F, Female glandular evider and associated structures, bar = 0.5 mm. G, Dorsal aspect of penis, bar = 0.5 mm. H, Ventral aspect of distal penis, scale as in G.

without sinuation. Umbilicus rimate or shallowly perforate. Pectostracum tan-brown.

Operculum ovate, ambex. nuclear region slightly dexter; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar slightly thickened all around.

Radialia $650 \times 100 \mu\text{m}$, with 60 rows of teeth. Central tooth 25 μm wide, with medium to highly indented dorsal edge; lateral cusps, 5-6; central cusp narrow, daggerlike;

basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth, formula 3(4)-1-(4); neck medium flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 19-22 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 26-29 cusps; cutting edge occupying 30% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

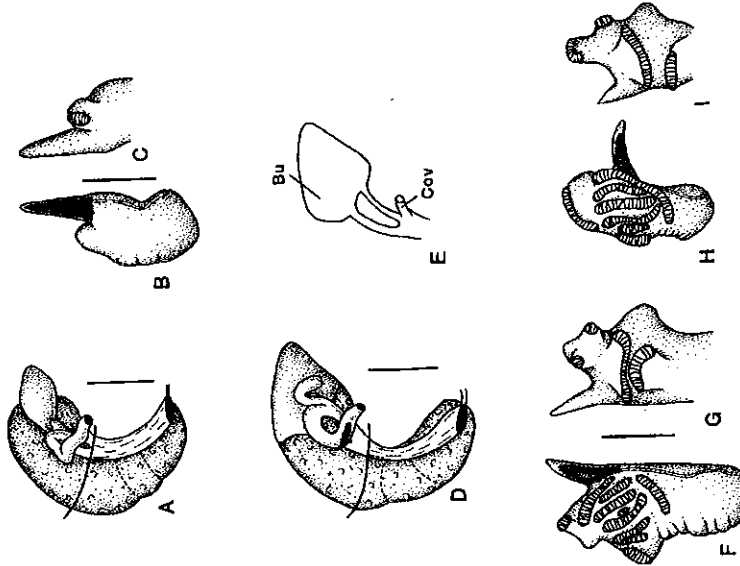


Figure 43
 Genitalia of *Pyrgulopsis* species (A-C, *P. hamillensis*, USNM 860695; D-G, *P. pectiniferis*, USNM 883602; H, *P. pectiniferis*, USNM 883603; I, *P. pectiniferis*, USNM 874766). A. Female gonostylar oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, bar = 0.25 mm. C. Ventral aspect of distal penis, scale as in B. D. Female gonostylar oviduct and associated structures, bar = 0.25 mm. E. Bursa copulatrix and bifid duct, scale as in D. F. Dorsal aspect of penis, bar = 0.5 mm. G. Ventral aspect of distal penis, scale as in F. A-E. Bars = 0.25 mm. F-I. Bars = 0.5 mm. Bu = bursa copulatrix. Cov = collared oviduct.

Species from the Oregon Lakes
Pyrgulopsis hendersoni (Pilsbry, 1933)
 1981:251-252 [locality records].
Pyrgulopsis hendersoni (Pilsbry, 1933), Hershler & Thompson, 1994:39, 41 [figures].

Fonticella hendersoni Pilsbry, 1933, pl. 2: figs. 2, 9, 10.
Fonticella hendersoni (Pilsbry, 1933), Taylor, 1975:94-95 [literature compilation].

Diagnosis: Large, with ovate to low-conical shell. Penis

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 distinct from the previously known range of *P. hendersoni* (Hansy 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; *Fonticella*, 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)

Ponticella intermedia Tryon, 1865, 1865, pl. 22, fig. 8.
Fonticella intermedia (Tryon, 1865), Taylor, 1975: 104 [literature compilation].—Taylor 1985:308-310.
Pyrgulopsis intermedia (Tryon, 1865), Hershler & Thompson, 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 Baren Valley (Figure 53), a small endemic drainage positioned between South Fork Malheur River and Owyhee River. Baren 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, Baren Valley, T. 28 S., R. 38 E., SW ¼ section 8, USNM 854126.—Spring, Dowell Ranch, Baren Valley, T. 27 S., R. 38 E., SW ¼ section 33, USNM 874179.

Species from the Bonneville Basin

Pyrgulopsis kolobensis (Taylor, 1987)
Paludetrina longiqua (Gould, 1855), Pilsbry, 1899:122 [not Gould, 1855; in part].—Hambl, 1912a:34 [in part].—Hambl, 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 longiqua Gould, 1855, Call, 1884:20-21 [not Gould, 1855; in part].—Henderson, 1924:137 [in part].—Chamberlin & Roscoe, 1948:11.—E.G. Berry, 1948:69.
Fonticella longiqua (Gould, 1855), Russell, 1971:223-223, fig. 4 [not Gould, 1855].
Fonticella kolobensis Taylor, 1987:19, fig. 8.
Fonticella 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 synonymy, *Fonticella 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 *Paludetrina longiqua* Gould, 1855 in the literature. As explained elsewhere (Hershler, 1994:47), *Pyrgulopsis longiqua* (Gould, 1855) is restricted to its type locality area in the Selton 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 mid/or

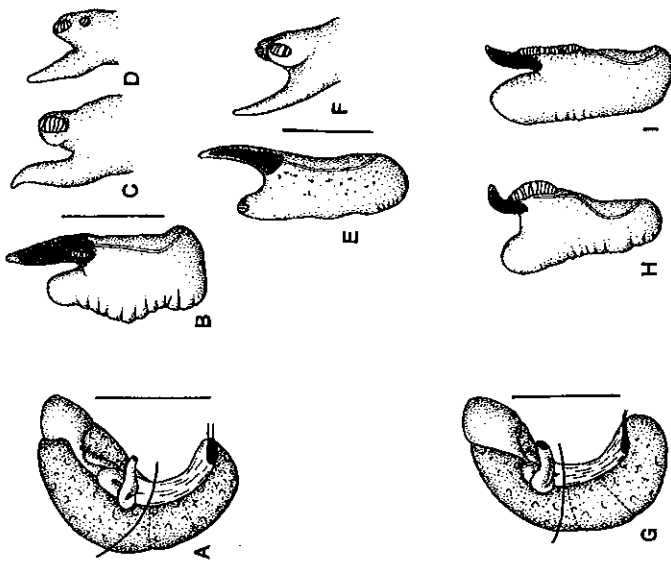


Figure 45

Genitalia of *Pygospio* species (A-D, *P. variegata*, USNM 883595; G-I, *P. horvathi*, USNM 874715). Bars = 0.5 mm. Drawings show (from left to right) female glansular oviduct and associated structure, dorsal aspect of penis, ventral aspect of penis (not shown for *P. horvathi*, 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 872161.—Spring, west side HWY 6, northwest of Preston, White River Valley, T. 13 N, R. 61 E, SW $\frac{1}{4}$ section 31, USNM 873530, USNM 874680.—Spring, Bull Creek, Railroad Valley, T. 14 N, R. 56 E, SE $\frac{1}{4}$ section 14, USNM 874774, USNM 874881.—Green Springs, Railroad Valley, T. 15 N, R. 57 E, SW $\frac{1}{4}$ section 33, USNM 874775, USNM 874874.—Bennett Spring, Steptoe Valley, T. 19 N, R. 63 E, SE $\frac{1}{4}$ section 33, USNM 874903.—Springs, northwest of Clark Spring,

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, Bunte 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.—Minoletsi 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.—Narcisse Springs, Ruby Valley, T. 25 N, R. 57 E, SW $\frac{1}{4}$ section 2, USNM 874307.—Springs, northwest of Narcisse Springs, Ruby Valley, T. 25 N, R. 57 E, NE $\frac{1}{4}$ section 3, USNM 873335.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, Mallard Valley, T. 15 N, R. 3 W, NE $\frac{1}{4}$ section 4, USNM 883490, USNM 883577.—Spring, ca. 1.6 km north of Pronomontory Point, Pronomontory Mountains, Great Salt Lake Desert, T. 6 N, R. 5 W, NE $\frac{1}{4}$ section 21, USNM 883611.—Shaw Spring, Pronomontory 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, Pronomontory Mountains, Great Salt Lake Desert, T. 8 N, R. 5 W, center section 5, USNM 883632.—Spring, east of Royal Flat, Pronomontory 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 Manana 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 883599.—Spring, Jesse's 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. Thornton, FMNH 178357.—Spring, north of Plymouth, Mallard Valley, FMNH 224314, Cache County: Spring, below (west of) Poncine Reservoir, Cache Valley, T. 9 N, R. 2 E, NW $\frac{1}{4}$ section 17, USNM 883853.—Pool along side 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. DENOT, 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. 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 883169.—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. Juab County: Springs, Mainway, Tintic Valley, T. 11 S, R. 3 W, SE $\frac{1}{4}$ section 28, USNM 883206.—Blair 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 Children 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, Moon, 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 888289, 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. Millard County: Coyote Spring, Beaver River drainage, T. 23 S, R. 9 W, NW $\frac{1}{4}$ section 33, USNM 883239.—The 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.—Pantler Spring, Tule Valley, T. 19 S, R. 14 W, NE $\frac{1}{4}$ section 5, USNM 883202.—Sinhob Spring, Tule Valley, T. 16 S, R. 13 W, NE $\frac{1}{4}$ section 33, USNM 883207, USNM 883424.—Spring, at conral, east of Horse Canyon, Snake Valley, T. 17 S, R. 19 W, NE $\frac{1}{4}$ section 29, USNM 883220.—Knoll

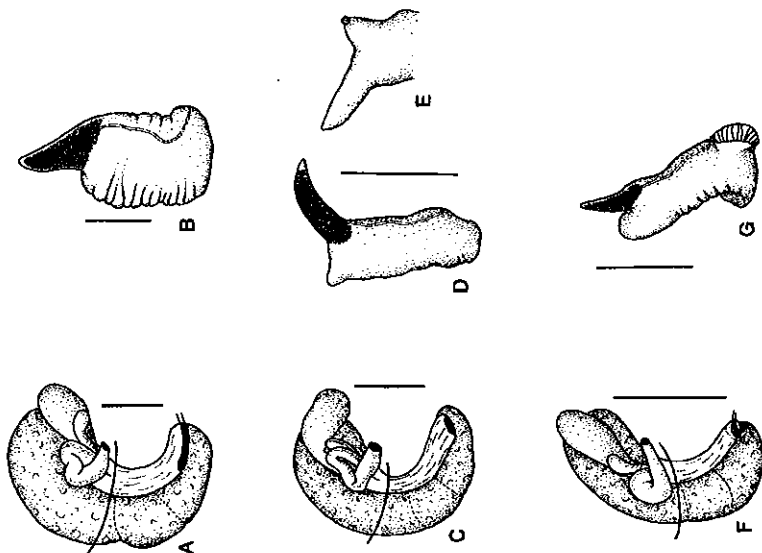


Figure 46
 Genitalia of *Pygospio* species (A, B, *P. millerrae*, USNM 860721; C-E, *P. filenta*, USNM 860722; F, *P. filenta*, USNM 860727). A, B, Bars = 0.25 mm. C-G, Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. millerrae* and *P. tenuigona*, which lack ventral ornament).
 Springs, Snake Valley, T. 18 S., R. 18 W., NE ¼ section 16, USNM 883218.—Twin Springs, Snake Valley, T. 16 S., R. 18 W., SW ¼ section 22, USNM 883208.—Cold Spring, Snake Valley, T. 16 S., R. 19 W., NW ¼ section 2, USNM 883213. *Mogyan County*. Spring, East Canyon, Weber River drainage, T. 1 N., R. 3 E., NW ¼ section 14, USNM 883389.—Spring, East Canyon, Weber River drainage, T. 1 N., R. 3 E., SE ¼ section 15, USNM 883485. *Salt Lake County*. Spring, Riverton, Jordan River

drainage, T. 3 S., R. 1 W., NW ¼ section 34, USNM 883236, USNM 883294.—Spring, HWY 80, Parleys Canyon (just below Parleys Summit), Jordan River drainage, T. 1 S., R. 3 E., SE ¼ section 8, USNM 883287, 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.—Lambe 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 178364.—Red Butte, Great Salt Lake Desert, FMNH 178369.—Tarpeys Spring, Salt Lake City, USNM 199398.—Salt Lake City, USNM 414181, USNM 424340.—Climans 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. *Sorensen 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 Alberry 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 886285, USNM 873436, USNM 883204.—Musk-rat Spring, Skull Valley, T. 2 S., R. 8 W., UMBZ 219484.—Big Spring, Skull Valley, T. 1 S., R. 7 W., SE ¼ section 8, USNM 883282, 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 Bonerville Service Station, near Timpi (Timpié), FMNH 178400 (mixed with *Trypania protea* [Goold, 1855]).—West side of Skull Valley (subfossil), FMNH 178423.—4.8 km south of Stockton, Rush Valley, FMNH 178380.—Spring before Koeple, Skull Valley, FMNH 178382 (mixed with *Trypania protea*).—First spring south of Josepha, Skull Valley, FMNH 178381.—Southeast of Tooele, FMNH 224405. *Utah County*. Springs, Warm Springs Ditch, Goeben 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, Wallenburg, Provo River drainage, T. 5 S., R. 5 E., section 18, USNM 883618.—Cascade Springs, Provo River drainage, T. 4 S., R. 3 E., NE ¼ section 24, USNM 873599, 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 883633.—Hot Springs, northwest of Midway, Heber Valley, Provo River drainage, T. 3 S., R. 4 E., SW ¼ section 27, USNM 883794, USNM 883804.—Spring, east of Haisilton, Provo River drainage, T. 2 S., R. 5 E., NE ¼ section 33, USNM 874372.—Spring, east of Haisilton, Provo River drainage, T. 2 S., R. 5 E., SE ¼ section 33, USNM 873440.—Drain Tunnel Creek, Provo River drainage, T. 2 S., R. 5 E., NE ¼ section 19, USNM 883284.—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, Fine 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.—Spring, Calif 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 883398.—Springs, North Fork Ogden River, T. 7 N, R. 1 E, NE ¼ section 18, USNM 883604.

Pyrgulopsis pitshryana (Bailey & Bailey, 1952)

Aminicola pitshryi Bailey & Bailey, 1951:50, pl. 4, fig. 3 [not *Aminicola pitshryi* Walker, 1906].
Aminicola pitshryana Bailey & Bailey, 1952:144 [new name for *Aminicola pitshryi* Bailey & Bailey, 1951].
Foneticella pitshryana (Bailey & Bailey, 1952), Taylor, 1975: 152 [literature compilation].
Foneticella pitshryi (Bailey and Bailey, 1951), Taylor, 1975: 153 [literature compilation].
Pyrgulopsis pitshryana (Bailey & Bailey, 1952), Herschler and Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Herschler, 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. kelobensis*, a similar species which differs in having a ventral gland on the penis. Populations of *P. pitshryana* 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 883281, USNM 883444.—Spring, northeast side Merkle Lake, Bear Lake drainage, T. 14 S, R. 44 E, NE ¼ section 26, USNM 883385.—Spring, Stauffer River, Bear River drainage, T. 11 S, R. 43 E, NE ¼ section 27, USNM 883387. CARIBOU COUNTY; Leader Creek, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, SE ¼ section 5, USNM 883337, 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.—Kadley Spring, Gem Valley, Bear River drainage, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883538, USNM 883891.—Spring (source), Whiskey Creek, Gentle Valley, Bear River drainage, T. 11 S, R. 41 E, SE ¼ section 7, USNM 883641. 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; Jacobson 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 Herschler, sp. nov.

Hamlin Valley DVF
 (Figures 91, 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 91, 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 distinct behind the aperture. Aperture ovate, usually distinct. 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 filled. 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. Spout medium grey. Foot light

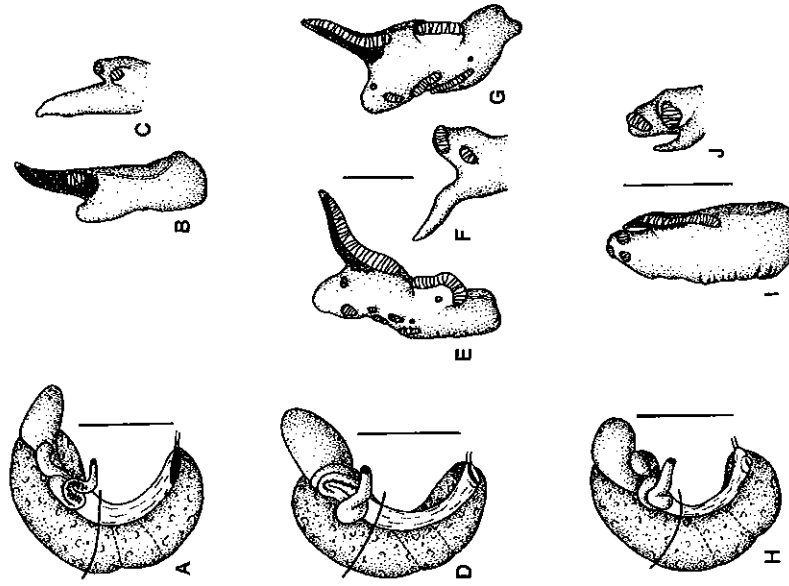


Figure 47

Genitalia of *Pyrgulopsis* species (A, P. favez, USNM 860728; B, P. favez, USNM 883484; D–G, P. chamberlaini, USNM 860729; H–J, P. longicauda, USNM 860740). Bars = 0.5 mm. Drawings show (from left to right) female glandular evictant and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the dorsal penis (B, G) are shown for *P. chamberlaini*.

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.

Ctenial filaments 15, weakly pleated; ctenidium connected to pericardium by short efferent vein. Oesophradium 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

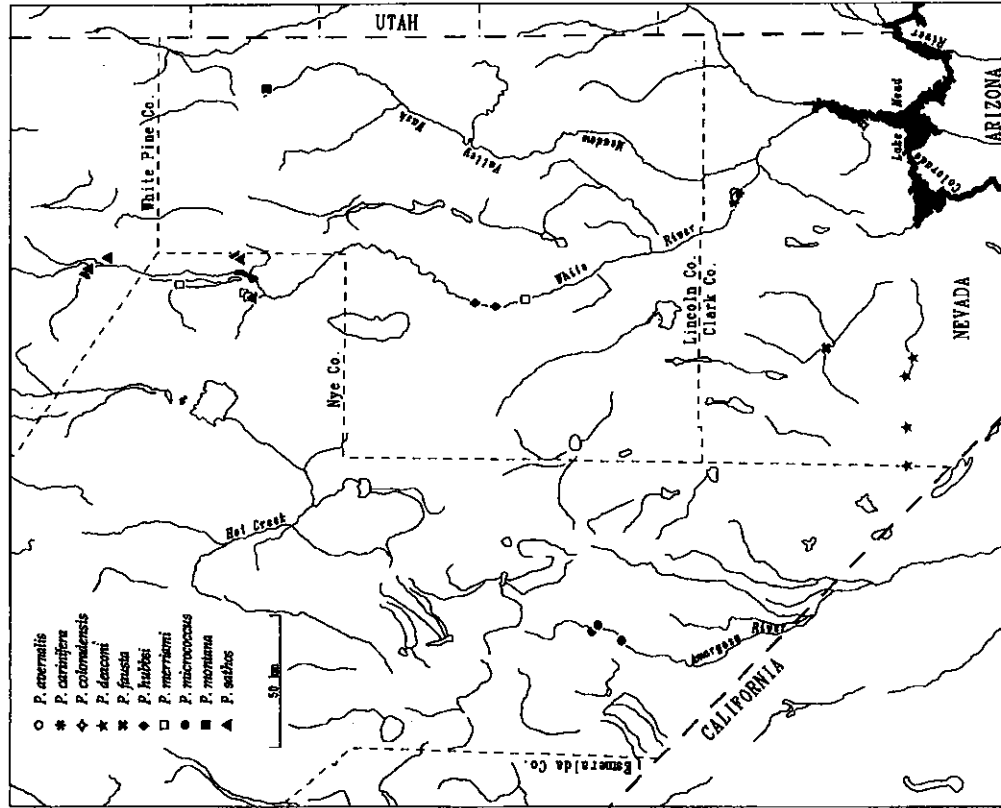


Figure 40

Map showing distributions of *Pygulopsis* species of southern Nevada. Previously known records for *P. microcoelus*, *P. oerensis*, *P. carinifera*, and *P. morrisi* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

palial wall. Bursa copulatrix short, narrow, globular-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 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, palial portion short, narrowly ovate in section. Proximal palial vas defersus with well-developed loop. Penis (Figure 44G, F) 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, glanular 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 863237 (Figure 23B), collected by R. Hershler and P. Hovvagh, 10 May 1993; paratypes, USNM 860726. The type locality is a series of large, thermal (26.9°C) rheocrenas issuing from the side of a hill.

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

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

Pygulopsis 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.

Diagnoses: 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).

Descriptions: 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, proscloine, without sinuation. Unoblique 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.

Rachula 665 x 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. Oopneuridium 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.

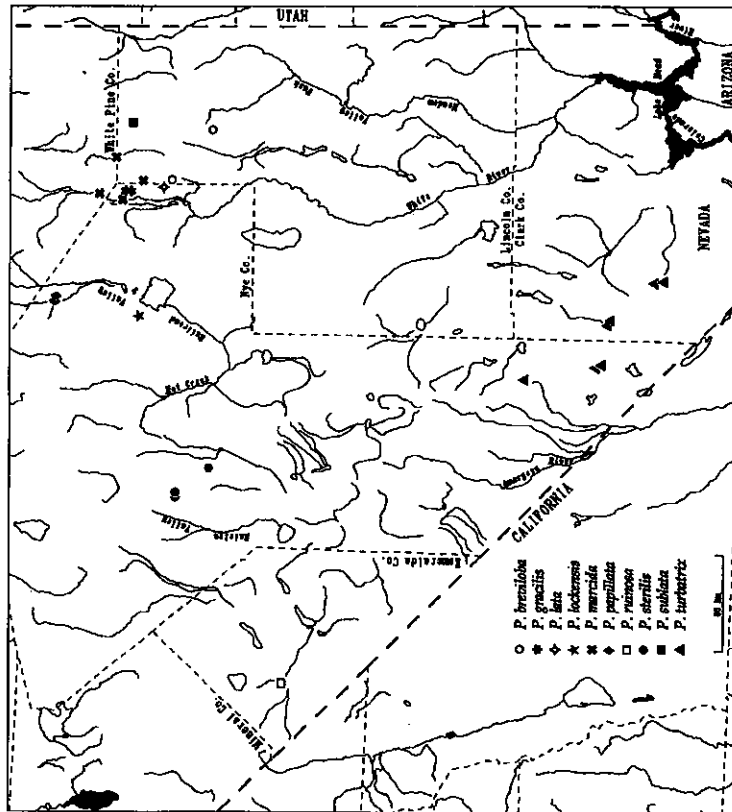


Figure 50
Map showing distributions of *Pyrgulopsis* species of the Colorado River drainage basin and isolated basins of Nevada. In cases where congeners are sympatric, symbols are slightly offset.

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 post-irio-oblique loop often preceded by weak posterio-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copularis 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 vesicle 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, sub-globular; entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 45B-P) 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 dentlike, 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 tanoecene.

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 gland; while those to the north and east (e.g., Grouse Creek, Park Valley) 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: Paxon Springs, Pilot Creek Valley, T. 36 N, R. 70 E, NE ¼ section 28, USNM 874713.—McCuisin Springs, Pilot Creek Valley, T. 37 N, R. 70 E, NE ¼ section 30, USNM 874723, USNM 883888.—Spring, lower Jay Creek, Grouse 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 23, 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 Elms Reservoir, Grouse Creek Valley (Figure 5E), T. 11 N, R. 18 W, NW ¼ section 6, USNM 883614.—North Beetle Spring, Grouse Creek Valley, T. 11 N, R. 17 W, NW ¼ section 32, USNM 883624.—South Beetle 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, Toole County, Spring, ca. 4.8 km south of Donner Spring, Pilot

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

Pyrgulopsis hovingsi Hershler, sp. nov.

Upper Thousand Spring pvs

(Figures 10B, 11I, 16D-E, 24E, 45C-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 11I) 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 annate or slightly disjunct. Inner lip slightly thickened, sometimes forming narrow columellar shelf. Outer lip thin, orthocone 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.

Radialia (Figure 16D-P) 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, daggertlike; 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.

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

Pyrgulopsis fusca Hershler, sp. nov.

Outer Creek pyrg

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

Etiymology: From *fusca* (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, petalid, 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. Teleconch whorls medium to high convexity, shoulders narrow to broad, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, acute or slightly disjunct, inner lip thin, sometimes having very narrow columellar shelf. Outer lip thin, slightly prosocline, without sinitation. Umbilicus rimate or shallowly perforate. Pterostacium dark tan.

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

Radula: 650 μ m, with 50 rows of teeth. Central tooth 24 μ m 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 teeth 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.

Caudal filaments: 19; pleated; ctenidium overlapping pterostacium posteriorly. Ophradium 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 lobe 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, Outer Creek, ca. 1.6 km above The Narrows, Piute County, Utah, T. 28 S. R. 1 W, SW $\frac{1}{4}$, 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 Outer 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, Outer Creek, USNM 860728, USNM 883439, USNM 883484. Sevier County: Burr Creek, Outer Creek drainage, T. 25 S. R. 1 W, SW $\frac{1}{4}$, 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)

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

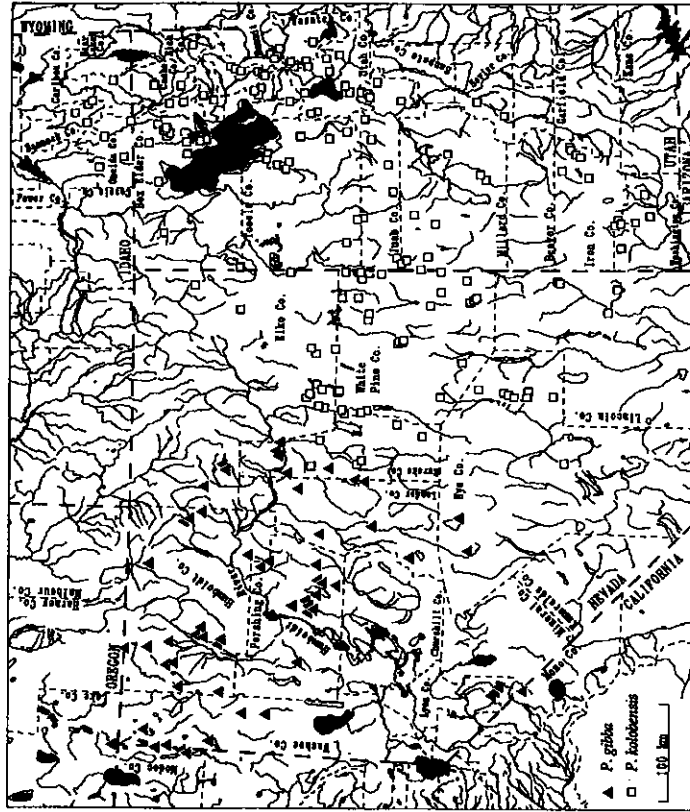


Figure 54

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

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 shell medium width. Outer lip usually thin, but slightly thickened in largest specimens, prosocline, without sinitation. Umbilicus absent or narrowly rimate. Pterostacium light green.

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

Radula: 710 \times 100 μ m, with 62 rows of teeth. Central tooth 28 μ m wide, with highly indented dorsal edge; lateral cusps, 4-6; central cusp narrow (sometimes long),

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 perial gland, large Dp1, small Dp2, small Dp3 (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. Teleconch whorls medium convexity,