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Rissooidean Snails from the Pit River Basin, California

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Abstract. A recent field survey of the Pit River basin in northeastern California resulted in the discovery of numerous undescribed populations of aquatic rissooidean snails which are treated in this paper. Based on morphological study and analysis of mitochondrial DNA sequences we describe a new species of the genus *Colligyrus* (family Amnicolidae) and four new species of the genus *Pyrgulopsis* (Hydrobiidae). Phylogenetic analysis of sequence data suggests that the new species of *Colligyrus* is sister to an undescribed congener from the Klamath basin. The four new species of *Pyrgulopsis* do not form a monophyletic group but instead are variously related to other regional congeners. We also describe Pit River basin populations of two species of *Pyrgulopsis* which were previously considered to be endemic to the northwestern Great Basin (*P. eremica*) and Klamath basin (*P. archimedis*).

INTRODUCTION

Rissooidean snails are one of the richest elements of aquatic biota in the western United States, with more than 170 species currently recognized, yet this fauna remains poorly known. Most of the previously described members of this fauna have been little studied and are in need of taxonomic revision. Existing collections document a large number of undescribed species, and discovery of additional novelties is anticipated as large expanses of the West still have not been thoroughly surveyed for these small, nondescript, highly speciose animals. One little explored region is the Pit River basin of northeastern California and southeastern Oregon, which is the major headwaters tributary of the Sacramento River. The only rissooidean snails that have been previously reported from this basin in the taxonomic literature are two species of *Fluminicola* (Hydrobiidae). One of these, *F. seminalis* (Hinds, 1842), is now extirpated from much of its historic range but persists in a few large springs and streams (Taylor, 1981; Hershler & Frest, 1996) while the other, *F. modoci* Hannibal, 1912, lives in springs along the margin of Goose Lake (Hershler & Frest, 1996). Two of us recently surveyed aquatic habitats throughout the Pit River basin and discovered numerous previously unstudied populations of rissooidean snails (Frest & Johannes, 1993a, b, 1994, 1995, 1996, 1997), including six species of *Pyrgulopsis* (Hydrobiidae), four of which are new. The other two congeners that were collected previously had been considered restricted to the Klamath (*P. archimedis*) and northwestern Lahontan (*P. eremica*) basins. A new species of *Colligyrus,* a small amnicolid genus previously known only from the Snake River basin and Great Basin of southeast Oregon (Hershler, 1999), also was discovered. All of this material is described herein. Inasmuch as species of freshwater rissooidean snails often are difficult to ascertain on the basis of morphological criteria alone, we have augmented our treatments with analyses of mitochondrial DNA sequences. These analyses also enabled evaluation of the phylogenetic relationships of the species treated herein. In a subsequent paper we will describe the numerous populations of another genus, *Fluminicola,* which were sampled during this survey.

PIT RIVER BASIN

The Pit River basin occupies about 17,000 km^2, contains a complex drainage (Pease, 1965), and is largely situated on the Modoc Plateau in Lassen, Modoc, Shasta, and Siskiyou counties (Figure 1). The mainstem Pit River originates near Alturas from the junction of two north-south streams, the North Fork and South Fork. These forks

Figure 1. Map of Pit River basin in northeastern California. Shaded polygons indicate portions of drainage shown in Figures 5, 9, 17.

drain the Warner Mountains, which form a western border of the California Great Basin. The North Fork also is the occasional outlet of the Goose Lake basin (Phillips & Van Denburgh, 1971) while the South Fork drains a small basin to the north of the Madeline Plains. From Alturas the Pit River flows nearly westward across a minor gap which separates Warm Springs Valley (Canby area) from the north-south oriented basins to the east. Several large streams (e.g., Turner and Canyon creeks) enter the river in this valley. Farther downstream the Pit River courses nearly southward through a series of northwest-southeast trending mountain ridges (e.g., Horsehead Mountain, Fox Mountain) into a flat plain, Big Valley (vicinity of Adin to Bieber). Several large, spring-fed creeks (Ash Creek, Taylor Creek, Willow Creek) enter the river in this valley. Along the southwest corner of this valley the river enters a deep canyon, which abuts the Big Valley Mountains and other small ranges, and curves around the Big Bend to assume a northwest-southeast orientation. The river then enters Fall River Valley where it is diverted into an adjacent northeast-southwest canyon formed in large part by several prominent peaks, including Chalk and Burney mountains. In the vicinity of Fall River Mills large north-south tributaries (Fall River on the north and Hat Creek to the south) augment the flow of the river. After exiting the downstream canyon section, the Pit River joins the McCloud and Sacramento rivers in Shasta Lake, north of Redding.

Most of the Pit River watershed as traditionally mapped consists of ephemeral water bodies. There are few natural, permanent lakes and ponds. The relatively few permanent streams include Ash Creek, Burney Creek, Fall and Tule "rivers," Hat Creek, Horse Creek, Lava "Creek," Lost Creek, Potem Creek, Rising "River," Rush Creek, Spring "Creek," Squaw Creek, Turner Creek, and Willow Creek, which are generally spring-fed. (Those listed in quotes are outlets of large springs. Similarly, many of the drainage's permanent "lakes" such as Big Lake, Baum Lake, Crystal Lake, Eastman Lake, Horr Pond, and Rising River Lake are large limnocrene springs.) The Pit River has steep canyon segments alternating with reaches that flow across flat plateaus and generally dry lake beds. The former river segments have moderate to steep gradients, coarse substrate, cold and clear water, limited aquatic macrophytes, low nutrients, high dissolved oxygen, and swift flow. The latter have more fine sediment, slower flow, abundant macrophytes, and higher dissolved nutrient but lower dissolved oxygen concentrations. Much of the Pit River drainage originates as rapid snow melt-off or from groundwater discharge, predominantly in the form of cold springs, although warm springs also are present, most commonly in the larger valleys. Some of the largest springs in the United States are found in this drainage (Waring, 1915; Meinzer, 1927), including Lava Creek, Spring Creek, Sucker Springs Creek, Thousand Springs, and the springs associated with Ahjumawi Lava Springs State Park and MacArthur-Burney Falls State Park. All of these are spring complexes (nasmodes) with one or more associated large limnocrenes (spring pools). Some of the larger springs are flowing rheocrenes, and these include several long spring runs issuing from a single spring (e.g., Bob Creek, Beaver Creek, Lost Creek). Springs typically originate from the edge of Pleistocene or Holocene basalt flows.

A large portion of the Pit River flow in some areas is diverted for irrigation, and some of the canyon sections have small hydroelectric dams and impoundments. As a consequence of water development, several reaches of the Pit River have dried on a seasonal basis in recent years, effectively segmenting the river. Many of the springs have diversions or other modifications and are utilized by fish hatcheries and for irrigation and watering of livestock.

MATERIALS AND METHODS

Specimens used in this study are deposited at the National Museum of Natural History, Smithsonian Institution (USNM) and in the collections of Deixis Consultants, Seattle, Washington (DEIX). Snails were relaxed with menthol crystals, fixed in dilute (4%) formalin, and preserved in 70% ethanol for morphological study; small subsamples were directly preserved in 90–95% ethanol for DNA analysis. Locality descriptions are followed by UTM coordinates (all from Zone 10), elevation, and locality codes (for sequences used in the phylogenetic analyses). Collector abbreviations are as follows: TF, Terrence J. Frest; EJ, Edward J. Johannes; JJ, James E. Johannes; JL, Jacquie S. Lee; JF, Joseph L. Furnish; FM, Francis W. Mangels; SR, Stewart Reid; and LA, James J. Landye. Common names are proposed for each new species. Treatments of the Pit River snails in agency and consulting reports are detailed in the synonymy sections as an aid to those who seek to track this literature as it pertains to snail conservation issues. Counts, measurements, and other methods of morphological study follow Hershler (1998). Whorl counts and measurements of 10–15 adult shells (as indicated by the completion of the inner shell lip) were taken from one or more samples of each species. Unless otherwise specified, 8–10 radulae from a single sample were examined for each species. The small sizes of many of the samples precluded analysis of sexual dimorphism of shells. Morphological terminology largely follows that of Hershler & Ponder (1998).

Genomic DNA was extracted from whole specimens for sequencing a partial segment of mitochondrial cytochrome-*c* oxidase subunit I (mtCOI) corresponding to Folmer's fragment (Folmer et al., 1994). Methods generally were those used by Liu et al. (2001). Forty-one new sequences were used in the phylogenetic analyses. Three sequences of one of the new species of *Pyrgulopsis* (from Sucker Springs Creek) were identical, and thus only one of these was submitted to GenBank. The new sequences were deposited under GenBank Accession Numbers AY196166–AY196175, and AY197577–AY197605. Sequences for *Pyrgulopsis archimedis* (from Upper Klamath Lake) and the outgroups were previously submitted by us to GenBank (*P. archimedis,* AF520950; also see Hershler et al., 2003; *Amnicola dalli,* AF354769; *Amnicola limosa,* AF354768; *Nymphophilus minckleyi,* AF354771; also see Liu et al., 2001).

Sequence divergences are reported as uncorrected p-distance (Nei, 1987) and are interpreted within the context of a previously published study which showed that species of *Tryonia* (family Cochliopidae), another western North American freshwater rissooidean genus, differed from one another by >1.3% (Hershler et al., 1999). In order to examine relationships between Pit River taxa and other members of the genera *Colligyrus* and *Pyrgulopsis,* phylogenetic trees were generated using PAUP 4.08b (Swofford, 2002). For *Colligyrus,* both previously described congeners were included in the analysis while for *Pyrgulopsis* we sampled other regional representatives of this huge genus. Trees were rooted with other North American representatives of the groups of concern. For these preliminary analyses neighbor-joining (NJ) trees were generated based on TrN (Tamura & Nei, 1993) (*Colligyrus*) and HKY (Hasegawa et al., 1985) (*Pyrgulopsis*) genetic distances. Modeltest 3.06 (Posada & Crandall, 1998) was used to determine which model of DNA substitution best fit these data. Bootstrapping (Felsenstein, 1985) with 1000 replications was used to estimate branch support.

TAXONOMY

Shell measurements are given in Table 1; radular counts are summarized in Table 2.

Superfamily Rissooidea
Family Amnicolidae

We follow Wilke et al. (2000, 2001) in treating the group composed of *Amnicola* and other genera which share its distinctive anatomical features (Hershler & Thompson, 1988) as a family separate from the Hydrobiidae.

Colligyrus Hershler, 1999

Type Species: *Hydrobia greggi* Pilsbry, 1935; original designation.

Diagnosis: The genus was diagnosed and discussed by Hershler (1999).

Colligyrus ***convexus*** Hershler, Frest, Liu & Johannes, sp. nov.
Canary duskysnail

(Figures 2, 3, 4A, 5, 6)

Lyogyrus n. sp. Frest & Johannes, 1993a:ii, 3, 30, 67 (fig. 2), 68 (fig. 3A), 71 (table 1), 73 (table 2), 76 (table 3), 78–89 (table 4), 101 (table 7).—Frest & Johannes, 1993b:73, 93, 98, addendum p. 12.—Frest & Johannes, 1994:18, 33 (fig. 2), 36 (table 1), 38 (table 2), 41 (table 3), 43–48 (table 4), 56 (table 8).—Furnish et al., 1998: 59.—Frest & Johannes, 1999:78.

Lyogyrus n. sp. 3 [canary duskysnail]. USDA, 1993a: unpaginated (Appendix A, table IV-A-5).—Frest & Johannes, 1993b: 69, 89.—USDA, 1994c:398.—USDI, 1994: 35306.—Furnish et al., 1997:6 (table 1), 7 (table 1), 8 (table 1), 10 (table 2), 32 (Appendix C), 58.—USDA, 1998: unpaginated (Appendix C Species IV.37).—Frest & Johannes, 1999:12 (table 1), 77.

Lyogyrus n. sp. 3. USDA, 1993a:IV-131 (table IV-22).—USDA, 1993b:3 & 4-83.—Frest & Johannes, 1994: 18.—USDA, 1994a:3 & 4-168 (table 3&4-27).—USDA, 1994b:B-160 (table B11-1).—USDA, 1994c:J2-74 (table J2-8f), J2-304.—USDA, 1994d:C-60 (table C-3).—Frest & Johannes, 1995:51.—Frest & Johannes, 1996:47, 113, 135.—Furnish et al., 1998:23 (Appendix A), 27 (Appendix B), 43.—USDA, 1998:23, 30.—Frest & Johannes, 1999:unpaginated (Table of Contents), 68, 78, 80 (figs. 31, 32, Map 15).—USDA, 1999:103 (table 2-2), 119 (table 2-8); 219, 395 (table C-3), 456 (table F-1).—USDA, 2000a:123 (table 2-2), 143 (table 2-8), 173 (table 2-12), 324, 325, 326.—USDA, 2000b:30 (table C-3), 105 (table F-2).—USDA, 2001:Standards and Guidelines, 49 (table 1-1).

Lyogyrus n. sp. 3 of Frest & Johannes (1993b). Frest & Johannes, 1994:18.—Frest & Johannes, 1995:68, 69.

Lyogyrus n. sp. 1. Frest & Johannes, 1995:3, 36, 68, 69, F14 (fig. 5), F16 (fig. 6A), T1 (table 1), T3 (table 2), T7 (table 3), T10–T31 (table 4), T61 (table 8), D12 (Appendix D map).—Frest & Johannes, 1997:T1 (table 1), T3 (table 2), T7 (table 3), T10 (table 10).—Furnish et al., 1998:59.—Frest & Johannes, 2002:17 (fig. 4).

Lyogyrus n. sp. 1 [canary duskysnail]. Frest & Johannes, 1995:50.

Lyogyrus n. sp. 3 Frest & Johannes, 1993 [canary duskysnail]. Furnish et al., 1998:58.

"*Lyogyrus*" n. sp. 8 Frest & Johannes, in press. Frest & Johannes, 1999:68.

"*Lyogyrus*" n. sp. 3. Frest & Johannes, 1999:77.

Lyogyrus n. sp. 8 Frest & Johannes, in press [canary duskysnail]. Frest & Johannes, 1999:77.

"*Lyogyrus*" n. sp. 8. Frest & Johannes, 1999:78.

Etymology: Referring to the well rounded aspect of the teleoconch shell whorls. Common name refers to the yellowish color of the shell periostracum in this species.

Diagnosis: *Colligyrus* ***convexus*** is smaller than its two congeners and is further distinguished by its highly convex teleoconch whorls and sinuate shell aperture. It differs also in having relatively few cusps on the marginal radular teeth, a narrow posterior seminal receptacle, an elongate bursal duct, and little or no pallial component of the albumen gland. *Colligyrus* ***convexus*** resembles *C. depressus* Hershler, 1999, in shell form, although the former has a taller spire.

Description: Shell (Figures 2A, B, 4A) 1.36–1.96 mm tall, SW/SL 84–101%, AL/SL 48–57%, whorls 3.0–3.5. Periostracum light tan or yellow. Protoconch (Figure 2E, F) markedly tilted, about 1.5 whorls, diameter about 440 μm, sculptured with numerous, evenly spaced narrow spiral lines. Teleoconch whorls evenly rounded, usually shouldered, sutures impressed, weak spiral striae often present on body whorl. Aperture ovate, slightly angled adapically. Inner lip slightly thickened, usually complete and narrowly adnate across parietal wall, sometimes narrowly disjunct; columellar lip sometimes reflected to form narrow shelf. Outer lip slightly thickened, prosocline, often strongly sinuate. Shell broadly umbilicate.

Outer (Figure 2C) and inner (Figure 2D) sides of operculum smooth.

Radula (Figure 2G) about 920 $\times$ 62 μm, with about 145 well formed rows of teeth. Central teeth (Figure 2H) about 20 μm wide; cutting edge straight or slightly convex, central cusp pointed, outer basal cusp often weakly developed. Basal tongue of central tooth V-shaped, base shorter than lateral margins, lateral margins distally expanded. Central

Table 1

Shell parameters. Ranges are followed by means and standard deviations. WH, total number of shell whorls; SL, shell height; SW, shell width; LBW, body whorl height; WBW, body whorl width; AL, aperture height; AW, aperture width.

Species	WH	SL	SW	LBW	WBW	AL	AW
Colligyrus ***convexus***							
holotype	3.00	1.52	1.40	1.40	1.12	0.76	0.78
USNM 1004536	3.0–3.25	1.42–1.78	1.32–1.56	1.22–1.42	1.08–1.29	0.79–0.90	0.73–0.85
n = 13	3.15	1.57	1.46	1.30	1.19	0.85	0.79
	0.13	0.095	0.073	0.057	0.054	0.035	0.041
Pyrgulopsis archimedis							
USNM 874369	4.50–5.25	3.94–5.66	2.88–3.64	2.98–3.97	2.41–3.33	1.73–2.26	1.60–2.06
n = 13	4.83	4.58	3.11	3.33	2.70	1.99	1.77
	0.30	0.49	0.22	0.27	0.28	0.16	0.15
USNM 892182	4.50–5.25	4.04–5.22	2.90–3.47	2.92–3.72	2.53–3.11	1.70–2.19	1.45–1.85
n = 12	4.77	4.49	3.13	3.25	2.75	1.94	1.65
	0.25	0.35	0.17	0.25	0.17	0.17	0.12
USNM 892186	4.75–5.50	4.40–5.19	2.92–3.27	3.18–3.74	2.71–3.10	1.82–2.12	1.64–1.87
n = 9	5.00	4.86	3.08	3.50	2.85	2.00	1.77
	0.22	0.28	0.12	0.16	0.11	0.093	0.078
USNM 1004548	4.75–5.75	4.04–5.85	2.73–3.54	2.79–3.88	2.34–3.21	1.60–2.23	1.43–1.90
n = 13	5.27	4.74	3.00	3.19	2.65	1.90	1.63
	0.26	0.53	0.25	0.31	0.25	0.17	0.12
Pyrgulopsis eremica							
USNM 1004528	4.00–4.25	2.16–2.37	1.46–1.65	1.58–1.82	1.32–1.51	0.88–1.05	0.80–0.94
n = 12	4.17	2.23	1.55	1.65	1.38	0.97	0.84
	0.12	0.055	0.056	0.062	0.053	0.043	0.038
Pyrgulopsis ***rupinicola***							
holotype	5.00	4.72	2.92	3.12	2.68	1.80	1.60
USNM 1004526	4.50–5.25	3.59–4.72	2.35–3.12	2.61–3.19	2.14–2.79	1.56–1.94	1.33–1.73
n = 11	4.84	4.04	2.77	2.87	2.44	1.74	1.53
	0.26	0.31	0.23	0.18	0.19	0.14	0.11
Pyrgulopsis ***falciglans***							
holotype	4.00	2.30	1.52	1.58	1.34	0.92	0.86
USNM 1004606	4.00–4.75	2.30–2.71	1.58–1.81	1.68–1.96	1.34–1.64	0.92–1.16	0.85–1.02
n = 10	4.45	2.47	1.69	1.82	1.51	1.04	0.93
	0.20	0.14	0.078	0.097	0.088	0.071	0.055
Pyrgulopsis ***cinerana***							
holotype	4.75	3.28	2.20	2.40	1.96	1.36	1.16
USNM 1004544	4.25–5.00	2.96–4.85	2.05–3.07	2.24–3.51	1.79–2.84	1.34–1.97	1.14–1.62
n = 11	4.61	3.42	2.36	2.58	2.08	1.52	1.30
	0.23	0.54	0.29	0.35	0.29	0.18	0.15
Pyrgulopsis ***lasseni***							
holotype	4.25	2.24	1.34	1.52	1.16	0.88	0.82
USNM 1004531	*4.25–4.75	2.06–2.58	1.31–1.74	1.41–1.89	1.10–1.41	0.82–1.16	0.73–1.05
n = 11	4.53	2.25	1.48	1.62	1.25	0.95	0.85
	0.079	0.20	0.13	0.14	0.097	0.10	0.086
USNM 1004533	*4.00–5.00	2.00–2.81	1.41–1.80	1.56–2.02	1.18–1.57	0.89–1.27	0.81–1.06
n = 13	4.42	2.37	1.58	1.75	1.34	1.04	0.92
	0.29	0.24	0.11	0.14	0.11	0.11	0.074

* Whorls not counted for one specimen with an eroded apex.

cusp of lateral tooth (Figure 2I) pointed; outer wing well flexed, length about 200% of tooth face length.

Animal generally pale. Pallial roof sometimes having transverse pigment streaks. Visceral coil with grey dusting on dorsal surfaces of stomach and digestive gland.

Efferent ctenidial vessel elongate. Ctenidial filaments about 15, narrow, lateral surfaces without ridges. Osphradium large, ovate, centrally positioned along ctenidium. Renal organ with small pallial section. Style sac about as long as remaining portion of stomach, stomach without

Table 2

Radular cusp counts. Data for *P. archimedis* are from three samples.

Species	Central tooth: lateral cusps	Central tooth: basal cusps	Lateral tooth: inner cusps	Lateral tooth: outer cusps	Inner marginal tooth	Outer marginal tooth
Colligyrus ***convexus***	5–7	1–2	2–3	3–4	19–23	15–19
Pyrgulopsis archimedis	2–6	1	3–4	3–5	17–29	14–31
P. ***rupinicola***	4–5	1–2	3	4–6	18–21	17–21
P. eremica	5–9	1	3–4	4–5	21–26	24–33
P. ***falciglans***	5–6	1	3–4	4–5	22–29	27–35
P. ***cinerana***	4–6	1	2–3	3–5	17–24	24–34
P. ***lasseni***	5–8	1	3–4	3–5	21–23	27–31

posterior caecum. Rectum forming weak furrow on capsule gland.

Testis 1.0 whorl, of compound lobes, overlapping stomach anteriorly. Seminal vesicle a small mass of thick coils. Prostate gland (Figure 3A) broadly ovate, almost entirely visceral, ventral section appearing nonglandular in dissection. Visceral vas deferens opening to prostate gland well behind posterior pallial wall; pallial vas deferens opening a little behind anterior edge of prostate gland in front of pallial wall, duct nearly straight. Penis (Figure 3B) medium-sized, squat base abruptly tapering; filament much longer than base, narrow, gently tapering; lobe narrowly rectangular, gently tapering, arising from base.

Ovary 0.5 whorl, a simple sac containing five to six oocytes, abutting posterior edge of stomach. Distal female genitalia shown in Figures 3C, D. Renal oviduct a single posterior-oblique or horizontal loop, slightly overlapped by albumen gland. Bursa copulatrix small, ovate or subglobular, horizontal to transverse, partly overlapped by albumen gland. Bursal duct longer than bursa copulatrix, narrow to medium width, shallowly imbedded in albumen gland. Posterior seminal receptacle about as long as bursa copulatrix, finger-shaped, overlapping anterior portion of bursa copulatrix. Anterior seminal receptacle small, globular. Albumen gland with very short pallial section; capsule gland slightly shorter than albumen gland, entirely pallial, composed of two glandular units. Spermathecal duct distally expanded. Genital opening broad, terminal.

Type material: Holotype (Figure 4A), USNM 1004535, Lava Creek at and west of Island Road bridge near mouth to Eastman Lake, Lava Creek Ranch, north side of The Island, about 8.3 km north of Glenburn, Shasta County, California (626,720E; 4,551,820N; 1007 m), 18 August 1991, TF, EJ, and JJ. Paratypes (from same lot), USNM 1004536, DEIX 3147, DEIX 3167.

Other material examined: CALIFORNIA. *Shasta County:* USNM 1004534, north side of Pit River south of FS 50 at Camp Nine Flat, about 1.8 km west of Rock Creek (607,670E; 4,539,780N; 743 m), October 21 1994, TF and EJ.—USNM 1004537, DEIX 3187, west side of Rising River at Schmidt Ranch, downstream of bridge of Cassel Road, about 2.4 km south of Cassel (622,405E; 4,528,400N: 972 m), 27 September 1996, TF, EJ, and JL.—USNM 1004538, DEIX 3148, Baum Lake (impoundment of Hat Creek) east of a boat ramp, northeast of parking lot of Baum Lake Public Fishing Access off Hat Creek Powerhouse Road, northwest of Crystal Lake State Hatchery, north of Cassel (622,440E; 4,532,280N; 908 m), 30 August 2001, TF and EJ.—USNM 1004539, DEIX 3188, Burney Creek at Falls Trail bridge, about 80 m upstream of Burney Falls, McArthur-Burney Falls Memorial State Park (613,420E; 4,540,640N; 881 m), 25 September 2001, TF and EJ.—USNM 1004540, DEIX 3189, Burney Creek above footbridge, about 0.48 km below Burney Falls, McArthur-Burney Falls Memorial State Park (613,360E; 4,541,140N; 841 m), 30 September 2001, TF and EJ.—USNM 1005153, DEIX 3186, spring source, Fall River, 21 September 2001, TF and EJ.

Distribution: Fall River, Hat Creek and lower Burney Creek drainages of the Pit River basin (Figure 5). Snails were collected from limnocrenes and hyporheic streams and were most abundant on the undersides of cobbles and boulders in shallow to moderate depths, especially in areas lacking macrophytes or dense epiphyte cover. *Colligyrus* ***convexus*** was often found in association with the Shasta crayfish, *Pacifastacus fortis* (Faxon, 1914).

Remarks: MtCOI sequences from four populations of *C.* ***convexus*** formed a strongly supported (97%) clade whose sister relationship with an undescribed species from the

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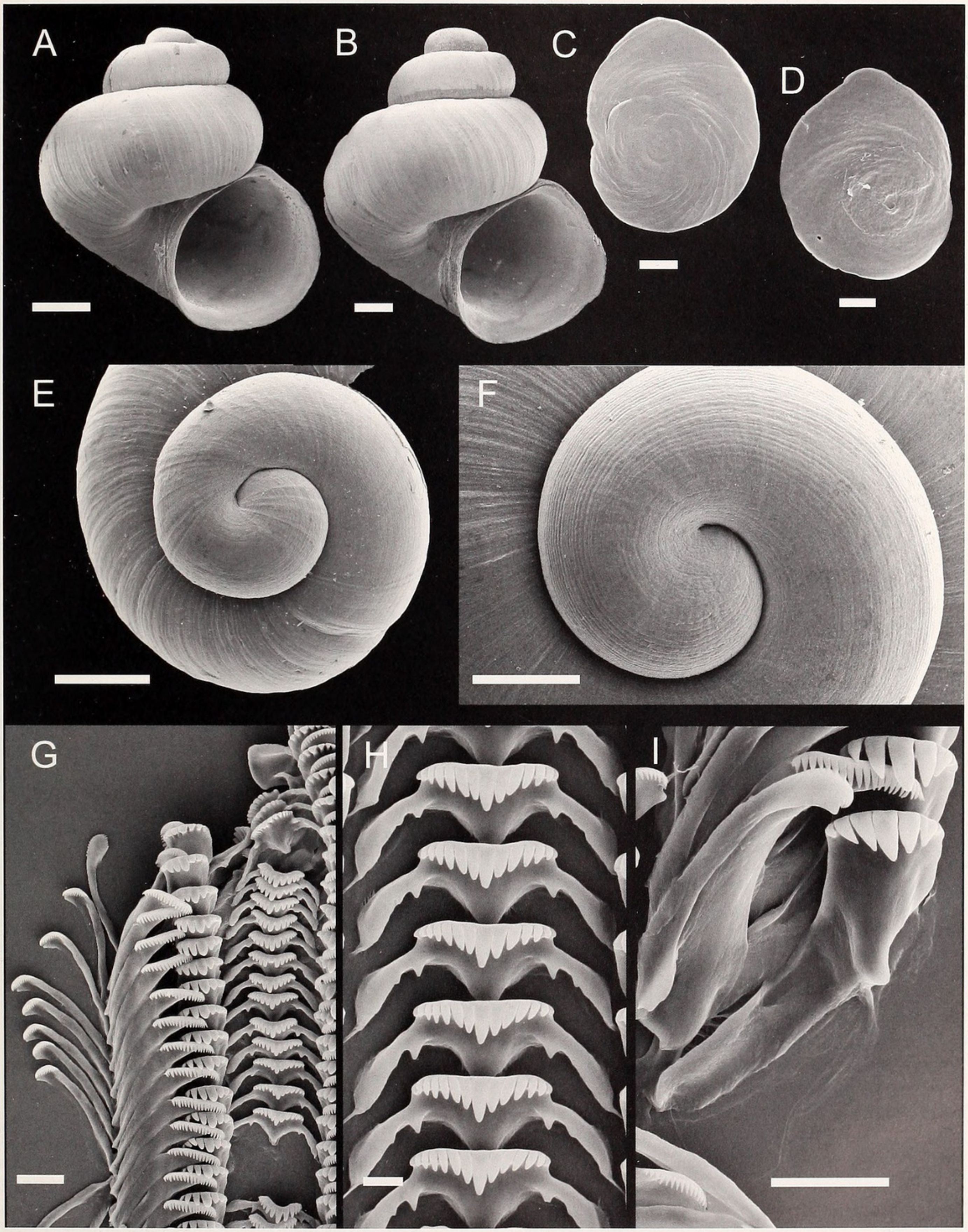
Figure 2. *Colligyrus* ***convexus*** Hershler, Frest, Liu & Johannes, sp. nov., shells, operculum, and radula, USNM 1004536, Lava Creek, Shasta Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Shell apex. F. Close up of apex showing protoconch sculpture. G. Radula. H. Detail of central teeth. I. Detail of lateral teeth. Scales: A = 300 μm; B = 200 μm; C–F = 100 μm; G, I = 10 μm; H = 3 μm.


A
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E
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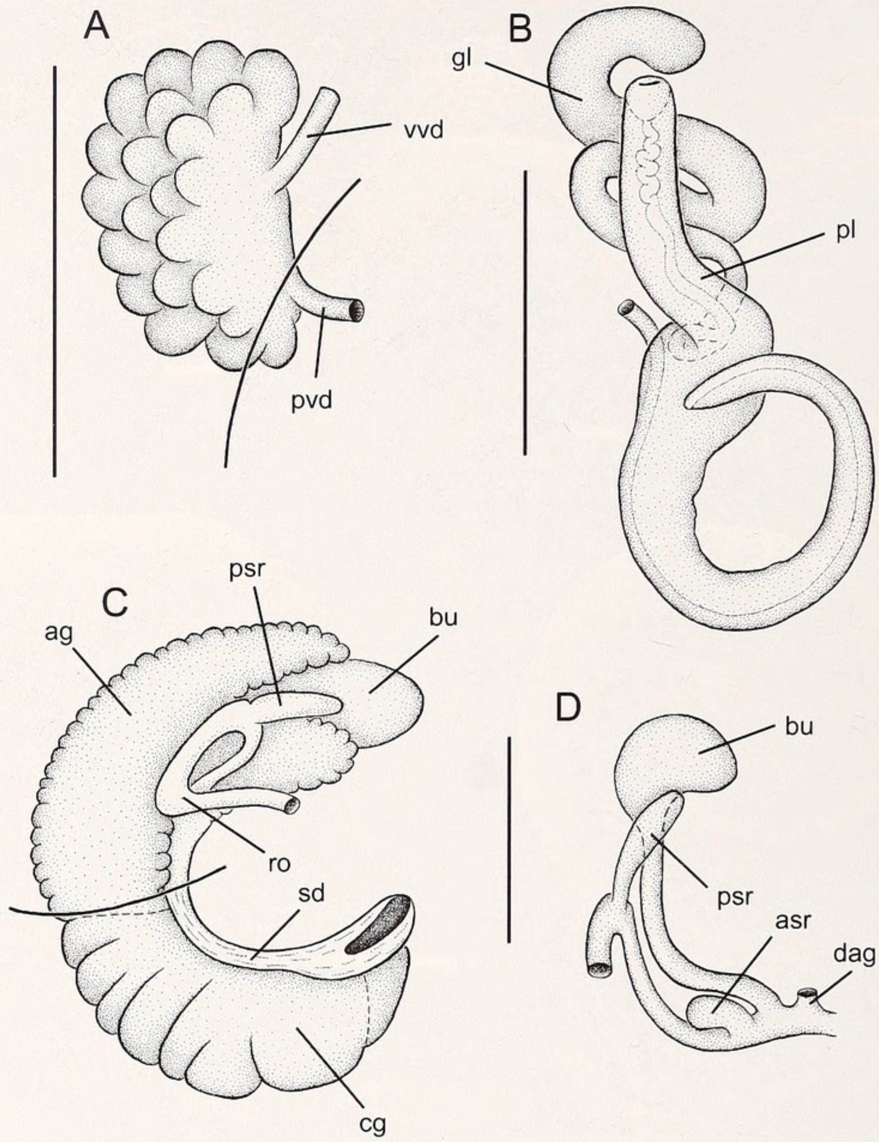


Figure 3. Genitalia of *Colligyrus* ***convexus*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004536. A. Prostate gland. B. Penis. C. Oviduct. D. Sperm pouches. Scales = 250 μm. ag = albumen gland, asr = anterior seminal receptacle, bu = bursa copulatrix, cg = capsule gland, dag = duct to albumen gland, gl = tubular gland of penis, pl = penial lobe, psr = posterior seminal receptacle, pvd = pallial vas deferens, ro = renal oviduct, sd = spermathecal duct, vvd =visceral vas deferens.

Klamath basin also was well supported (91%) (Figure 6). Sequence divergence among these four populations was only 0.0–0.50% (≤ 3 bp differences) while these differed from *C. depressus, C. greggi,* and the undescribed species from the Klamath basin by 7.8–8.2%, 10.0–11.2%, and 3.8–4.2%, respectively. *Colligyrus* ***convexus*** is a Record of Decision (ROD) Survey and Manage species on certain public lands (USDA, 1994d)

Family Hydrobiidae
Pyrgulopsis Call & Pilsbry, 1886

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

Diagnosis: The genus was recently diagnosed and discussed by Hershler (1994) and Thompson & Hershler (2002).

Pyrgulopsis archimedis Berry, 1947
Archimedes pyrg

(Figures 7–10)

Pyrgulopsis archimedis Berry, 1947:76, pl. 7: fig. 6.—Hershler, 1994:17–18, figs. 4a, 8a–c, 32c, 43c.

Pyrgulopsis intermedia (Tryon, 1865). Frest & Johannes, 1993a:ii, 3, 8, 71 (table 1), 73 (table 2), 76 (table 3), 101 (table 7).—Frest & Johannes, 1994:18, 36 (table 1), 38 (table 2), 41 (table 3), 56 (table 8). (All *non* Tryon, 1865).

Pyrgulopsis intermedia (Tryon, 1865) [Crooked Creek

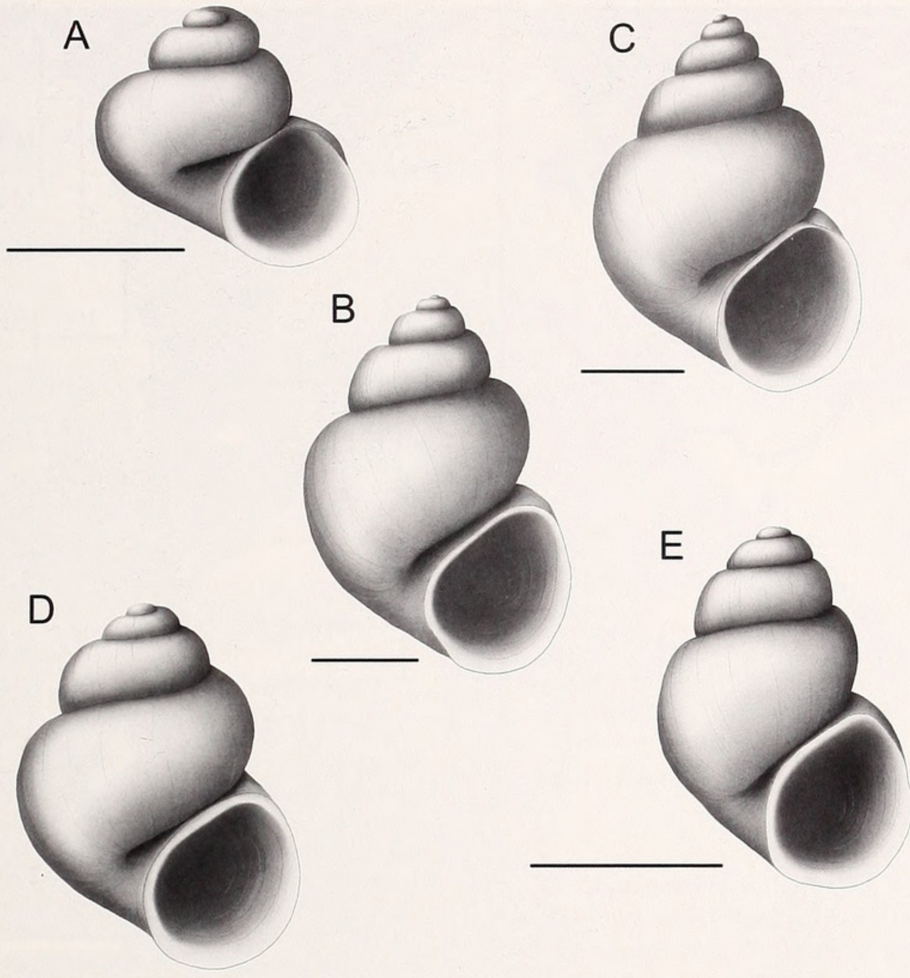


Figure 4. Holotypes (dried shells) of new species described in this paper. A. *Colligyrus* ***convexus*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004535. B. *Pyrgulopsis* ***rupinicola*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 892187. C. *Pyrgulopsis* ***falciglans*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004605. D. *Pyrgulopsis* ***cinerana*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004543. E. *Pyrgulopsis* ***lasseni*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004532. Scales = 1.0 mm.

springsnail]. Frest & Johannes, 1993a:29. (*non* Tryon, 1865).

Pyrgulopsis intermedia. Frest & Johannes, 1993a:67 (fig. 2), 78–89 (table 4).—Frest & Johannes, 1994:19, 33 (fig. 2), 43–48 (table 4). (All *non* Tryon, 1865).

Pyrgulopsis n. sp. 1 [Pit River springsnail]. Frest & Johannes, 1995:51.

Pyrgulopsis n. sp. 1. Frest & Johannes, 1995:70, F14 (fig. 5), T1 (table 1), T3 (table 2), T7 (table 3), T10–T31 (table 4), T61 (table 8), D10 (Appendix D map).—Frest & Johannes, 1997:T1 (table 1), T3 (table 2), T7 (table 3).

Pyrgulopsis n. sp. 1 Frest & Johannes, 1995. Frest & Johannes, 1997:T10 (table 10).

Revised diagnosis: Shell medium-large (up to 7.16 mm tall), variably shaped, teleoconch whorls near flat to moderately convex, sometimes angulate or prominently keeled basally. Penial ornament a variably oriented terminal gland; short, basally positioned penial gland; and stalked ventral gland.

Description (of Pit River basin material): Shell (Figures 7C, D) broad- to narrow-conic, 2.48–7.16 mm tall, SW/SL 59–75%, AL/SL 39–48%, whorls 4.0–5.75. Periostracum brown or tan. Protoconch 1.25–1.30 whorls, diameter about 430 μm, smooth or weakly wrinkled at apex. Teleoconch whorls slightly to moderately convex, usually evenly rounded but sometimes wider above, shoulders absent or narrow, sometimes sculptured with numerous weak spiral threads. Aperture ovate, angled above. Inner lip usually thin and adnate, sometimes incomplete across parietal wall, sometimes narrowly disjunct in large specimens; columellar lip rarely thickened and having narrow shelf. Outer lip usually thin, orthocline or weakly prosocline. Umbilicus absent to perforate.

Outer side of operculum shown in Figure 7E. Attachment scar margin sometimes slightly thickened near nucleus; inner side sometimes having narrow rim along outer edge (Figure 7F).

Radula (Figure 7G) 800–900 × 125–150 μm, with about 42 well formed rows of teeth. Central teeth (Figure 7H) about 48 μm wide; cutting edge weakly concave;

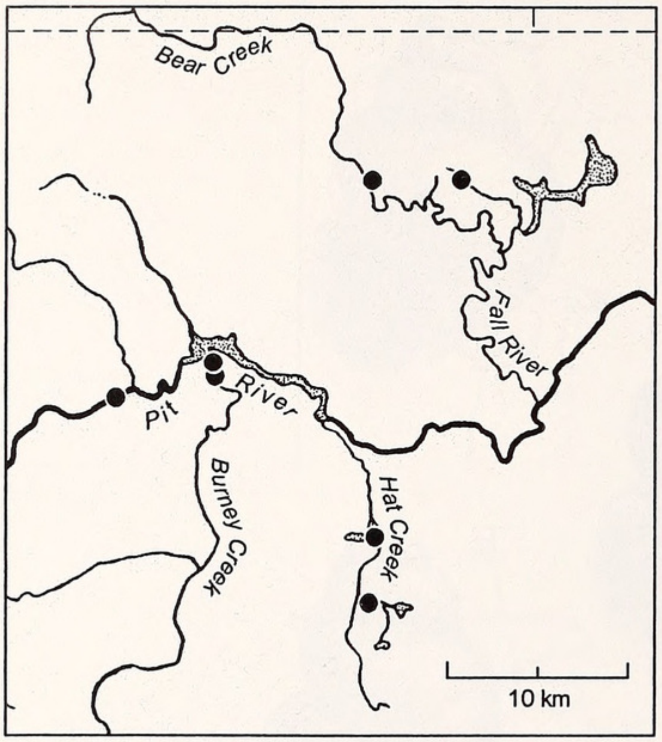


Figure 5. Map showing distribution of *Colligyrus* ***convexus*** Hershler, Frest, Liu & Johannes, sp. nov.

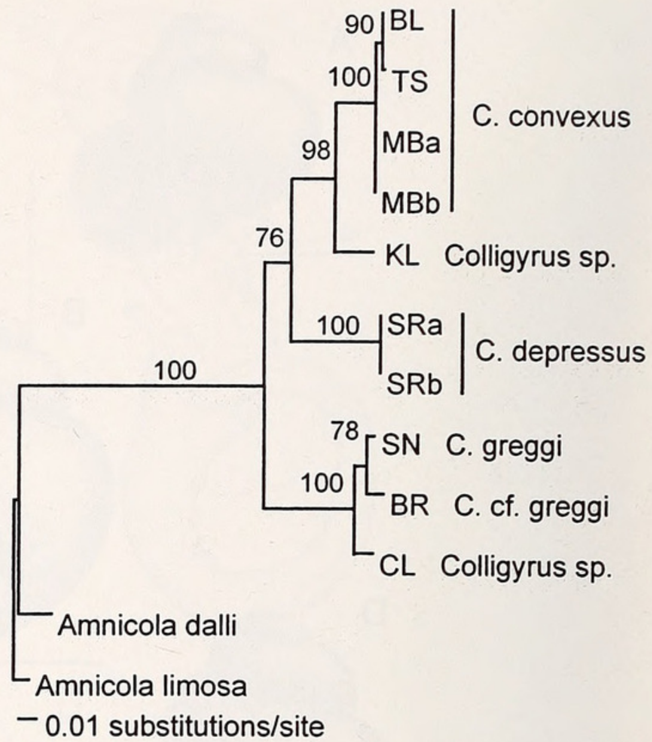


Figure 6. Phylogram from NJ distance analysis of mtCOI sequences of *Colligyrus* species and two outgroups (*Amnicola*). Bootstrap values ≥ 50% are given. BL = Baum Lake, Pit River basin, Shasta Co., California. BR = Saint Charles Spring, Bear Lake basin, Bear Lake Co., Idaho. CL = Oak Grove Fork, Clackamas River, Willamette basin, Clackamas Co., Oregon. KL = Link River, Klamath basin, Klamath Co., Oregon. MBa = Burney Creek (at Falls Trail bridge), Pit River basin, Shasta Co., California. MBb = Burney Lake (above footbridge), Pit River basin, Shasta Co., California. SN = springs, Cliff Creek, upper Snake River basin, Sublette Co., Wyoming. SRa = second spring south of Turner Ranch, Silvies River basin, Harney Co., Oregon. SRb = third spring south of Turner Ranch, Silvies River basin, Harney Co., Oregon. TS = Fall River (spring source), Pit River basin, Shasta Co., California.

outer basal cusp very small, sometimes incompletely developed. Basal tongue broadly rounded, almost U-shaped, base about even with distal ends of lateral margins, lateral margins proximally broad. Central cusp of lateral tooth (Figure 7I) hoelike, outer wing near straight to moderately flexed, length 200% length of tooth face. Inner marginal tooth with narrow, weakly developed wing on inner side. Outer marginal tooth with well developed rectangular wing on outer side.

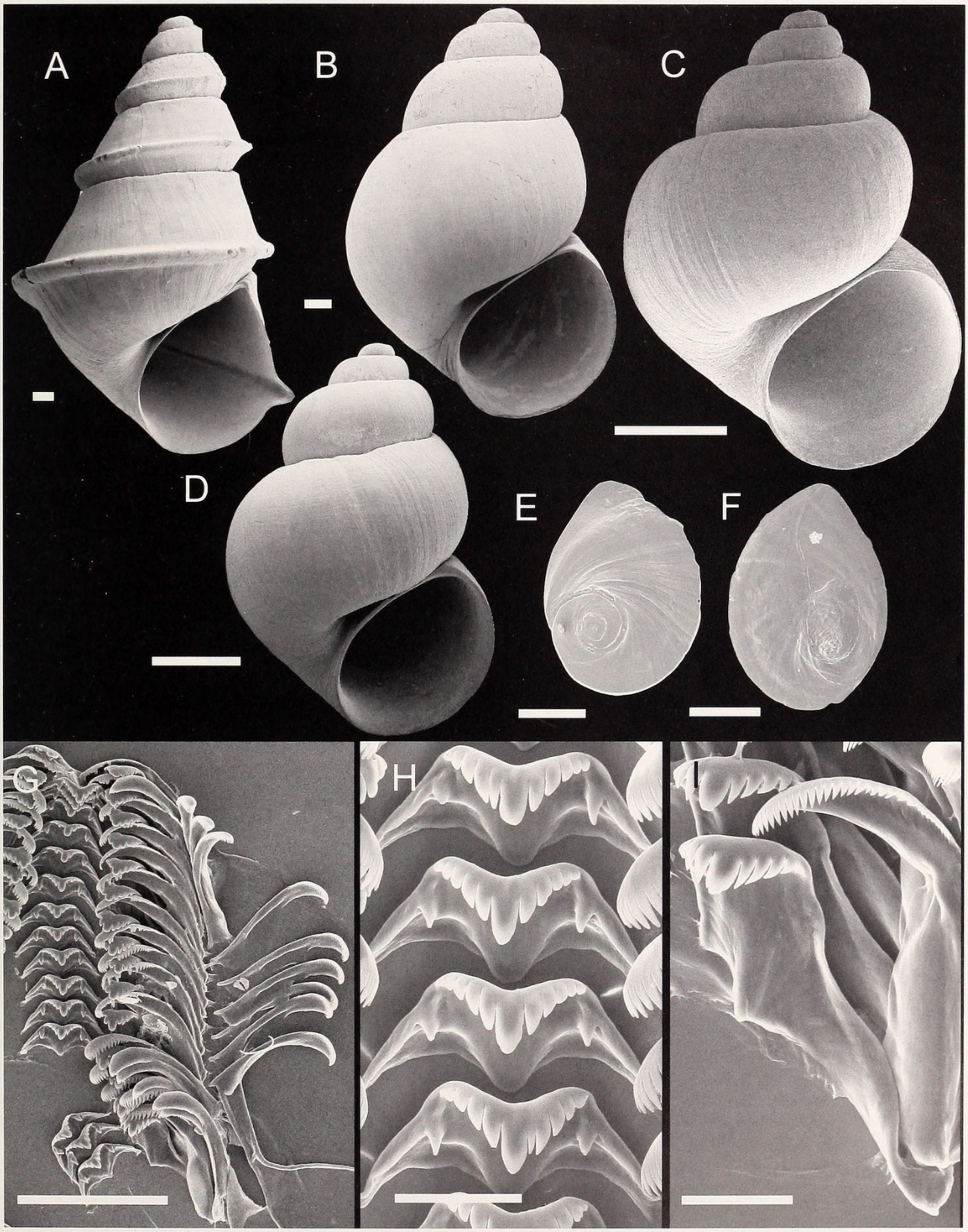
Animal darkly pigmented. Cephalic tentacles light to medium brown, dorsal sides sometimes having narrow, pale zone centrally. Snout dark brown. Pallial roof, visceral coil dark brown or black. Penial filament darkly pigmented along most of length.

Efferent ctenidial vessel short. Ctenidial filaments 28, well developed, lateral surfaces ridged. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal organ with short pallial section. Style sac a little longer than remainder of stomach; stomach with prominent triangular posterior caecum. Rectum forming furrow on capsule gland.

Testis 2.0 whorls, very large, of >10 compound lobes, overlapping stomach to edge of style sac. Seminal vesicle of a few, thick coils. Prostate gland (Figure 8A) ovate or bean-shaped, with short pallial section. Visceral vas deferens opening anteriorly a little behind posterior pallial wall; pallial vas deferens opening near middle of prostate gland; duct with proximal kink. Penis (Figures 8B–E) medium-sized to large; base rectangular, weakly folded along inner edge; filament short, narrow, tapering, horizontal; lobe short, rectangular, horizontal or slightly

→

Figure 7. *Pyrgulopsis archimedis,* shells, operculum, radula. A Shell, USNM 874887, Klamath Lake, Klamath Co., Oregon. B. Shell, USNM 1006053, 5th spring, Link River, Klamath Co., Oregon. C. Shell, USNM 874365, Fall River, Shasta Co., California. D. Shell, USNM 874369, Baum Lake, Shasta Co., California. E. Outer side of operculum, USNM 874365. F. Inner side of operculum, USNM 874365. G. Radula, USNM 874365. H. Detail of central teeth, USNM 874365. I. Detail of lateral and inner marginal teeth. Scales: A, B = 200 μm; C–E = 1.0 mm; F = 500 μm; G = 100 μm; H, I = 20 μm.


A
B
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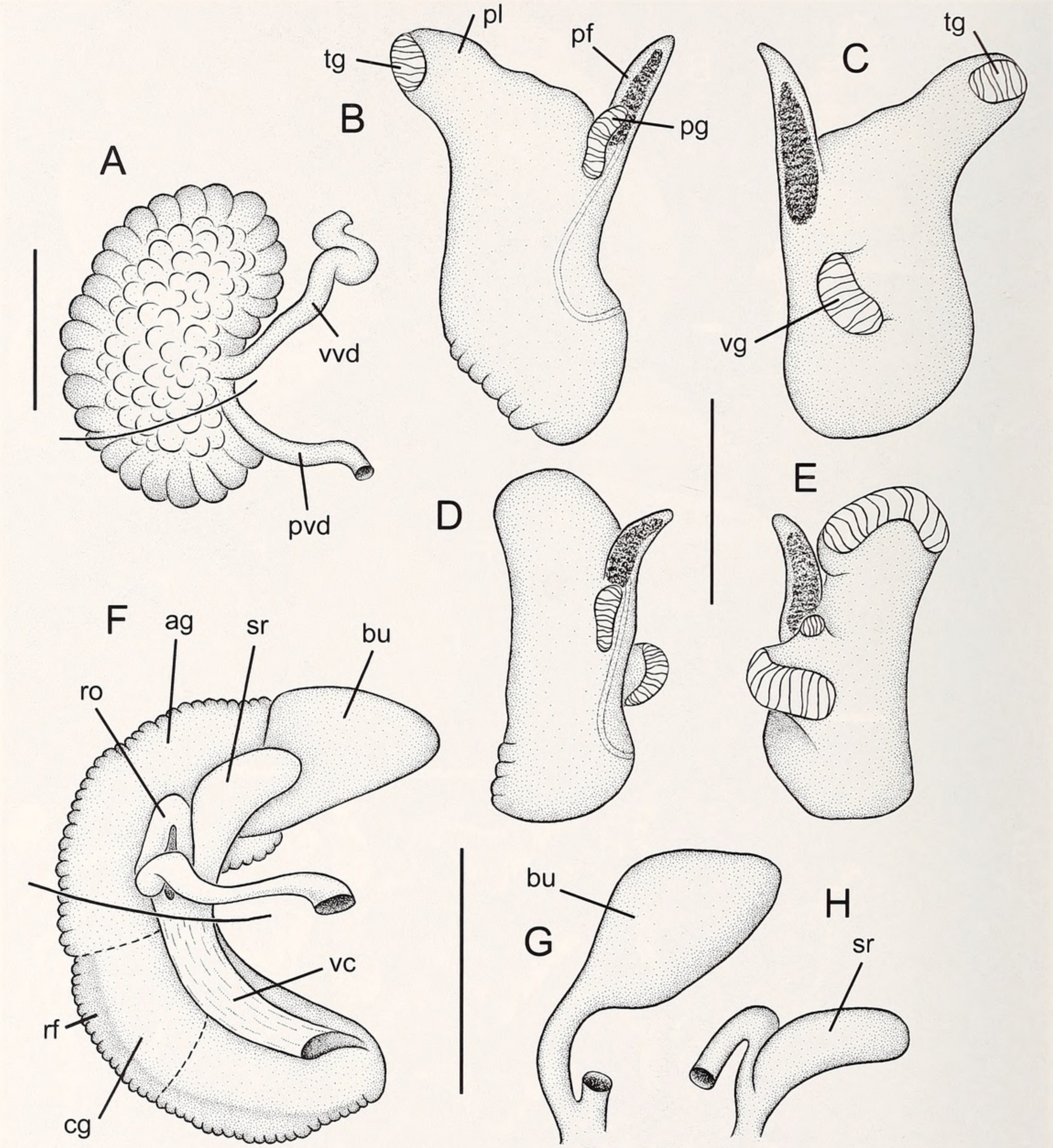

Figure 8. Genitalia of *Pyrgulopsis archimedis*. A. Prostate gland, USNM 874365. B–E. Penes, USNM 874369. F. Oviduct, USNM 874365. G. Bursa copulatrix. H. Seminal receptacle. Scales: A = 250 μm; B–H = 500 μm. ag = albumen gland, bu = bursa copulatrix, cg = capsule gland, pf = penial filament, pl = penial lobe, pvd = pallial vas deferens, rf = rectal furrow, ro = renal oviduct, sr = seminal receptacle; tg = terminal gland, vc = ventral channel of oviduct, vvd = visceral vas deferens.

oblique. Terminal gland well developed, ovate (Figure 8C) to elongate (Figure 8E), transverse to oblique. Penial gland short, slightly narrower than filament, basally positioned on filament. Ventral gland well developed, positioned near inner edge a little behind filament, borne on weak stalk, sometimes accompanied by second, dotlike unit.

Ovary 0.5 whorl, of four simple lobes, abutting pos-

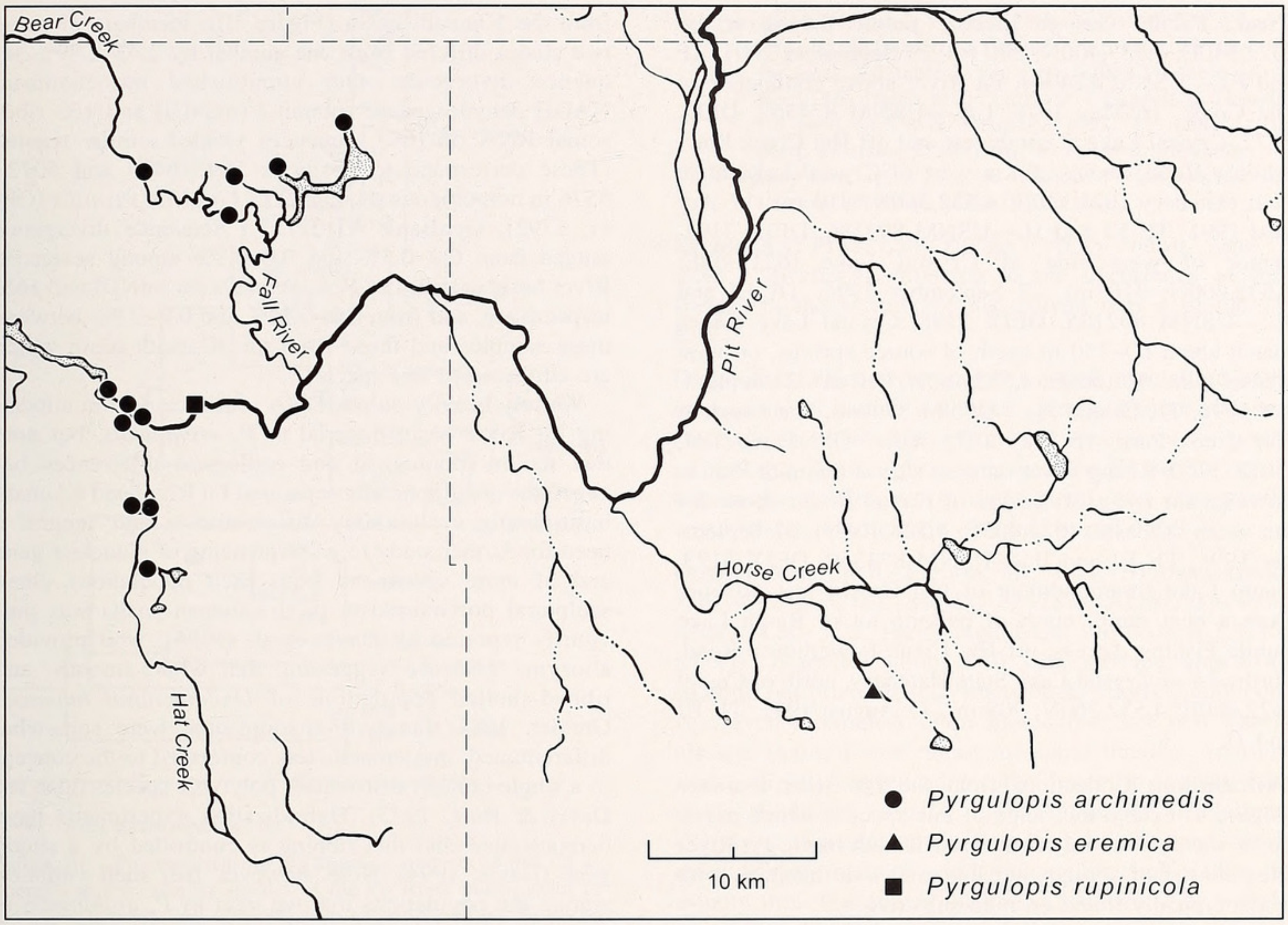

Figure 9. Map showing distribution of *Pyrgulopsis archimedis*, *P. eremica*, and *P.* ***rupinicola*** Hershler, Frest, Liu & Johannes, sp. nov. in the Pit River basin.

terior edge of stomach. Distal female genitalia shown in Figure 8F. Renal oviduct a single, large, horizontal or posterior-oblique loop, kinked anteriorly. Bursa copulatrix (Figure 8G) small or medium-sized, narrow ovate to hatchet-shaped, horizontal or oblique, slightly overlapped by albumen gland. Bursal duct short to slightly longer than bursa copulatrix, narrow, superficial or shallowly embedded in albumen gland. Seminal receptacle (Figure 8H) smaller than bursa copulatrix, finger-shaped, overlapping anterior section of bursa copulatrix, duct short to fairly long. Albumen gland entirely visceral or with very short pallial section; capsule gland a little shorter than albumen gland, composed of two glandular units. Genital opening broad, subterminal.

Material examined: CALIFORNIA. *Shasta County:* USNM 874365, DEIX 3190, Fall River at Caltrout Public Fishing Access Area just east of Island Road bridge, south of The Island, north of Glenburn (626,700E; 4,549,500N; 1007 m), 18 August 1991, TF, EJ and JJ.—USNM 894699, DEIX 3191, *ibid.*, 16 August 2000, TF and EJ.—USNM 1004545, DEIX 3192, spring source, Fall River, 1 September 2001, TF and EJ.—USNM 1004542, DEIX 3193, Big Lake Springs west spring pool, north end of Big Lake, Ahjumawi Lava Springs State Park (633,640E; 4,554,560N; 1007 m), 27 September 2001, TF and EJ.—USNM 892182, DEIX 3194, Lava Creek about 60 m west of Island Road bridge, Lava Creek Ranch, north side of The Island, about 8.4 km north of Glenburn (626,620E; 4,551,960N; 1007 m), 29 September 1996, TF, EJ and JL.—USNM 1004546, DEIX 3195, Ja She Creek on southeast side of bridge of Lava Springs Rim Trail, Ahjumawi Lava Springs State Park (629,680E; 4,552,170N; 1007 m), 26 September 2001, TF and EJ.—USNM 1005052, DEIX 3177, Eastman Lake on northeast side, at Lava Creek Lodge (627,120E; 4,551,740N; 1006 m), 25 July 2002, TF and EJ.—USNM 892183, DEIX 3144, three unnamed springs on point opposite large island in Pit River (northeast side), about 805 m northwest of CA 299 bridge across Pit River (621,680E; 4,537,580N; 840 m), 12 September 1993, TF and EJ.—USNM 1004548, DEIX 3196, Pit River on southeast side of CA 299 bridge near (upstream of) confluence of Hat

Creek, Pacific Gas & Electric public fishing access (622,340E; 4,537,400N; 840 m), 29 September 2001, TF and EJ.—USNM 874044, Pit River above confluence of Hat Creek, 16 May 1978, LA.—USNM 874367, DEIX 3172, Crystal Lake at southwest end off Hat Creek Powerhouse Road, about 1.0 km west of Crystal Lake State Fish Hatchery (621,140E; 4,532,360N; 910 m), 17 August 1991, TF, EJ and JJ.—USNM 892186, DEIX 3197, center of west side of Crystal Lake (621,060E; 4,532,400N; 910 m), 27 September 1996, TF, EJ and JL.—USNM 892185, DEIX 3198, Crystal Lake *Chara* marsh about 60–150 m south of source springs, on west side of lake (621,020E; 4,532,430N; 910 m), 27 September 1996, TF, EJ and JL.—USNM 874046, Hat Creek at Hat Creek Park, 16 May 1978, LA.—USNM 892184, DEIX 3200, Rising River on west side at Schmidt Ranch, downstream (west of) bridge of Cassel Road, about 2.4 km south of Cassel (622,405E; 4,528,400N), 27 September 1996, TF, EJ and JL.—USNM 874369, DEIX 3173, Baum Lake (impoundment of Hat Creek) just offshore from a boat ramp, north of parking lot of Baum Lake Public Fishing Access, off Hat Creek Powerhouse Road, northwest of Crystal Lake State Hatchery, north of Cassel (622,400E; 4,532,260N; 908 m), 17 August 1991, TF, EJ and JJ.

Distribution: Collections from the Pit River drainage (Figure 9) extend the range of this species, which previously was known only from the Klamath basin. Pit River sites consist of springs, streams, and lotic habitats, with snails typically found on mud substrate.

Remarks: The Pit River populations that we assign to *P. archimedis* differ from previously described material of this species which has a narrower shell, shorter body whorl, and nearly flat teleoconch whorls sculptured with a well developed basal keel (Figure 7A). Shells from one of the populations distributed along the Link River (the outlet of Klamath Lake) are somewhat intermediate in appearance in that they lack a peripheral keel, but have rather flat, sometimes basally angulate teleoconch whorls (Figure 7B). Klamath basin populations live in Klamath Lake and springs that are occasionally or permanently submerged under this lake or its outlet (Frest & Johannes, 1998, 2000) while Pit River basin snails inhabit (more typical) springs and streams. Despite these differences, conspecificity is strongly supported by mtCOI data sequences, which indicate that individuals from seven Pit River basin populations are nearly identical to each other (0.0–0.17% divergence; 0–1 bp differences) and to four specimens from the Klamath basin, including one specimen of typical *P. archimedis* (0.17–0.34%; 1–2 bp differences). (We subsequently analyzed a second specimen of typical *P. archimedis* and observed no sequence variation in either this gene or the two discussed below.) These 11 populations formed a strongly supported (100%) clade which was sister to an undescribed species from the Klamath basin (Figure 10); members of these two clades differed from one another by 2.42–2.89% sequence divergence. Our unpublished mitochondrial NADH dehydrogenase subunit I (mtNDI) and 16S ribosomal RNA (mt16S) sequences yielded similar results. (These correspond to positions 5896–6478 and 5072–5576 in homologous sequences of *Littorina saxatilis* [Olivi, 1792]; GenBank AJ132137.) Sequence divergence ranged from 0.0–0.5% and 0.0–0.2% among seven Pit River basin samples of *P. archimedis* for mtNDI and 16S, respectively; and from 0.0–0.34% and 0.0–0.8% between these samples and those from the Klamath basin which are attributed to this species.

We rely heavily on our DNA sequence data in allocating Pit River basin material to *P. archimedis,* but note that the morphological and ecological differences between the geographically separated Pit River and Klamath basin imply evolutionary differentiation and suggest a need for further study (e.g., sequencing of a nuclear gene and of more specimens from each population). Shell sculptural polymorphism in rissooidean snails was previously reported by Davis et al. (1995), who provided allozyme evidence suggesting that while smooth- and ribbed-shelled populations of *Oncomelania hupensis* Gredler, 1881 (family Pomatiopsidae) were somewhat differentiated, they nonetheless conformed to the concept of a single broadly distributed, polytypic species (also see Davis & Ruff, 1973). Hybridization experiments have demonstrated that this ribbing is controlled by a single gene (Davis, 1994). Note, however, that shell variation among the populations that we treat as *P. archimedis* is more complex than in *O. hupensis* (e.g., a basal keel and flattened shell whorls probably represent separate characters; Hershler & Ponder, 1998:5).

The smooth-shelled Pit River populations resemble *P. intermedia* (Tryon, 1865), which was recorded in this watershed by Taylor (1985: 308–309) in a biogeographic paper (although specimen and locality details were not included therein). *Pyrgulopsis intermedia* differs from *P. archimedis* in having a larger penial gland, pigmented coiled oviduct, and a smaller, more ventrally positioned seminal receptacle (Hershler, 1994). Sequences of *P. archimedis* differ from those of *P. intermedia* by 5.95–6.43%. Phylogenetic analysis of mtCOI data indicates that *P. intermedia* is not closely related to *P. archimedis,* but instead is sister to *P. hendersoni* (Pilsbry, 1933), which also lives in southeast Oregon (Figure 10). Our data suggest that *P. intermedia* is not widely distributed but instead is restricted to its type locality area in the Owyhee Desert of southeastern Oregon.

Pyrgulopsis ***rupinicola*** Hershler, Frest, Liu & Johannes, sp. nov.

Sucker Springs pyrg

(Figures 4B, 9–12)

Pyrgulopsis n. sp. 2 [Willow Creek springsnail]. Frest & Johannes, 1995:51 [in part].

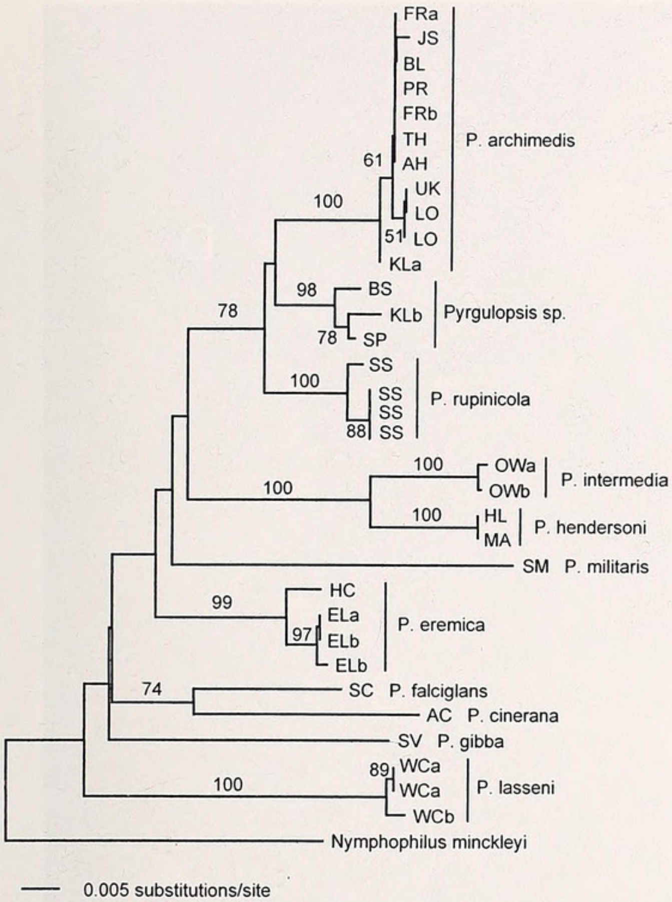

Figure 10. Phylogram from NJ distance analysis of mtCOI sequences of *Pyrgulopsis* species of the Pit River basin, other regional congeners, and one outgroup (*Nymphophilus*). Bootstrap values ≥50% are given. AC = Ash Creek, Pit River basin, Lassen Co., California. AH = Big Lake Springs, Pit River basin, Shasta Co., California. BL = Baum Lake, Pit River basin, Shasta Co., California. BS = Big Springs at Bonanza, Klamath basin, Klamath Co., Oregon. ELa = Troxel Point Spring, Honey-Eagle Lakes basin, Lassen Co., California. ELb = Murrers Upper Meadow, Honey-Eagle Lakes basin, Lassen Co., California. FRa = Fall River (Caltrout Access), Pit River basin, Shasta Co., California. FRb = spring source, Fall River, Pit River basin, Shasta Co., California. HC = spring west of Russell Dairy Spring, Pit River basin, Lassen Co., California. HL = Hughet Spring, Harney-Malheur Lakes, Harney Co., Oregon. JS = Ja She Creek, Pit River basin, Shasta Co., California. KLa = 5th Link River spring, Klamath basin, Klamath Co., Oregon. KLb = 7th Link River spring, Klamath basin, Klamath Co., Oregon. LO = Lost River near Horsefly Irrigation District, Klamath basin, Klamath Co., Oregon. MA = spring at South Fork (Malheur River) Reservoir, middle Snake River basin, Malheur Co., Oregon. OWa = Crooked Creek, Hwy 95 crossing, middle Snake River basin, Malheur Co., Oregon. OWb = Crooked Creek Spring State Wayside, middle Snake River basin, Harney Co., Oregon. PR = Pit River at confluence with Hat Creek, Shasta Co., California. SC = Smokey Charley Spring, Modoc Co., California. SM = spring west of Soldier Meadow Ranch, Black Rock Desert, Humboldt Co., Nevada. SP = Sprague River north of Beatty, Klamath basin, Lake Co., Oregon. SS = Sucker Springs Creek, Shasta Co., California. SV = springs west of Fee Reservoir, Surprise Valley, Lassen Co., California. TH = three unnamed springs, Pit River basin, Shasta Co., California. UK = Upper Klamath Lake at

←

Hagelstein Park outlet, Klamath basin, Klamath Co., Oregon. WCa = Willow Creek west of Lower Mcbride Springs, Lassen Co., California. WCb = Willow Creek downstream from Willow Creek Campground, Lassen Co., California.

Pyrgulopsis n. sp. 2. Frest & Johannes, 1995:70 [in part], F14 (fig. 5) [in part], T1 (table 1) [in part], T3 (table 2) [in part], T7 (table 3) [in part], T10–T31 (table 4) [in part], T61 (table 8) [in part], D11 (Appendix D map) [in part].—Frest & Johannes, 1997. T1 (table 1) [in part], T3 (table 2) [in part], T7 (table 3) [in part].

Pyrgulopsis n. sp. 2 Frest & Johannes, 1995. Frest & Johannes, 1997:T10 (table 10) [in part].

Etymology: From Latin *rupina* ("rocky chasm") and *-cola* ("dweller"), referring to the occurrence of this species in the vicinity of the canyon region of the Pit River.

Diagnosis: Differs from smooth-shelled populations of *P. archimedis* in having a shorter spire and more rounded shell whorls. Also differs from this species anatomically in having a large osphradium, weak rectal furrow on albumen gland, elongate prostate gland, and consistently small sperm pouches and elongate bursal duct.

Description: Shell (Figures 4B, 11A, B) ovate-conic, 3.40–4.92 mm tall, SW/SL 62–78%, AL/SL 39–49%, whorls 4.50–5.25. Periostracum tan. Protoconch 1.5–1.6 whorls, diameter about 440 μm, surface appearing smooth, but often eroded. Teleoconch whorls highly convex, evenly rounded, often shouldered, last two whorls often sculptured with numerous spiral threads. Aperture ovate, slightly angled adapically. Inner lip usually thin, rarely thickened, usually narrowly adnate, sometimes slightly separated from body whorl; thick-lipped specimens having medium width columellar shelf. Outer lip usually thin, sometimes thickened, orthocline or weakly prosocline. Shell narrowly umbilicate.

Outer and inner sides of operculum (Figure 11C, D) smooth.

Radula (Figure 11E) about 820 × 130 μm, with about 50 well formed rows of teeth. Central teeth (Figure 11F) about 38 μm wide; cutting edge slightly concave, central cusps hoelike; outer basal cusp often incomplete. Basal tongue of central teeth convex, sometimes almost straight, base about even with distal ends of lateral margins, lateral margins broad. Central cusp of lateral tooth (Figure 11G) hoelike, outer wing weakly flexed, length 200–240% length of tooth face; basal tongue weakly developed. Inner marginal teeth with enlarged cusp near outer edge.

Animal moderately pigmented. Cephalic tentacles near pale to dark brown (with pale central strip). Snout dark brown or grey. Pallial roof, visceral coil usually dark brown or grey, sometimes more lightly pigmented. Penial filament darkly pigmented.

Efferent ctenidial vessel short. Ctenidial filaments 22–

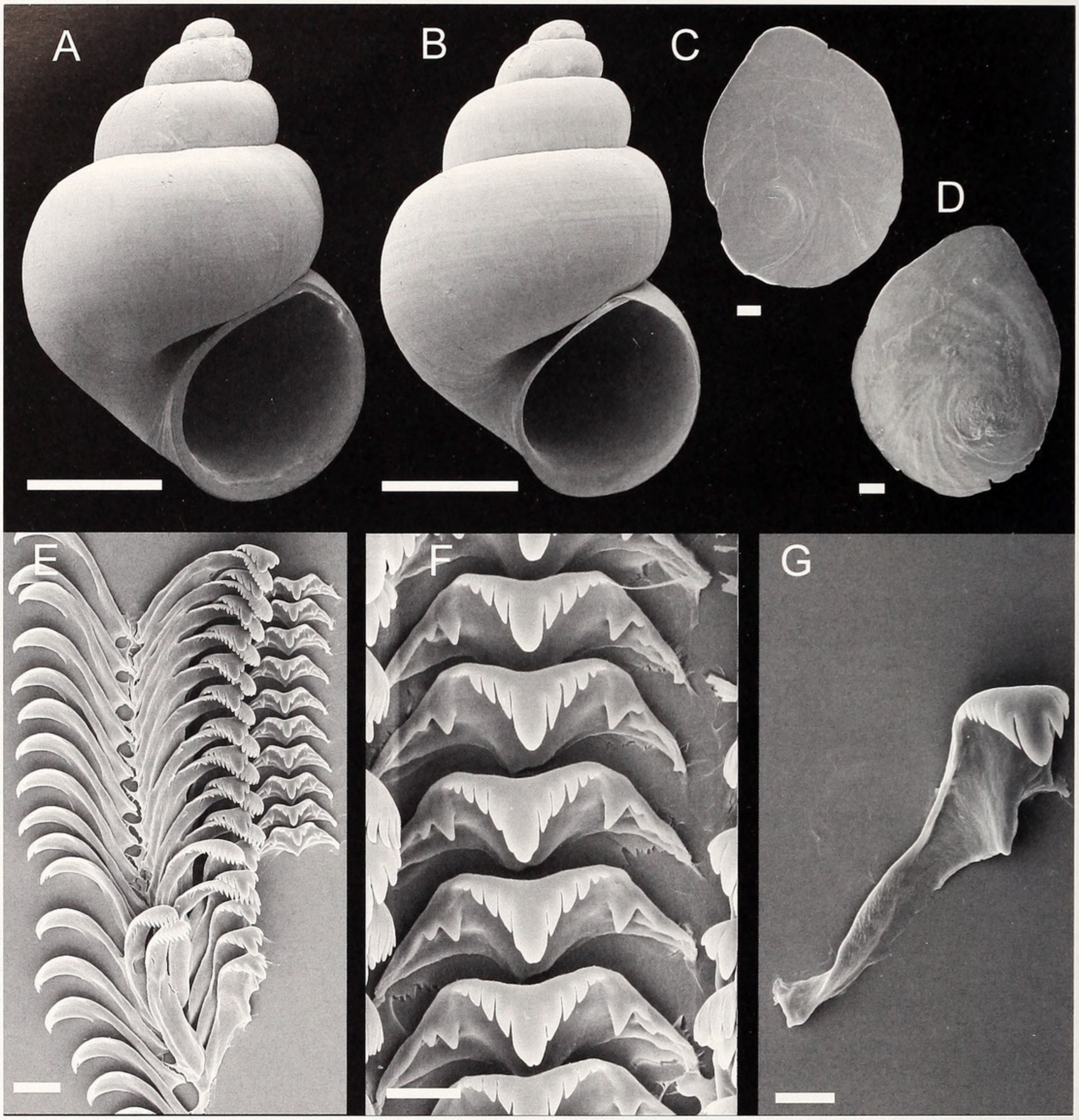

Figure 11. *Pyrgulopsis* ***rupinicola*** Hershler, Frest, Liu & Johannes, sp. nov., shells, operculum, radula, USNM 892187, Sucker Springs Creek, Shasta Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Radula. F. Detail of central teeth. G. Detail of lateral tooth. Scales: A, B = 1.0 mm; C, D = 100 μm; E, F = 20 μm; G = 10 μm.

26, well developed, lateral surfaces ridged. Osphradium large, narrow, positioned posterior to middle of ctenidium. Renal organ with short pallial section. Style sac about as long as remainder of stomach; stomach with large, triangular posterior caecum. Capsule gland with weak rectal furrow.

Testis 2.0 whorls, of numerous compound lobes, broadly overlapping stomach anteriorly. Seminal vesicle consisting of a few coils. Prostate gland (Figure 12A) elongate, with short pallial section. Visceral vas deferens opening a little behind posterior pallial wall; pallial vas deferens opening well behind anterior edge of prostate gland, duct having proximal bend. Penis (Figures 12B, C) small or medium-sized; rectangular base with inner edge weakly folded or smooth; filament short, medium width, tapering, slightly oblique; lobe medium length, almost

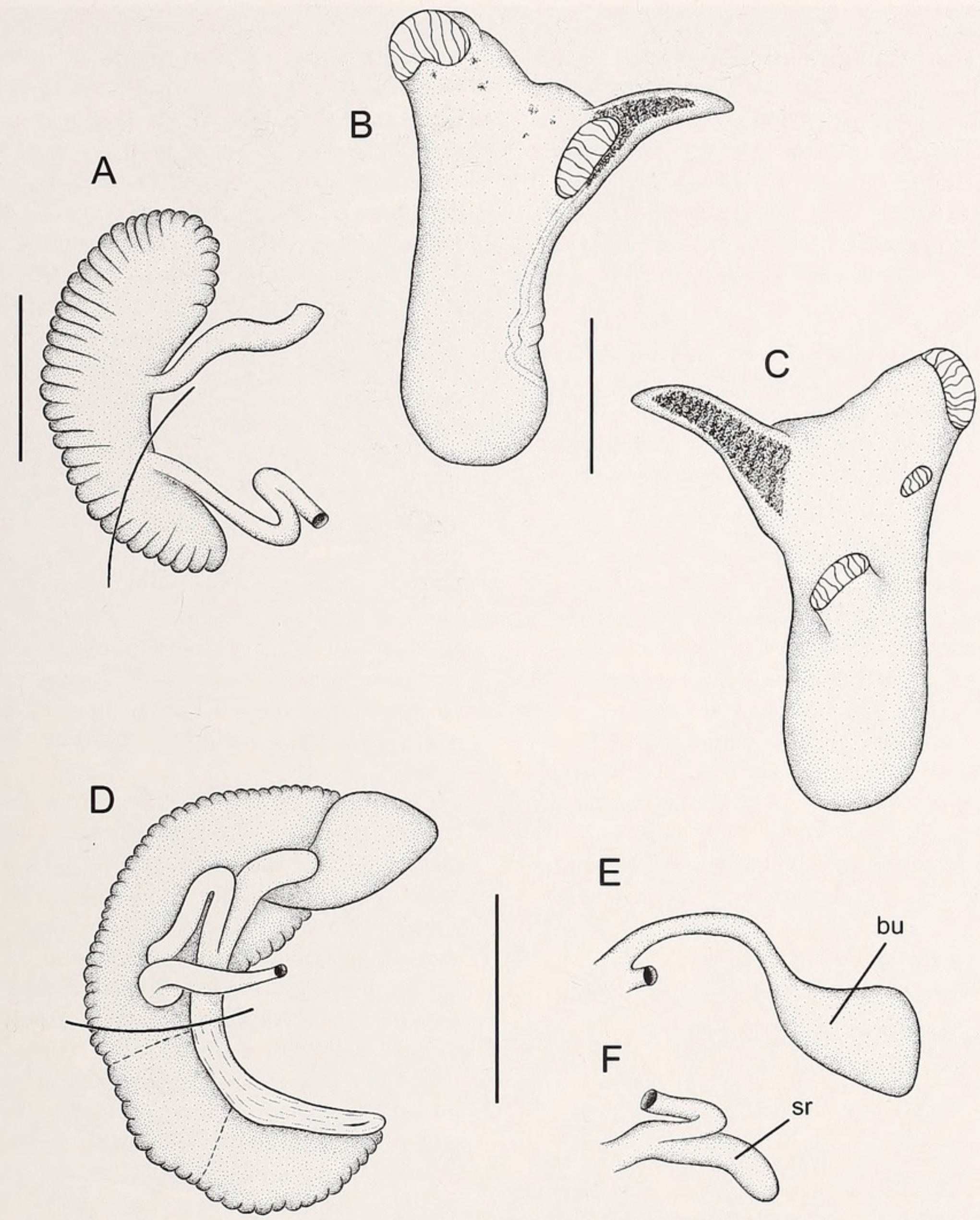

Figure 12. Genitalia of *Pyrgulopsis* ***rupinicola*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 892187. A. Prostate gland. B, C. Penis. D. Oviduct. E. Bursa copulatrix. F. Seminal receptacle. Scales = 250 μm. bu = bursa copulatrix, sr = seminal receptacle.

square, slightly oblique. Terminal gland narrow, weakly curved, transverse. Penial gland about 50% length of filament, slightly narrower than filament, positioned on basal half of filament medially. Ventral gland well developed, medially positioned, stalked, sometimes accompanied by separate glandular dot. Penial duct weakly undulating proximally.

Ovary 1.25 whorl, of compound lobes, overlapping stomach anteriorly. Distal female genitalia shown in Figure 12D. Renal oviduct a single, posterior-oblique or horizontal loop, kinked anteriorly. Bursa copulatrix (Figure 12E) small, ovate or pyriform, horizontal, partly overlapped by albumen gland. Bursal duct longer than bursa copulatrix, narrow, superficial or slightly embedded in albumen gland. Seminal receptacle (Figure 12F) shorter than bursa copulatrix, finger-shaped, positioned near medially on albumen gland, overlapping anterior section of bursa copulatrix. Albumen gland with very short pallial section; capsule gland shorter than albumen gland, entirely pallial, composed of one to two glandular units (as discerned in dissection). Genital opening a small, subterminal slit.

Type material: Holotype (Figure 4B), USNM 892187, from Sucker Springs Creek east of California Fish and Game Pit River Hatchery on northwest side of access road above intake for the fish hatchery, northwest of Pit River, over 1.6 km southwest of Pit 1 Powerhouse (Pacific Gas & Electric), Shasta County, California (625,320E; 4,538,180N; 875 m), 18 October 1994, TF and EJ. Paratypes (from same lot), USNM 1004526, DEIX 3161. Additional paratype series, USNM 1004527, DEIX 3201, collected from same locality on 31 August 2001, TF and EJ.

Distribution: Endemic to a single site in the Pit River basin (Figure 9). Snails were collected from a large, cold spring outflow with slow to moderate current and substrate of mud, silt, sand, fine gravel, scattered cobbles. Snails were most abundant in open, muddy areas of this nasmode.

Remarks: The endemic locality of this snail is in close proximity to populations of morphologically similar *P. archimedis*. However, the distinctiveness of ***P. rupinicola*** is strongly supported by the phylogenetic analysis of mtCOI data, which depicts a strongly supported clade (99%) composed of four specimens of this species positioned outside of (sister to) a clade composed of *P. archimedis* and an undescribed species from the Klamath basin (Figure 10). MtCOI sequences of ***P. rupinicola*** differ from those from 10 populations of *P. archimedis* by 2.55–3.06% and from three populations of the undescribed species by 2.38–3.06%.

Pyrgulopsis eremica Hershler, 1995
Smoke Creek pyrg

(Figures 9, 10, 13, 14)

Pyrgulopsis eremica Hershler, 1995:349–351, 354, fig. 5B, 7–9.

Diagnosis: Distinguished from other regional congeners by its distinctive bladelike penis, which has lobe absent or very reduced and lacks any glandular ornament.

Description (of Pit River basin material): Shell (Figures 13A, B) ovate-conic, 1.58–2.37 mm tall, SW/SL 66–74%, AL/SL 41–45%, whorls, 4.0–4.25. Periostracum tan, very thin. Protoconch 1.25–1.3 whorls, diameter about 0.340 μm, smooth. Teleoconch whorls well rounded, wider above, smooth apart from growth lines. Aperture ovate, slightly angled adapically. Inner lip slightly thickened, narrowly adnate or slightly separated from body whorl. Outer lip slightly thickened. Shell broadly umbilicate.

Outer side of operculum (Figure 13C) with edge of last whorl frilled. Attachment scar margin sometimes slightly thickened along inner edge (Figure 13D).

Radula (Figure 13E) about 460 × 92 μm, with about 50 well-formed rows of teeth. Central teeth (Figure 13F) about 20 μm wide; cutting edge concave, central cusp bi- or trifurcate in anterior tooth rows. Basal tongue of central tooth V-shaped, base even with distal edges of lateral margins. Central cusp of lateral tooth (Figure 13G) hoe-like; outer wing well flexed, length about 200% of tooth face length; basal tongue well developed.

Animal darkly pigmented. Snout, cephalic tentacles dark brown or black; bases of tentacles around eyes pale. Pallial roof, visceral coil dark brown or black.

Efferent ctenidial vessel short. Ctenidial filaments about 16, much wider than tall, lateral surfaces without ridges. Osphradium large, narrow, positioned well posterior to middle of ctenidium. Renal organ without pallial section. Style sac a little shorter than remainder of stomach.

Testis 1.25 whorls, of 8–10 compound lobes, broadly overlapping stomach anteriorly. Seminal vesicle a small mass of loose coils. Prostate gland (Figure 14A) ovate or bean-shaped, with very short pallial section. Visceral vas deferens opening a little behind posterior pallial wall; pallial vas deferens opening well behind anterior edge of prostate gland just in front of pallial wall, duct with proximal bend or twist. Squat base of penis (Figure 14B) folded along inner edge; filament longer than base; lobe absent or a very short, broad swelling. Penial duct fairly broad.

Ovary 0.75 whorl, of three to four simple lobes, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 14C. Renal oviduct a small, posterior-oblique loop strongly kinked anteriorly. Bursa copulatrix (Figure 14D) small, ovate or club-shaped, horizontal, partly overlapped by albumen gland. Bursal duct about as long as bursa copulatrix, narrow or medium width, expanded distally, usually shallowly embedded in albumen gland along entire length. Seminal receptacle (Figure 14E) short, finger-shaped, sometimes folded, positioned near ventral edge of albumen gland, anterior to or slightly overlapping bursa copulatrix. Albumen gland with large pallial section; capsule gland longer than albumen gland, entirely pallial, composed of single glandular unit. Genital opening a short, subterminal slit.

Material examined: CALIFORNIA. *Lassen County:* USNM 1004529, DEIX 3160, from spring on north side of FS 22, west of Russell Dairy Spring (666,010E; 4,521,420N), 24 September 2001, TF & EJ.

Distribution: Collected from a single site in the lower Pit River basin (Figure 9). This species is otherwise restricted to the geographically proximal northern Lahontan and Black Rock Desert regions (Hershler, 1995, fig. 6). The Pit River locality is a cold spring with mud and cobble bottom.

Remarks: The Pit River basin population closely conforms morphologically to *P. eremica* in both shell and anatomical features, although it differs in having a more

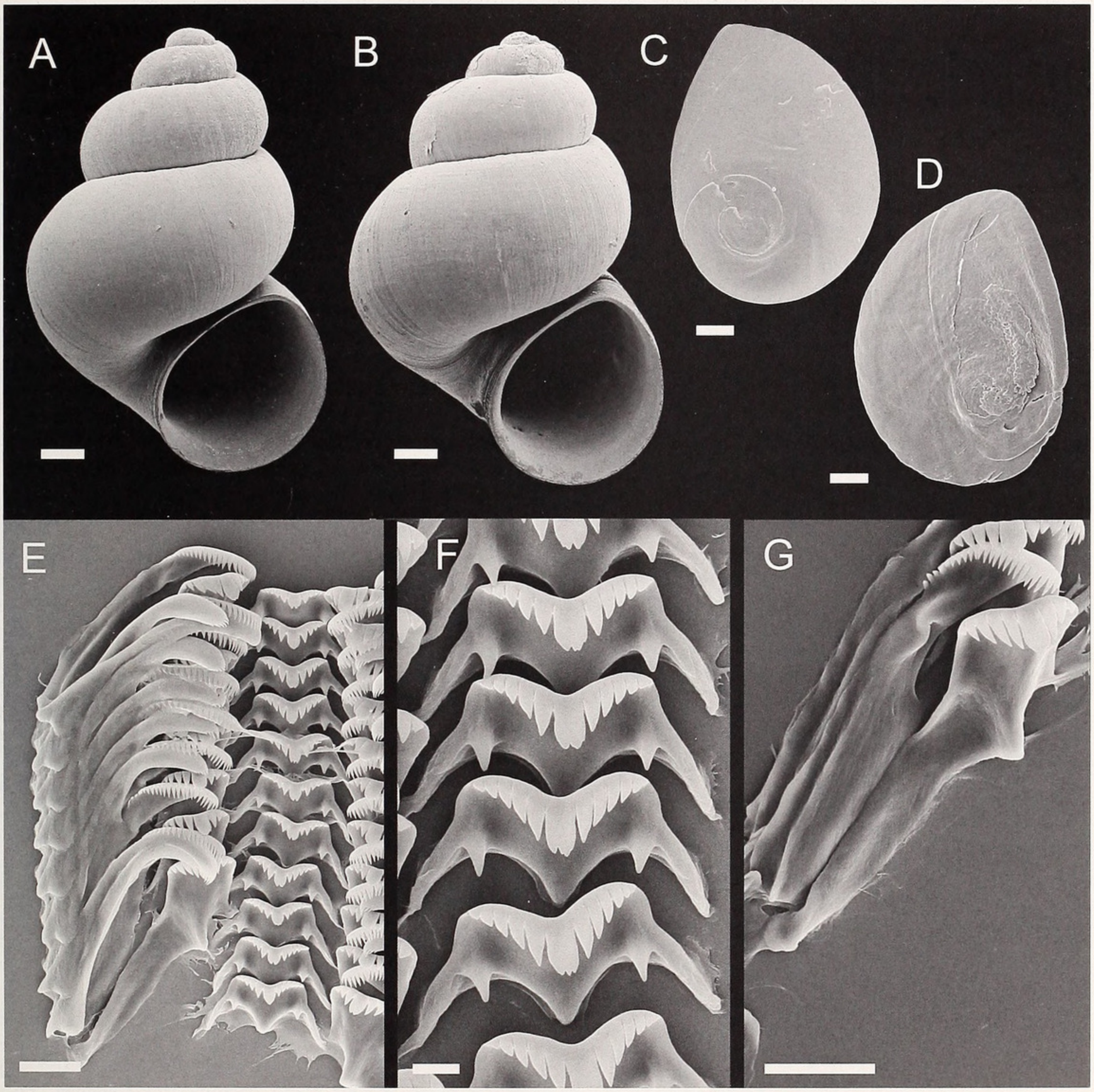

Figure 13. *Pyrgulopsis eremica,* shells, operculum, radula, USNM 1004529, spring west of Russell Dairy Spring, Lassen Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Radula. F. Detail of central teeth. G. Details of lateral and inner marginal teeth. Scales: A, B = 200 μm; C, D = 100 μm; E, G = 10 μm; F = 3 μm.

posterior position of the osphradium, and an entirely visceral position of renal organ. Snails from this population also are slightly differentiated from three sequences (two localities) of *P. eremica* from the Eagle Lake basin based on mtCOI sequence divergences (0.85–1.02%), suggesting that this geographically isolated population warrants recognition as an evolutionarily significant unit within this species. These sequences collectively form a well supported (95%) clade (Figure 10).

Pyrgulopsis ***falciglans*** Hershler, Frest, Liu & Johannes, sp. nov.
Likely pyrg

(Figures 4C, 10, 15–17)

Pyrgulopsis n. sp. 2 [Willow Creek springsnail]. Frest & Johannes, 1995:51 [in part].

Pyrgulopsis n. sp. 2. Frest & Johannes, 1995:70 [in part], F14 (fig. 5) [in part], T1 (table 1) [in part], T3 (table 2)

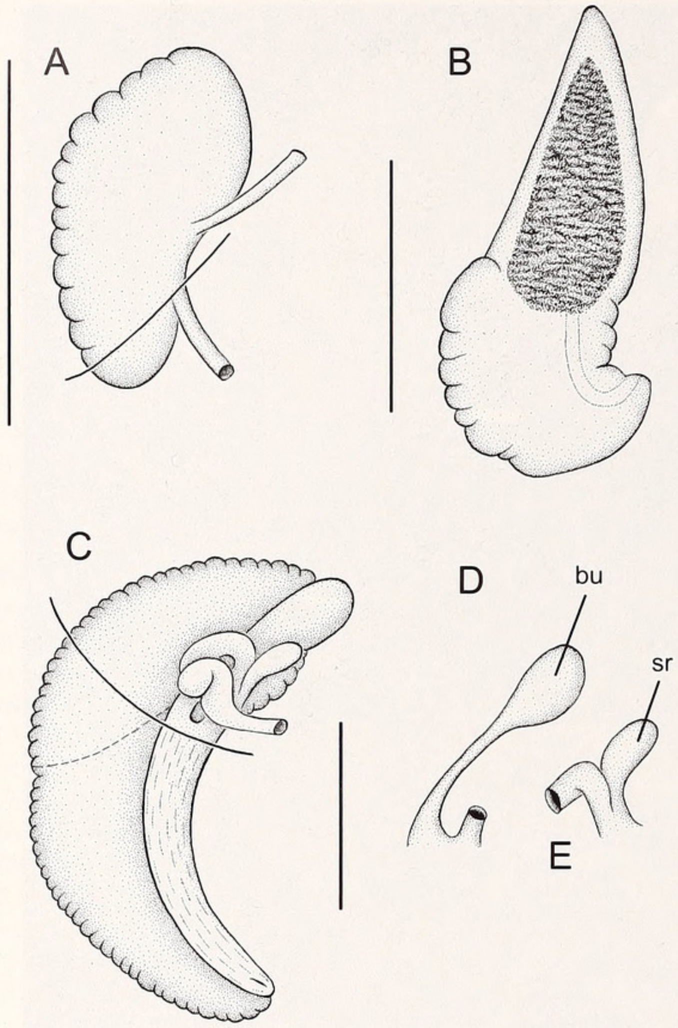

Figure 14. Genitalia of *Pyrgulopsis eremica,* USNM 1004529. A. Prostate gland. B. Penis. C. Oviduct. D. Bursa copulatrix. E. Seminal receptacle. Scales: A, C–E = 250 μm; B = 200 μm. bu = bursa copulatrix, sr = seminal receptacle.

[in part], T7 (table 3) [in part], T10–T31 (table 4) [in part], T61 (table 8) [in part], D11 (Appendix D map) [in part].—Frest & Johannes, 1997. T1 (table 1) [in part], T3 (table 2) [in part], T7 (table 3) [in part].

Pyrgulopsis n. sp. 2 Frest & Johannes, 1995. Frest & Johannes, 1997:T10 (table 10) [in part].

Etymology: Latin *falcis* ("sickle"), referring to the shape of the prominent penial gland of this species. Common name refers to distribution of snail in proximity of town of Likely, California.

Diagnosis: Distinguished from other regional congeners by its unique pattern of penial ornament, consisting of a weakly developed terminal gland and a sickle-shaped penial gland.

Description: Shell (Figures 4C, 15A, B) ovate-conic, 1.95–2.71 mm tall, SW/SL 66–73%, AL/SL 39–43%, whorls, 4.25–4.75. Periostracum brown. Protoconch slightly tilted, 1.3–1.4 whorls, diameter about 330 μm, surface wrinkled with sculpture more pronounced near apex. Teleoconch whorls convex, wider above, narrowly shouldered, weak spiral threads sometimes present. Aperture ovate, slightly angled adapically. Inner lip slightly thickened, complete, usually slightly separated from body whorl. Outer lip thin, prosocline. Shell narrowly umbilicate.

Outer side of operculum with edge of last whorl weakly frilled (Figure 15C). Attachment scar margin slightly thickened along inner edge (Figure 15D).

Radula (Figure 15E) about 460 × 60 μm, with about 50 well formed rows of teeth. Central teeth (Figure 15F) about 25 μm wide; cutting edge weakly concave, central cusp distally rounded or pointed. Basal tongue of central tooth broadly rounded, base shorter than lateral margins, lateral margins narrow. Central cusp of lateral tooth (Figure 15G) broad, hoelike; outer wing weakly to moderately flexed, length about 200% of tooth face length, basal tongue well developed. Inner marginal teeth with broad wing on inner side. Outer marginal teeth with rectangular wing on outer side.

Animal darkly pigmented. Snout, cephalic tentacles light grey to black. Pallial roof, visceral coil grey-black. Penial filament black, pigment granules scattered on base.

Efferent ctenidial vessel short. Ctenidial filaments about 20, well developed, lateral surfaces with ridges. Osphradium short, narrow, centrally positioned along ctenidium. Renal organ with small pallial section. Style sac about as long as remainder of stomach; stomach with small posterior caecum.

Testis 1.5 whorls, of numerous compound lobes, overlapping stomach anteriorly. Seminal vesicle a small, tightly coiled mass. Prostate gland (Figure 16A) bean-shaped, with short pallial section. Visceral vas deferens opening to prostate gland a little behind posterior pallial wall; pallial vas deferens opening behind anterior edge of prostate just in front of pallial wall, duct with proximal bend. Penis (Figures 16B, C) medium-sized; base rectangular, folded along inner edge; filament slightly shorter than base, fairly broad, distally pointed, slightly oblique; lobe short, narrow, hemispherical, horizontal. Terminal gland transverse or oblique, narrow, positioned largely on ventral surface. Penial gland narrow, sickle-shaped, positioned along inner edge of base of filament.

Ovary 1.0 whorl, of five to six simple stalked lobes, filling less than 50% of digestive gland behind stomach, slightly overlapping stomach anteriorly. Distal female genitalia shown in Figure 16D. Renal oviduct a single, horizontal, weakly pigmented loop, slightly kinked proximally. Bursa copulatrix (Figure 16E) medium-sized, ovate or subglobular, horizontal, partly overlapped by albumen gland. Bursal duct about as long as bursa copulatrix, medium width, positioned on surface of albumen gland. Seminal receptacle (Figure 16F) considerably shorter than bursa copulatrix, finger-shaped, slightly folded, positioned near ventral edge of albumen gland just

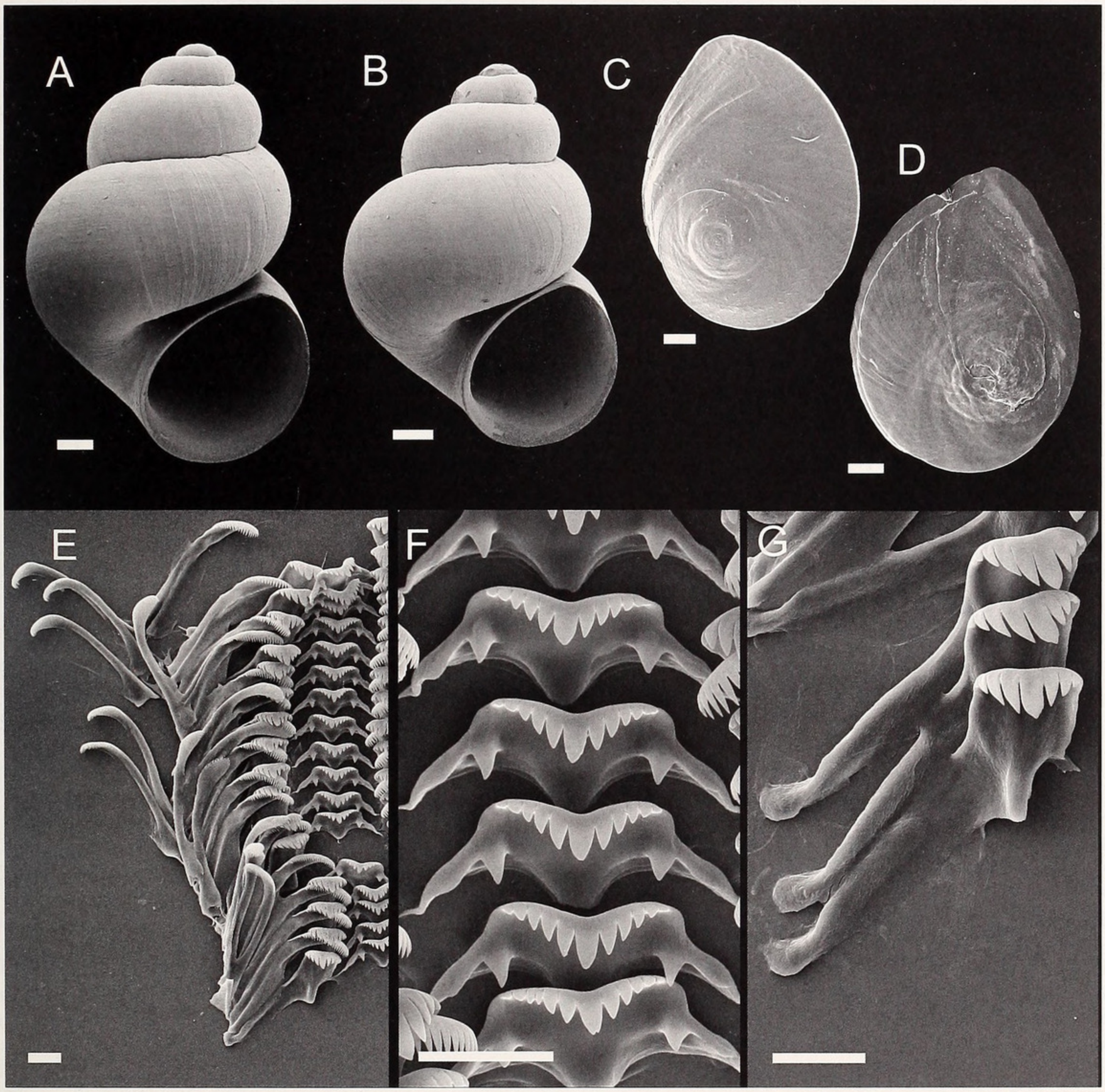

Figure 15. *Pyrgulopsis* ***falciglans*** Hershler, Frest, Liu & Johannes, sp. nov., shells, operculum, radula, USNM 1004606, spring southeast of Smokey Charley Spring, Modoc Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Radula. F. Detail of central teeth. G. Details of lateral teeth. Scales: A, B = 200 µm; C, D = 100 µm; E, G = 10 µm; F = 3 µm.

anterior to bursa copulatrix. Albumen gland with short pallial section; capsule gland shorter than albumen gland, entirely pallial, composed of single glandular unit. Genital opening broad, terminal.

Type material: Holotype (Figure 4C), USNM 1004605, from cold spring about 0.40 km southeast of Smokey Charley Spring and 0.32 km west of Modoc County 63, at source next to homestead cabin, Modoc County, California (705,090 E; 4,566,300 N; 1366 m), 19 September 2001, TF and EJ. Paratypes (from same lot), USNM 1004606, DEIX 3155.

Other material examined: CALIFORNIA. *Modoc County:* USNM 1004604, DEIX 3202, Smokey Charley Spring at source on hillside, about 0.40 km west of Modoc County 63 (704,900E; 4,560,570N; 1366 m), 19 September 2001, TF and EJ.

Distribution: Restricted to two closely adjacent springs along the South Fork Pit River (Figure 17).

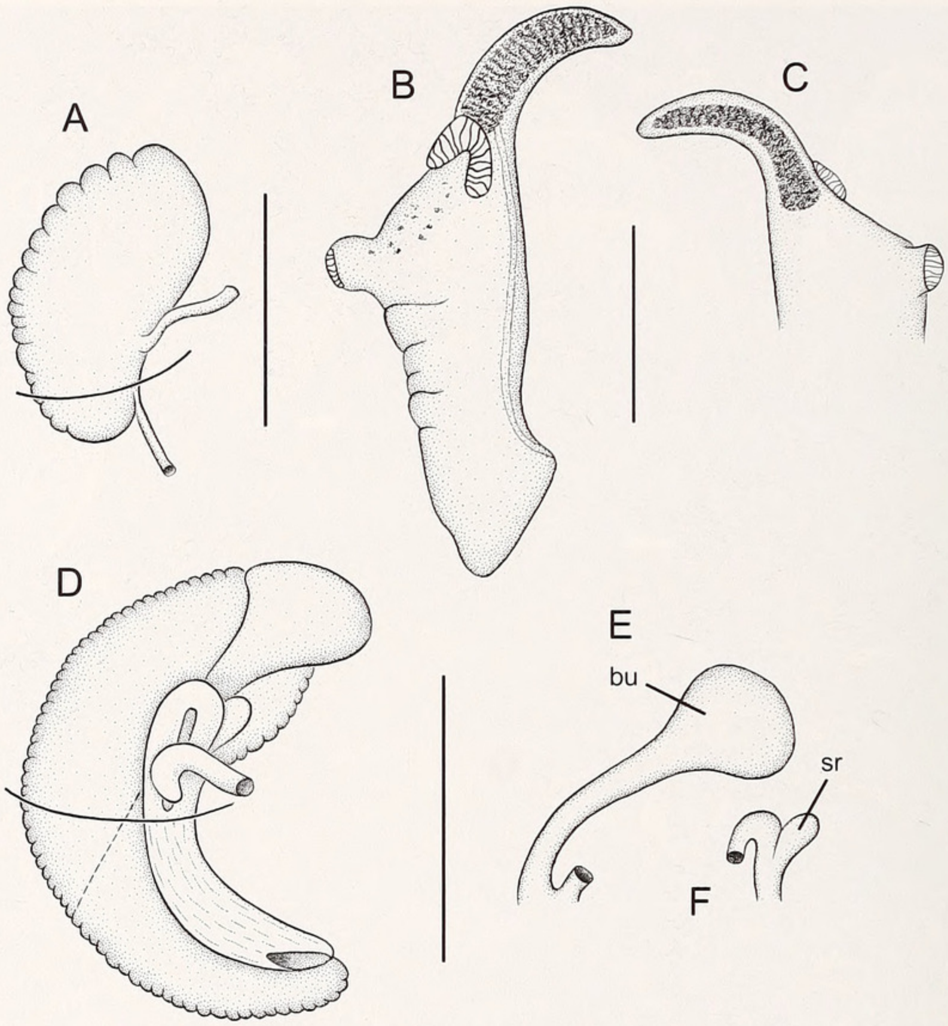

Figure 16. Genitalia of *Pyrgulopsis* ***falciglans*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004606. A. Prostate gland. B, C. Penis. D. Oviduct. E. Bursa copulatrix. F. Seminal receptacle. Scales: A–C = 250 μm; D–F = 500 μm. bu = bursa copulatrix, sr = seminal receptacle.

Remarks: This snail is not closely similar morphologically to other regional congeners. MtCOI sequences provide moderate support (73%) for a sister relationship with another species from the upper Pit River basin, *P.* ***cinerana*** (Figure 10). Sequence divergence between these two species is 4.6%.

Pyrgulopsis **cinerana** Hershler, Frest, Liu & Johannes, sp. nov. Ash Valley pyrg

(Figures 4D, 10, 17–19)

Etymology: From Latin *cineris* ("ashes"), referring to distribution of this snail in Ash Valley.

Diagnosis: Distinguished from other regional congeners by its broad, strongly shouldered shell and pattern of penial ornament consisting of a small terminal gland.

Description: Shell (Figures 4D, 18A, B) subglobose to ovate-conic, 2.48–4.85 mm tall, SW/SL 63–76%, AL/SL 41–48%, whorls 4.1–5.0. Periostracum thick, brown. Protoconch 1.3 whorls, diameter about 380 μm, appearing smooth but somewhat eroded. Teleoconch whorls convex, shoulders well developed, usually broad; evenly rounded. Aperture ovate, narrower adapically. Inner lip rarely thickened, complete, slightly separated in larger specimens, otherwise narrowly adnate. Outer lip usually thin, orthocline or weakly prosocline, sometimes weakly sinuate. Shell umbilicate.

Outer side of operculum with edge of last 0.5 whorl frilled (Figure 18C). Attachment scar margin sometimes slightly thickened near nucleus (Figure 18D).

Radula (Figure 18E) about 650 × 120 μm, with about 30–34 well formed rows of teeth. Central teeth (Figure 18F) about 33 μm wide; cutting edge weakly concave, central cusp rounded or pointed. Basal tongue of central tooth broadly rounded, base even with distal ends of lateral margins, lateral margins broad. Central cusp of lat-

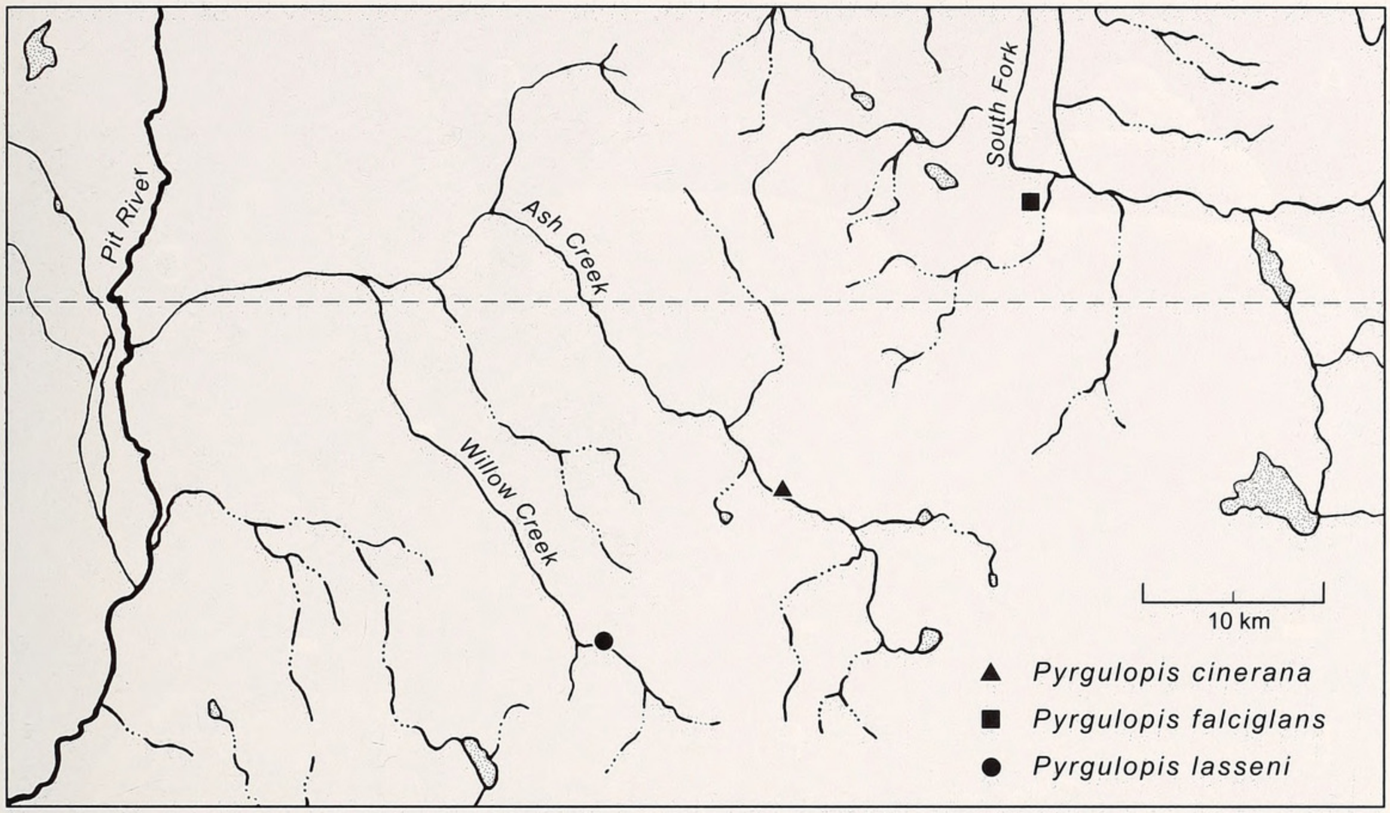

Figure 17. Map showing distribution of *Pyrgulopsis* ***cinerana*** Hershler, Frest, Liu & Johannes, sp. nov., *P.* ***falciglans*** Hershler, Frest, Liu & Johannes, sp. nov., and *P.* ***lasseni*** Hershler, Frest, Liu & Johannes, sp. nov. in the Pit River basin.

eral tooth (Figure 18G) large, hoelike; outer wing weakly flexed, length about 170–190% of tooth face length; basal tongue well developed. Inner marginal teeth with rectangular wing on inner side; outer marginal teeth with similar wing on outer side.

Animal darkly pigmented. Snout, cephalic tentacles light grey to near uniform black, tentacle pigmentation lighter centrally. Pallial roof, visceral coil dark brown to almost uniform black. Penial filament darkly pigmented along proximal 66% of length, distal portion of base pigmented with scattered granules.

Efferent ctenidial vessel very short. Ctenidial filaments about 27, well developed, lateral surfaces having ridges. Osphradium medium-sized, narrow, positioned slightly posterior to center of ctenidium. Renal organ with medium pallial section. Style sac about as long as remainder of stomach; stomach with medium-sized posterior caecum. Capsule gland with rectal furrow.

Testis 2.0 whorls, of numerous compound lobes, broadly overlapping stomach anteriorly. Seminal vesicle of a few loose coils. Prostate gland (Figure 19A) bean-shaped, with very short pallial section. Visceral vas deferens opening to prostate gland just behind posterior pallial wall; pallial vas deferens opening a little behind anterior edge of prostate gland just in front of pallial wall, duct with prominent proximal bend. Penis (Figures 19B, C) medium-sized; base elongate-rectangular, inner edge smooth or weakly undulating; filament short, narrow, tapering, slightly oblique; lobe short, rectangular but slightly tapering, horizontal or slightly oblique. Terminal gland small, transverse, ovate, positioned largely on ventral edge.

Ovary 1.0 whorl, a single mass of numerous oocytes, filling more than 50% of digestive gland behind stomach, partly overlapping stomach anteriorly. Distal female genitalia shown in Figure 19D. Renal oviduct a single posterior-oblique or horizontal coil, slightly kinked proximally. Bursa copulatrix (Figure 19E) small, subglobular or ovate, horizontal, partly overlapped by albumen gland. Bursal duct longer than bursa copulatrix, fairly broad but narrowing distally, shallowly embedded in albumen gland. Seminal receptacle (Figure 19F) very small, fingerlike, straight, positioned near ventral edge of albumen gland well anterior to bursa copulatrix. Albumen gland with short pallial section; capsule gland much shorter than albumen gland, entirely pallial, composed of one to two glandular units. Genital opening broad, terminal.

Type material: Holotype (Figure 4D), USNM 1004543, nearest spring east of Ash Valley Road (Modoc County 527) crossing of Ash Creek, north side of creek, JJJ Ranch, Lassen County, California (692,180E, 4,551,090N; 1536 m), 23 July 2002, TF, EJ and SR. Paratypes (from same sample), USNM 1004544, DEIX 3181.

Other material examined: CALIFORNIA. *Lassen*

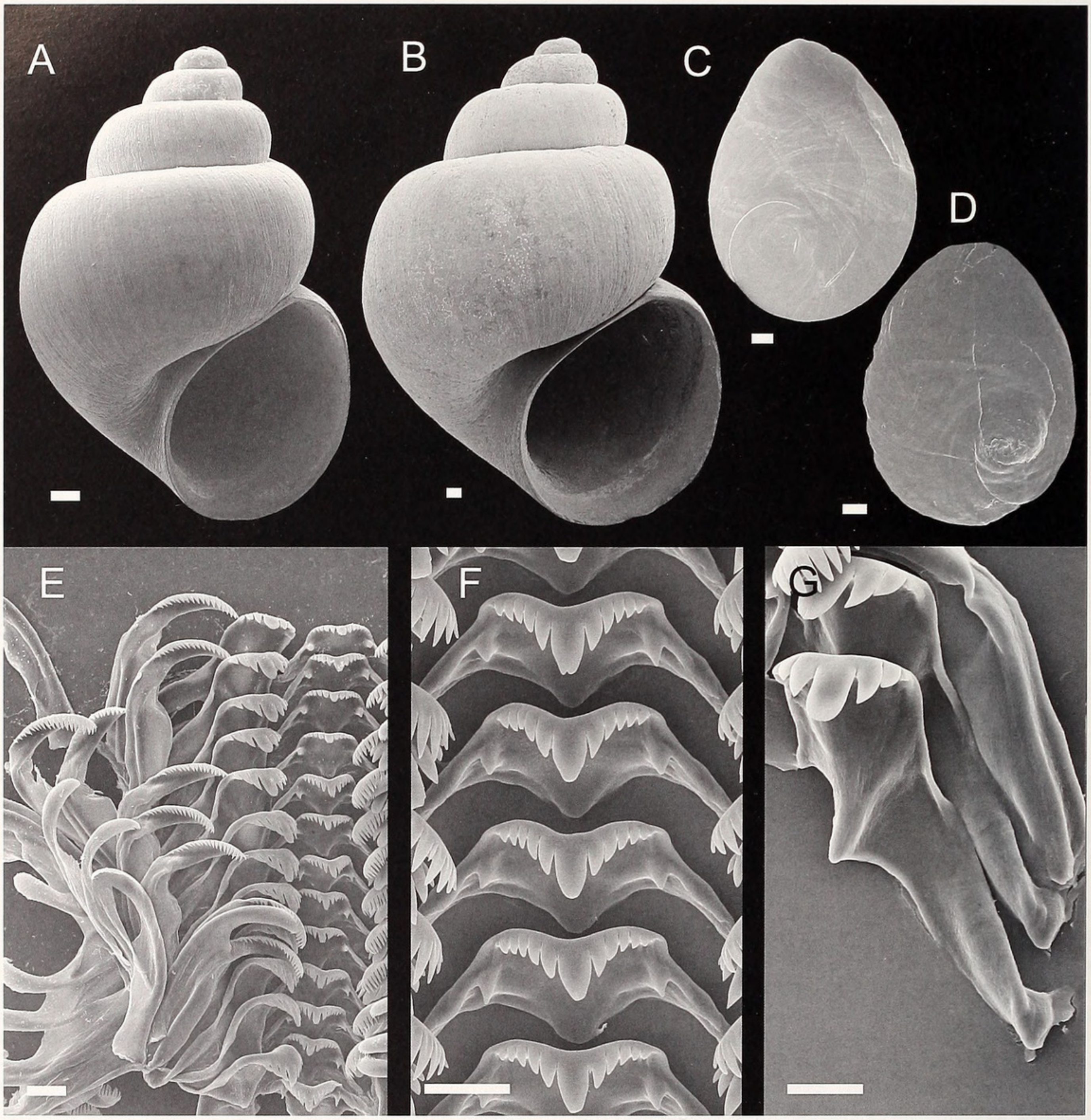

Figure 18. *Pyrgulopsis* ***cinerana*** Hershler, Frest, Liu & Johannes, sp. nov., shells operculum, radula, USNM 1004544, spring east of Ash Valley Road, Lassen Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Radula. F. Detail of central teeth. G. Detail of lateral teeth. Scales: A, B = 200 μm; C, D = 100 μm; E–G = 10 μm.

County: USNM 1004525, DEIX 3205, Ash Creek on west side of Ash Valley Road (Modoc County 527), Ash Valley (692,080 E; 4,551,080 N; 1535 m), 19 September 2001, TF and EJ.—USNM 1004524, DEIX 3178, *ibid.*, 23 July 2002, TF and EJ.—USNM 1004541, DEIX 3184, Ash Creek south culvert channel on west side of Ash Valley Road (Modoc County 527), Crown D Ranch (692,060E; 4,551,010N; 1535 m), 23 July 2002, TF, EJ and SR.—USNM 1004547, DEIX 3182, Second closest spring east of Ash Valley Road (Modoc County 527) crossing of Ash Creek, north side of creek, JJJ Ranch (692,240E; 4,551,080N; 1535 m), 23 July 2002, TF, EJ and SR.—USNM 1004528, DEIX 3180, DEIX 3183, farthest spring east of Ash Valley Road (Modoc County 527)

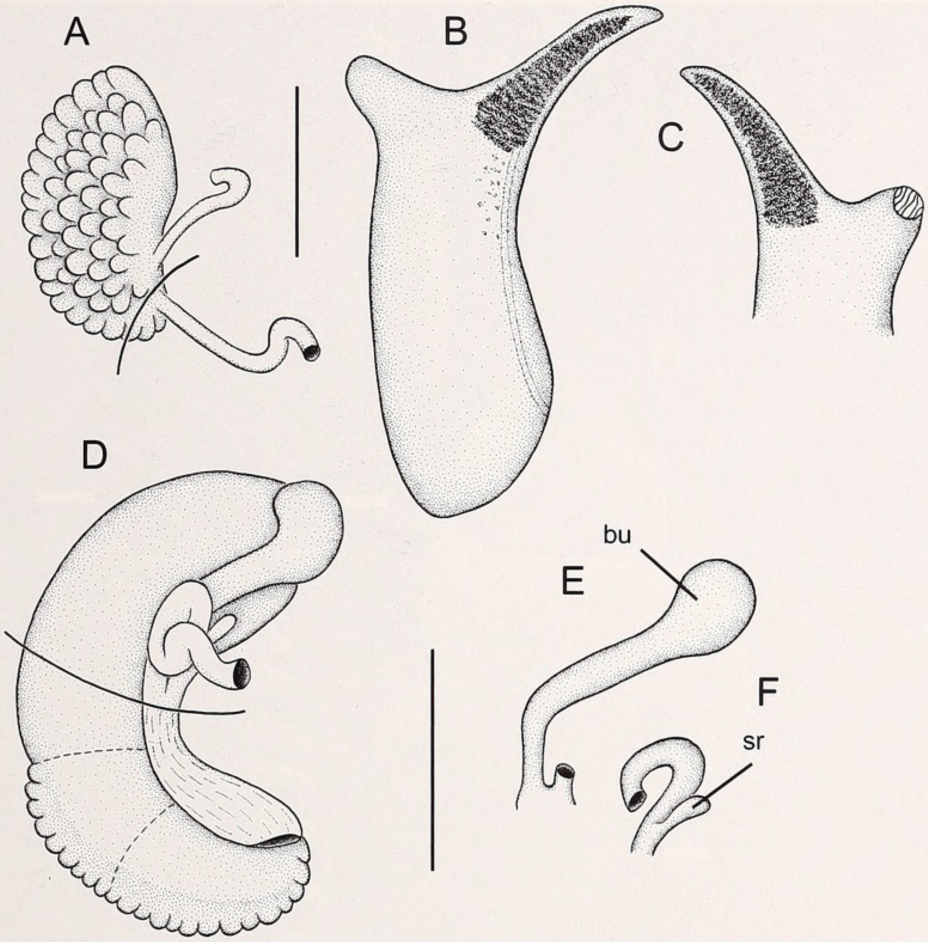

Figure 19. Genitalia of *Pyrgulopsis* ***cinerana*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004528. A. Prostate gland. B, C. Penis. D. Oviduct. E. Bursa copulatrix. F. Seminal receptacle. Scales: A–C = 250 μm; D–F = 500 μm. bu = bursa copulatrix, sr = seminal receptacle.

crossing of Ash Creek, north side of creek, JJJ Ranch (692,310E; 4,551,060N; 1536 m), 23 July 2002, TF, EJ and SR.—USNM 1005152, DEIX 3203, Chisolm Spring on south side of Ash Creek, west side of Ash Valley Road (Modoc County 527), Crown D Ranch (692,030E; 4,550,990N; 1536 m), 23 July 2002, TF and EJ.

Distribution: Cold springs associated with upper Ash Creek, Ash Valley, upper Pit River basin (Figure 17). These snails live in small helocrenes.

Pyrgulopsis ***lasseni*** Hershler, Frest, Liu & Johannes, sp. nov. Willow Creek pyrg

(Figures 4E, 10, 17, 20, 21)

Pyrgulopsis n. sp. [Willow Creek springsnail]. Frest & Johannes, 1994:13.

Pyrgulopsis n. sp. Frest & Johannes, 1994:18, 19, 33 (fig. 2), 36 (table 1), 38 (table 2), 41 (Table 3), 43–48 (table 4), 56 (table 8).

Pyrgulopsis n. sp. 2 [Willow Creek springsnail]. Frest & Johannes, 1995:51 [in part].

Pyrgulopsis n. sp. 2. Frest & Johannes, 1995:70, F14 (fig. 5), T1 (table 1), T3 (table 2), T7 (table 3), T10–T31 (table 4), T61 (table 8), D11 (Appendix D map).—Frest & Johannes, 1997:T1 (Table 1) [in part], T3 (table 2) [in part], T7 (table 3) [in part].

Pyrgulopsis n. sp. 2 Frest & Johannes, 1995. Frest & Johannes, 1997: T10 (table 10) [in part].

Etymology: For Peter Lassen, intrepid early explorer of northeastern California.

Diagnosis: Differs from other regional congeners in its strongly angled shell aperture, frequently solute body whorl, and pattern of penial ornament, consisting of the combination of well developed penial and terminal glands and absence of a ventral gland.

Description: Shell (Figures 4E, 20A, B) broad to narrow conic, 1.52–2.81 mm tall, SW/SL 61–73%, AL/SL 39–47%, whorls 3.5–5.0. Periostracum tan or brown. Protoconch 1.25–1.30 whorls, diameter about 310 μm, surface smooth. Teleoconch whorls weakly convex, narrowly shouldered, weak spiral threads sometimes present. Aperture ovate, strongly angled above. Inner lip usually

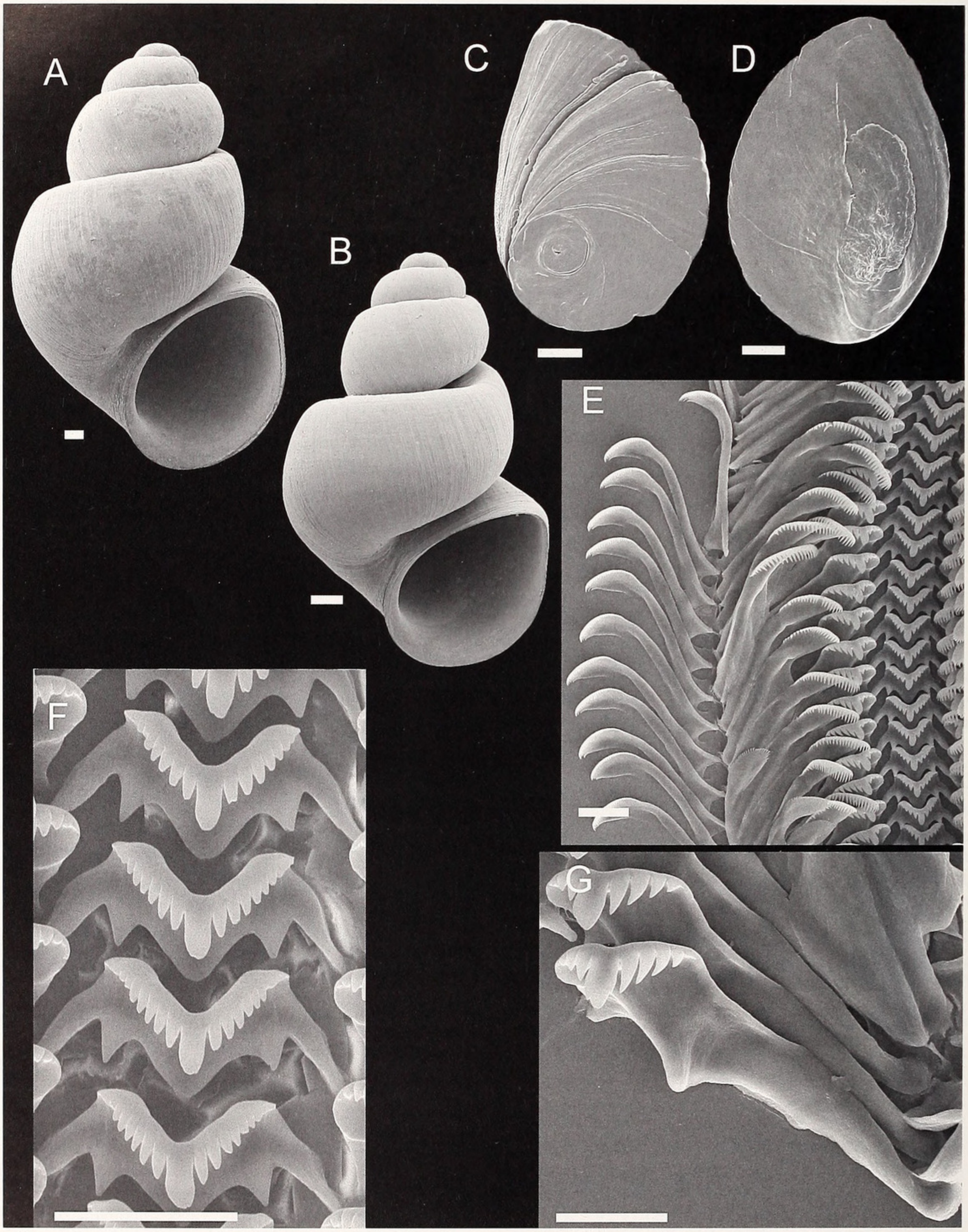

Figure 20. *Pyrgulopsis* ***lasseni*** Hershler, Frest, Liu & Johannes, sp. nov., shells, operculum, radula, USNM 1004533, Willow Creek, Lassen Co., California. A, B. Shells. C. Outer side of operculum. D. Inner side of operculum. E. Radula. F. Detail of central teeth. G. Detail of lateral teeth. Scales: A = 200 μm; B–D = 100 μm; E–G = 10 μm.

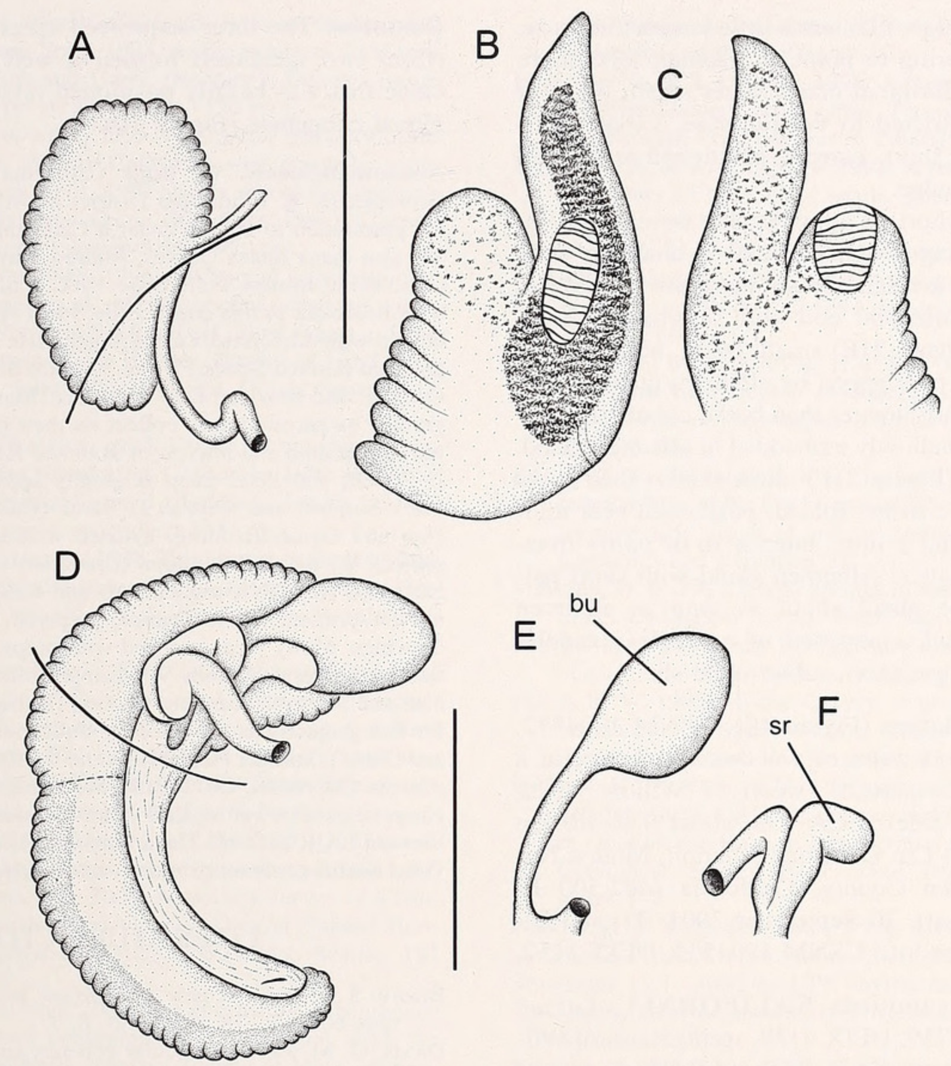

Figure 21. Genitalia of *Pyrgulopsis* ***lasseni*** Hershler, Frest, Liu & Johannes, sp. nov., USNM 1004533. A. Prostate gland. B, C. Penis. D. Oviduct. E. Bursa copulatrix. F. Seminal receptacle. Scales = 250 μm. bu = bursa copulatrix, sr = seminal receptacle.

slightly thickened, rarely thick, last 0.25 whorl to entire body whorl often disjunct. Outer lip thin, orthocline or weakly prosocline. Umbilicus rimate or chinklike.

Outer side of operculum shown in Figure 20C. Attachment scar margin thickened along inner edge near nucleus (Figure 20D).

Radula (Figure 20E) about 460 × 82 μm, with about 65 well formed rows of teeth. Central teeth (Figure 20F) about 17 μm wide; cutting edge strongly indented, central cusp hoelike or spoonlike. Basal tongue of central tooth broadly angled, almost V-shaped, base about even with distal edges of lateral margins, lateral margins narrow. Central cusp of lateral tooth (Figure 20G) hoelike; outer wing weakly flexed, length about 200% of tooth face length; basal tongue well developed.

Animal darkly pigmented. Cephalic tentacles grey or black, pigment darker along midline. Pallial roof, visceral coil black dorsally, ventral surface pale or grey. Penial filament black along proximal 66% of length; penial lobe sometimes darkly pigmented, but less so than filament.

Efferent ctenidial vessel short. Ctenidial filaments 11–13, narrow, lateral surfaces without ridges. Osphradium large (> 50% of length of ctenidium), narrow, posteriorly positioned along ctenidium. Renal organ, pericardium with short pallial sections. Style sac about as long as remainder of stomach; stomach with small posterior caecum. Rectum producing distinct furrow on capsule gland.

Testis 1.25–1.50 whorls, of compound lobes, broadly overlapping stomach anteriorly. Seminal vesicle a large mass of loose coils filling about 0.5 whorl. Prostate gland (Figure 21A) bean-shaped, with short pallial section. Visceral vas deferens opening to prostate gland just behind posterior pallial wall; pallial vas deferens opening near middle of prostate gland (sometimes on left side rather than along ventral edge) at pallial wall, duct with proximal bend. Penis (Figures 21B, C) small; base square, folded along inner edge; filament a little longer than base, medium width, tapering to point, horizontal; lobe short, square, horizontal. Terminal gland rather small, ovate or circular, usually restricted to ventral edge, variably oriented. Penial gland short, narrow, positioned at base of filament near inner edge.

Ovary 0.5–0.75 whorl, of a few weakly developed simple lobes, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 21D. Renal oviduct a small, horizontal coil with a proximal kink. Bursa copulatrix (Figure 21E) small, ovate, horizontal or oblique, about 50% overlapped by albumen gland. Bursa duct as long or slightly longer than bursa copulatrix, narrow, superficial or shallowly embedded in albumen gland. Seminal receptacle (Figure 21F) much shorter than bursa copulatrix, narrow or ovate, folded, positioned near midline of albumen gland a little anterior to or partly overlapping bursa copulatrix. Albumen gland with short pallial section; capsule gland about as long as albumen gland, entirely pallial, composed of a single glandular unit. Genital opening a short, subterminal slit.

Type material: Holotype (Figure 4E), USNM 1004532, Willow Creek on both sides of wooden foot bridge at a picnic area just downstream (west) of Willow Creek Campground, north side of CA 139, about 0.16 rd. km west of Hayden Hill Cut Off Road junction, Modoc National Forest, Lassen County, California (682,500 E; 4,542,280 N; 1521 m), 20 September 2001, TF and EJ. Paratypes (from same lot), USNM 1004533, DEIX 3152.

Other material examined: CALIFORNIA. *Lassen County:* USNM 883759, DEIX 3149, spring north of Willow Creek and north of CA 139, about 0.49 km east of Willow Creek Campground, Modoc National Forest, Lassen County, California (683,090E; 4,542,320N; 1543 m), 10 September 1993, TF and EJ.—USNM 1004530, Willow Creek just upstream (south) of Hayden Hill Road (Lassen County Road 534, FS37N42) junction, along west side of CA 139, mouth of Hayden Canyon, Modoc National Forest, Lassen County, California (680,680E; 4,542,990N; 1487 m), 20 September 2001, TF and EJ.—USNM 1004531, DEIX 3151, Willow Creek at lower end (west) of Lower McBride Springs, northeast side of CA 139, about 0.64 rd. km east of Hayden Hill Cut Off Road junction, Modoc National Forest, Lassen County, California (682,030E; 4,542,680N; 1503 m), 20 September 2001, TF and EJ.

Distribution: Upper reaches of Willow Creek and an associated warm nasmode, upper Pit River basin (Figure 17). This species lives in an area of recent geyser activity. Snails were collected from exposed travertine in a warm (20–22°C) nasmode (composed of about seven springs) and from cobble, mud, and rooted macrophytes in the adjoining, cooler Willow Creek. Snails were most abundant in Willow Creek.

Remarks: The three sequenced specimens of *P. **lasseni*** (from two localities) formed a well supported (100%) clade that was basally positioned relative to all other regional congeners (Figure 10).

Acknowledgments. We thank California State Parks District Ecologist H. W. Elliott and District Superintendent K. V. Foley for permission to collect under a California State Parks permit. We also thank Susan Groves, Andrew Scotti, and Andrew Urlie (MacArthur-Burney Falls State Park, California) for assistance with fieldwork in this area. Leslie Steidl (California State Parks) helped with Ahjumawi Lava Springs State Park fieldwork. Stewart Reid (United States Fish & Wildlife Service, Klamath Falls, Oregon) also provided field assistance. Many private landowners granted us permission to collect on their property. In particular, the cooperation and interest of Tom and Kathy DeForest (Crown D Ranch) and Peter Stent is greatly appreciated. Richard Lis, Mark Stopher, and Stephen L. Turek (California Department of Fish and Game, Redding) assisted with various stages of this project. We thank Tom Quinn (University of Denver) for sharing lab space (for DNA sequencing) and Kayla Clift for providing mtNDI primers. Karie Darrow prepared shell and anatomical drawings, Molly Ryan assisted with preparation of the distributional maps, and Yolanda Villacampa collected shell and radular data and prepared scanning electron micrographs. Fiscal support for this project was provided by California Department of Fish and Game (Contract FG2016R1) and the Cantara Trustee Council (Grants C0010010, C0110013). We thank Martin Haase and an anonymous reviewer for their helpful criticism of the manuscript. Richard Lis (California Department of Fish and Game) also provided useful comments on draft manuscript.

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