A Review of the North American Freshwater Snail Genus *Pyrgulopsis* (Hydrobiidae)

ROBERT HERSHLER

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ABSTRACT

Hershler, Robert. A Review of the North American Freshwater Snail Genus *Pyrgulopsis* (Hydrobiidae). *Smithsonian Contributions to Zoology*, 554, 115 pages, 53 figures, 2 tables, 1994.—The Recent nominal species belonging to the hydrobiid snail genus *Pyrgulopsis* Call and Pilsbry, 1886, are reviewed. *Pyrgulopsis* is a large group of 65 Recent species inhabiting diverse inland waters of North America. This genus is distinguished from other members of the subfamily Nymphophilinae by the combination of small size; generally simple, ovate-conic shell; and penis ornamented with relatively few glands.

Members of this genus have a globose to elongate-conic shell with near smooth to strongly punctate protoconch, smooth or rarely carinate teleoconch, and simple apertural lip often loosened from the body whorl. The taenioglossate radula features a central radular tooth with well-developed lateral angles, narrow basal process, and, usually, a single pair of basal cusps. The operculum generally is paucispiral with eccentric nucleus. The ventral operculum is notable for its variably thickened attachment scar margin and central callus. The caecal chamber of the stomach is variably developed. Animal pigmentation is variable, sometimes including dark stripes along the mantle. Cephalic tentacle ciliation generally is weak. The gonads usually are of simple lobes, and sometimes overlap the stomach. The prostate gland usually has a small pallial section and the vas deferens usually exits from the gland sub-terminally. The penis is generally large and distally bifid; with a terminal filament bearing the vas deferens, and accessory lobe (sometimes absent). The penis surface is very weakly ciliated and is variably ornamented with dorsal and ventral glands. The albumen gland usually has a small pallial section. The capsule gland is almost always bipartite, and contains a well-developed ventral channel. The genital aperture is either simple or opens to an anterior vestibule. The coiled oviduct usually is simple, and joins the bursal duct just behind, to well anterior to, the pallial wall. Both bursa copulatrix and seminal receptacle usually are present, the former being larger and often at least partly posterior to the albumen gland. The bursal duct is of variable size and shape, and often embedded, sometimes deeply so, within the albumen gland. The seminal receptacle is usually just behind the coiled oviduct and typically has a short duct. Females are oviparous, and lay single, hemispherical egg capsules.

A cladistic analysis of relationships among 60 species was conducted using *Nymphophilus* Taylor as single outgroup. Monophyly of *Pyrgulopsis* was supported by 15 character-state transformations, including six non-homoplasious synapomorphies. Four large clades were recognized: a group of nine species distributed in Mississippi River drainage and other waters to the east, a group of six species from southern Nevada and southeastern Arizona; a group of 10 species from eastern California, northern Arizona, and Snake River drainage; and a group of 18 species scattered throughout the West. The remaining 17 western taxa included four species occupying basal positions on the cladogram, a poorly resolved group of eight species, and two small clades consisting of two species from northern Arizona; and three widely disjunct species from northern Mexico, Snake River drainage, and southeastern California.

The following genera herein are added to the list of junior subjective synonyms of *Pyrgulopsis: Savaginius* Taylor, 1966a, *Apachecoccus* Taylor, 1987, and *Yaquicoccus* Taylor, 1987. *Fluminicola avernalis carinifera* Pilsbry, 1935, is elevated to full species status herein —this and fifteen other species are newly allocated to *Pyrgulopsis*. *Fontelicella pinetorum* Taylor, 1987, is a junior subjective synonym of *Pyrgulopsis kolobensis* (Taylor, 1987); and *Pyrgulopsis wabashensis* Hinkley, 1908a, is a junior subjective synonym of *Pyrgulopsis scalariformis* (Wolf, 1869). A new name, *Pyrgulopsis bryantwalkeri*, is proposed for *Fluminicola nevadensis* Walker, 1916 (not *Pyrgula nevadensis* Stearns, 1883).

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Contents

A Review of the North American Freshwater Snail Genus *Pyrgulopsis* (Hydrobiidae)

Robert Hershler

Introduction

Prosobranch snails of the genus *Pyrgulopsis* are widespread in the United States (extending into southern Canada) and northern Mexico, where they occur in lakes, springs, seeps, marshes, and diverse lotic waters. These small (about 1–8 mm shell length) animals often are found in densities exceeding >1000/m^2 (for example see Noel, 1954), comprising a prominent element of the benthic epifauna. *Pyrgulopsis*, as recognized herein, is the second most diverse genus of North American freshwater gastropods (the pleurocerid *Elimia* ranking as first) and includes many narrowly localized species. Numerous undescribed species also are known, and large physiographic regions still await exploration by those interested in these easily overlooked organisms. These snails are beginning to draw the attention of wildlife agencies and groups seeking to preserve and manage North American aquatic ecosystems: over half (52%) of the *Pyrgulopsis* species recognized herein currently are candidates for addition to the Federal List of Threatened and Endangered Species (USDI, 1991a) and three snails (from New Mexico and Idaho) recently were listed as endangered (USDI, 1991b, 1992, 1993). At least three members of the genus have gone extinct since their original description during the early part of this century.

Call and Pilsbry (1886) erected *Pyrgulopsis* for four species from the United States having a small, fairly elongate shell whose single basal carina distinguished the group from multicarinate European *Pyrgula*. Ancey (1888) early reviewed *Pyrgulopsis*, and described 13 new Central American taxa, all of which were later transferred to the hydrobiid subfamily Cochliopinae, genus *Pyrgophorus*, by Hershler and Thompson (1992). Wenz (1926) also provided an early review of fossil species assigned to this genus. The concept of this group varied little since that time (even recent workers such as Burch (1982) and Taylor (1985) used *Pyrgulopsis* in the original sense) until Hershler and Thompson (1987) redefined the genus in a broader fashion based on penial (rather than shell) characters. They consequently placed five other North American genus-level taxa in synonomy with our group, which as a result swelled to 24 Recent species. The relationship between *Pyrgulopsis* (sensu Hershler and Thompson) and two similar genera recently described from the West (Taylor, 1987) has not been addressed in the literature.

The scope and content of *Pyrgulopsis* remain incompletely known because the anatomy of relatively few North American freshwater hydrobiids has been studied—this includes some of the species allocated to the genus, on a provisional basis, by Hershler and Thompson (1987) and other, mostly western hydrobiids with simple, ovate-conic shells that were early described as members of "catch-all" genera such as *Amnicola* and *Paludestrina*.

There has been no comprehensive review of the species of *Pyrgulopsis* since that of Ancey (1888), at which time only two of the 65 species considered valid herein had been described. The present review is intended to provide nomenclatural stability for *Pyrgulopsis* and its Recent species, and is based on evaluation of available type and other museum material as well as anatomical study of almost all Recent North American hydrobiid snails potentially referable to the genus.

Pyrgulopsis species usually are readily distinguished from one another by combinations of qualitative characters, and thus I have not gathered and analyzed quantitative morphological data as part of this broad review. Note, however, that analysis of such data has been previously pursued with good results in studies of local *Pyrgulopsis* faunas (Hershler and Sada, 1987; Taylor, 1987; Hershler and Landye, 1988), and use of this and other means of comparing populations (i.e., biochemical) will be necessary to better resolve the lingering species-level problems in this group.

Only nominate taxa are included in this review, as my intention is to provide herein a framework for future studies describing new species. Eastern American *Pyrgulopsis* were included despite the fact that most of them recently were well

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reviewed (as *Marstonia*) by Thompson (1969, 1977), for sake of completeness and to add additional morphological details where necessary. Recent species incorrectly assigned to *Pyrgulopsis* in the literature are listed, for the reader's convenience, in Appendix 1. Fossils largely have been excluded from consideration owing to the difficulty of assigning empty shells to hydrobiid genera, but those species described as or previously allocated to *Pyrgulopsis* (or junior synonyms thereof) are listed in Appendix 2.

MATERIALS AND METHODS.—*Pyrgulopsis* species were characterized based on examination of type and other dry museum material (principally USNM) as well as anatomical study of topotypes and/or other specimens as available. Anatomical material used to characterize species are listed in the "Material Examined" sections. Institutional repositories of examined specimens are indicated by the following abbreviations:

ANSP	Academy of Natural Sciences, Philadelphia
CAS	California Academy of Sciences, San Francisco
FSM	Florida Museum of Natural History, Gainesville
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
SBMNH	Santa Barbara Museum of Natural History
UCM	University of Colorado Museum, Boulder
UIMNH	University of Illinois at Urbana-Champaign Museum of Natural History
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UTEP	University of Texas at El Paso

Anatomical study was of alcohol-preserved snails that had been relaxed with menthol crystals and fixed in dilute (4%) formalin. Examination of live animals, while especially desireable for accurate description of head-foot features such as size and shape of cephalic tentacles and snout, was limited given the broad scope of this project and logistical difficulties inherent in setting up field laboratories. Alcohol material, when properly prepared, nevertheless is rich in information as hydrobiid viscera fixes well and head-foot features relax in a near life-like state.

Inorganic shell material was removed by soaking specimens in Bouin's Solution or hydrochloric acid. Animals were dissected in dilute Bouin's Solution. Specimens were first examined entire, after which the visceral coil was separated from the proximal portion of the animal by tearing between the anterior edge of style sac and kidney/pericardium. The pallial roof then was torn from the head-foot, flattened out, and pinned. The female glandular oviduct and associated structures were examined from the left side. In cases where alcohol material was not available, study was of dried animals resuscitated by soaking in Bouin's Solution. Anatomical illustrations were prepared from camera lucida drawings of pinned out specimens.

Three or four specimens of each sex (topotypes, when available) were usually dissected for each species, although additional series were added when species were widely distributed or geographically variable in shell features.

Shell, opercula, and radulae were cleansed in commercial bleach (CLOROX), rinsed in water, and then studied and photographed using a Hitachi S-570 Scanning Electron Microscope (SEM). With the exception of a few species, study of radula was limited to the central radular teeth owing to the perceived lack of variation in lateral and marginal teeth. Animals were dried using a Denton DCP-1 Critical Point Drier and studied with SEM to ascertain ciliation patterns on dorsal cephalic tentacles and penis. Whole mounts of penes were prepared by staining in hematoxylin followed by dehydration, clearing, and mounting in balsam.

The following morphologic features were routinely scrutinized while preparing species descriptions:

1. Shell: size, shape, thickness, number of whorls; protoconch, teleoconch sculpture; whorl convexity; adapical shoulder of whorls; aperture size, shape; thickness of inner shell lip, relationship between lip and body whorl; inclination of outer lip relative to coiling axis; umbilical development; periostracal thickness, color.

2. Operculum: shape, thickness, color, number of whorls, location of nucleus, frilling of whorl outlines on dorsal surface, thickening of (ventral) attachment scar margin, development of attachment region callus.

3. Digestive system: indentation of dorsal edge of central radular tooth; number of lateral cusps; size (relative to lateral cusps), shape of central cusp; number, size, shape, position of basal cusp(s); robustness of dorsal support of basal cusps; depth of basal sockets; width of basal process; thickness of lateral angles; prominence of neck along outer edge of lateral angles; size, shape of posterior caecum of stomach.

4. Animal pigmentation: color, intensity, pattern of pigment on cephalic tentacles, snout, neck, foot, opercular lobe, pallial roof, visceral coil.

5. Pallial cavity: length of ctenidium (relative to pallial cavity); height, width, number of ctenidial filaments; size, position of osphradium (relative to ctenidial axis); bulge of kidney into pallial cavity (relative to total length of kidney); nature of kidney opening to pallial cavity.

6. Male animal: total whorls; testis whorls, position; size, shape, thickness of prostate gland; extent of pallial portion of prostate gland; coiling of vas deferens in pallial roof; size, shape of penis, penial filament, distal lobe; orientation of lobe, filament; number, size, position, orientation, fusion of penial glands; pigmentation of penial filament.

7. Female animal: total whorls; ovary whorls, position; extent of pallial portion of albumen gland (relative to total length of gland); relative lengths of albumen, capsule glands; number of distinct capsule gland regions; size, shape, position of capsule gland opening; development of vestibule extending anteriorly from capsule gland opening along pallial roof;

position of coiled oviduct; number, size, orientation of oviduct coils; shape, length and width (relative to length and width of albumen gland), position of bursa copulatrix; origin, length, and width (relative to bursa copulatrix) of bursal duct; extent to which bursal duct is embedded in albumen gland; position of junction between bursal duct and oviduct; shape, length (relative to length of bursa copulatrix), position (relative to bursa copulatrix, coiled oviduct, albumen gland) of seminal receptacle; length of seminal receptacle duct.

Shell, operculum, central radular teeth, and penis are illustrated for each species, while other aspects of morphology are shown only for a subset of the above. Diagnoses focus on features of shell and penis that permit identification of material. Given that phylogenetic relationships among *Pyrgulopsis* species are poorly resolved, I have not adopted any formal sub-generic groupings and taxa are treated alphabetically, with the exception of separating the well-differentiated eastern and western faunas. For elucidation of phylogenetic relationships among *Pyrgulopsis* species, a data set of 64 characters (24 multistate) for 60 Recent species, comprising all those for which anatomical material was available, plus one outgroup was analyzed using HENNIG86 (Farris, 1988). The type species of *Nymphophilus* was selected as the outgroup based on its suspected close relationship with *Pyrgulopsis* (see generic description). For this preliminary analysis, character states found in the outgroup were uniformly treated as plesiomorphic despite the likelihood that *Nymphophilus* has various derived morphological attributes associated with its unusual habitat of large limnocrene springs. Descriptions of characters and their states are in Table 1. Character states for each species are in Appendix 3. Inapplicable characters and those for which data were not available were scored as missing ("?"). Continuous characters were divided into states separated by gaps. Multistate characters were treated as unordered. Characters that were polymorphic within a species generally were scored for the presumed apomorphic state. Owing to the large size of the data set, exact methods for calculating shortest trees were not feasible and thus an approximate method (m*;bb*;) was used. Character state evolution on the preferred tree was studied using CLADOS (Nixon, 1992).

TABLE 1.—Character definition and state codes. "0" indicates the plesiomorphic state for *Pyrgulopsis* species.

1. Shell form. 0 = globose-trochoid, 1 = ovate-elongate.
2. Shell inner lip. 0 = complete, 1 = usually incomplete.
3. Protoconch microsculpture. 0 = scattered, elevated wrinkles; 1 = weakly pitted; 2 = coarsely pitted.
4. Teleoconch sculpture. 0 = basally carinate, 1 = smooth.
5. Operculum whorls. 0 = multisipiral, 1 = paucispiral.
6. Operculum nucleus. 0 = subcentral, 1 = eccentric.
7. Outer edge of operculum. 0 = simple, 1 = indented.
8. Extent of operculum attachment scar. 0 = extending through nucleus, 1 = to side of nucleus.
9. Attachment scar margin. 0 = faint, 1 = thickened along part or entirety of perimeter.
10. Ventral callus of operculum. 0 = weak-absent, 1 = moderate to well developed.
11. Central radular tooth face. 0 = elongate-rectangular, 1 = near square.
12. Dorsal edge of central tooth. 0 = slightly-moderately indented, 1 = deeply indented.
13. Width of central cusp of central tooth. 0 = narrow-moderate relative to length of cusp row, 1 = very broad.
14. Shape of central cusp. 0 = blunt or rounded, 1 = pointed.
15. Pairs of basal cusps on central tooth. 0 = 2 or more, 1 = 1.
16. Basal process of central tooth. 0 = very broad, 1 = moderate-narrow.
17. Lateral angles of central tooth. 0 = weakly developed, 1 = well developed.
18. Mantle pigment. 0 = diffuse or uniform, 1 = distinctly banded, 2 = absent.
19. Ctenidial filaments. 0 = 30 or more, 1 = less than 30.
20. Osphradium. 0 = elongate, 1 = short.
21. Caecal chamber of stomach. 0 = small, 1 = absent, 2 = large.
22. Testis position. 0 = overlapping stomach, 1 = behind or abutting stomach.
23. Prostate gland. 0 = with pallial portion, 1 = without pallial portion.
24. Pallial vas deferens. 0 = kinked or coiled, 1 = simple.
25. Anterior vas deferens. 0 = in raised ridge on neck, 1 = simple in neck.
26. Penis size. 0 = moderate-large relative to head, 1 = small.
27. Distal edge of penis. 0 = distinct from filament, 1 = continuous with filament.
28. Penial filament. 0 = shorter than base of penis, 1 = as long or longer than base.
29. Orientation of penial lobe. 0 = horizontal, 1 = strongly oblique.
30. Length of penial lobe. 0 = moderate, 1 = as long as base, 2 = highly reduced, 3 = absent.
31. Distal edge of lobe. 0 = simple, 1 = strongly bifurcate, ? = lobe absent.
32. Terminal gland. 0 = short, straight strip; 1 = long, curved strip; 2 = circular; 3 = absent.
33. Number of penial glands. 0 = glands absent, 1 = single; 2 = multiple.
34. Extent of penial glands. 0 = glands absent, 1 = confined to proximal filament, 2 = filling most of length of filament.

TABLE 1.—Continued.

35. Proximal edge of penial gland. 0 = glands absent, 1 = simple, 2 = bifurcate.
36. DG1. 0 = absent, 1 = weak dot, 2 = short strip, 3 = elongate strip.
37. Position of dg1 relative to penis surface. 0 = gland absent, 1 = superficial, 2 = borne on swelling.
38. Position of dg1 relative to filament. 0 = gland absent, 1 = overlapping filament, 2 = posterior to filament.
39. DG2. 0 = absent, 1 = present.
40. DG3. 0 = absent, 1 = present.
41. Fusion of DG1-3. 0 = glands absent; 1 = only one gland present; 2 = glands unfused; 3 = glands often fused.
42. Additional dorsal glands. 0 = absent; 1 = single, large; 2 = multiple, small.
43. Number of ventral glands. 0 = gland absent, 1 = single; 2 = two or more.
44. Size and shape of ventral glands. 0 = glands absent; 1 = dot-like or narrow, 2 = large, circular.
45. Position of ventral glands. 0 = glands absent, 1 = superficial, 2 = borne on stalk.
46. Ovary position. 0 = overlapping stomach, 1 = behind or abutting stomach.
47. Albumen gland. 0 = without pallial portion, 1 = with pallial portion.
48. Anterior vestibule of capsule gland. 0 = absent, 1 = present.
49. Junction between coiled oviduct and bursal duct. 0 = behind pallial wall, 1 = in front of wall.
50. Shape of primary coil of oviduct. 0 = circular, 1 = narrowly vertical, 2 = posterior-oblique.
51. Coiled oviduct. 0 = kinked or of two coils, 1 = single coil, 2 = complexly coiled.
52. Length of bursa copulatrix. 0 = short-moderate, 1 = almost as long as albumen gland.
53. Width of bursa copulatrix. 0 = moderate, 1 = almost as wide as albumen gland, 2 = narrow.
54. Shape of bursa copulatrix. 0 = ovate, 1 = pyriform, 2 = globular, 3 = narrow sac.
55. Orientation of bursa copulatrix. 0 = transverse, 1 = horizontal.
56. Position of bursa copulatrix relative to albumen gland. 0 = mostly or entirely posterior to gland, 1 = slightly-moderately overlapping gland, 2 = entirely lateral to gland.
57. Position of bursal duct relative to coiled oviduct. 0 = partly or entirely lateral to oviduct, 1 = dorsal to coiled oviduct.
58. Length of bursal duct. 0 = moderate relative to length of bursa copulatrix, 1 = considerably longer than bursa copulatrix, 2 = very short.
59. Position of bursal duct relative to albumen gland. 0 = lateral to gland, 1 = partly imbedded in gland, 2 = largely or entirely embedded in gland.
60. Seminal receptacle length. 0 = moderate relative to length of bursa copulatrix, 1 = short, 2 = seminal receptacle absent.
61. Position of seminal receptacle relative to coiled oviduct. 0 = just behind coiled oviduct, 1 = anterior to posterior edge of coiled oviduct, ? = seminal receptacle absent.
62. position of seminal receptacle relative to bursa copulatrix. 0 = well anterior, 1 = slightly anterior or overlapping bursa copulatrix, ? = seminal receptacle absent.
63. Position of seminal receptacle relative to ventral edge of albumen gland. 0 = near or along edge, 1 = between mid-line and edge, ? = seminal receptacle absent.
64. Position of seminal receptacle relative to posterior edge of albumen gland. 0 = anterior to edge, 1 = extending to edge, ? = seminal receptacle absent.

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Superfamily RISSOOIDEA Gray, 1847

Family HYDROBIIDAE Troschel, 1857

Subfamily NYMPHOPHILINAE Taylor, 1966b

Genus *Pyrgulopsis* Call and Pilsbry, 1886

Pyrgulopsis Call and Pilsbry, 1886:9. [Type species, *Pyrgula nevadensis* Stearns, 1883; original designation.]
Marstonia Baker, 1926:195. [Type species, *Amnicola lustrica* Pilsbry, 1890; original designation.]
Fontelicella Gregg and Taylor, 1965:103. [Type species, *Fontelicella californiensis* Gregg and Taylor, 1965; original designation.]
Natricola Gregg and Taylor, 1965:108. [Type species, *Pomatiopsis robusta* Walker, 1908; original designation.]
Microamnicola Gregg and Taylor, 1965:109. [Type species, *Amnicola micrococcus* Pilsbry *in* Stearns, 1893; original designation.]
Savaginius Taylor, 1966a:130. [Type species, *Paludestrina nanna* Chamberlain and Berry, 1933; original designation.]
Mexistiobia Hershler, 1985:46. [Type species, *Mexistiobia manantiali* Hershler, 1985; original designation.]
Apachecoccus Taylor, 1987:32. [Type species, *Apachecoccus arizonae* Taylor, 1987; original designation.]
Yaquicoccus Taylor, 1987:34. [Type species, *Yaquicoccus bernardinus* Taylor, 1987; original designation.]

DIAGNOSIS.—A North American freshwater genus distinguished from other Nymphophilinae by combination of small size, generally ovate to ovate-conic shell, and penis with relatively few glands.

DESCRIPTION.—Shell globose to elongate-conic or turriform, 1–8 mm tall, with 4–5 whorls. Protoconch flattened to dome-like, of 1.25–1.50 whorls, near smooth or variably punctate, often with weak spiral lines on later portion (Figure 1). Teleoconch whorls near flat to highly convex, often shouldered adapically. Teleoconch sculpture usually only of fine growth lines and occasional spiral striae, although periphery of later whorls sometimes strongly angled or keeled. Aperture near circular to ovate, usually angled adapically. Apertural lip usually complete and slightly loosened from body whorl, sometimes adnate, rarely incomplete across parietal region; columellar lip usually slightly reflected. Inner lip often slightly thickened; outer lip thinner, usually prosocline. Umbilicus absent to perforate. Periostracum thin, gray-brown.

Operculum thin to moderately thick, amber-red, paucispiral-multispiral, with near central to highly eccentric nucleus. Dorsal operculum near smooth or with whorl outlines frilled; outer edge usually simple, rarely slightly indented. Ventral attachment scar margin variably thickened and raised along portion or entirety of perimeter; attachment area near smooth to with modest callus.

Well-developed pair of chitinous jaws present. Radula taenioglossate; ribbon moderately elongate, slightly coiled behind buccal mass, with numerous (>50) rows of teeth. Central radular tooth usually trapezoidal, rarely near square, with well-developed basal process; basal sockets usually deep; central cusp blunt, rounded or pointed, usually broader and longer than laterals, often markedly so; lateral cusps, 3–7. Central tooth with single pair of basal cusps (second, outer pair rarely present) arising from lateral angles or outer portion of tooth face. Lateral angles well developed, often thickened, often with prominent neck along outer edge. Lateral teeth with prominent central cusp flanked by 2–6 smaller cusps; marginal teeth with 14–37 fine cusps, usually more numerous on outer tooth. Stomach chambers about equal in length. Posterior caecum absent to prominent. Rectum without bend or coil in pallial roof. Anus positioned near mantle edge.

Animal pigmentation ranging from pale, except for black eyespots, to uniformly dark brown-black. Epithelial melanic pigment usually prominent on head/foot, pallial roof, visceral coil. Pallial roof pigmentation uniform-diffuse; or of 2–3 narrow-broad bands, extending along sides of ctenidium and (sometimes) dorsal edge of pallial gonoduct and often uniting over pericardium (Figure 2*e*).

Snout slightly longer than broad, with prominent distal lips. Cephalic tentacles extending beyond tip of snout, with little or no taper distally; tentacle tips rounded. Dorsal tentacle ciliation varying from small, scattered patches to one or more prominent longitudinal bands; weak transverse ciliation sometimes present along side of left tentacle (Figure 3). Foot large, rounded posteriorly, truncate anteriorly.

Ctenidium usually filling most of length of pallial cavity; filaments, 10–35, generally broadly triangular. Osphradium usually short, narrow, centered slightly posterior to middle of ctenidial axis. Kidney usually with prominent pallial bulge; kidney opening simple or slightly thickened and whitened. Hypobranchial gland weakly developed in posterior pallial roof.

Gonads usually simple lobate, often occupying at least one whorl and at least the posterior stomach chamber. Prostate gland bean-shaped to fan-like, usually with small to prominent pallial component, rarely positioned entirely posterior to pallial wall. Anterior vas deferens exiting from anterior portion of prostate gland (proximal to tip); pallial vas deferens usually with proximal twist or bend. Penis (Figure 2*a–d*) originating well behind right cephalic tentacle; generally large, extending beyond edge of mantle and as wide as or wider than snout. Base of penis square to broadly rectangular; distal penis usually bifurcate, with distal lobe and penial filament. Filament usually narrow, tapering, variable in length, rarely longer than base of penis, usually horizontal to slightly oblique (to right), rarely highly oblique. Lobe small and slender to broadly rectangular (as long as base), horizontal or (rarely) oblique (to left), rarely absent. Penial vas deferens slender, coursing straight along

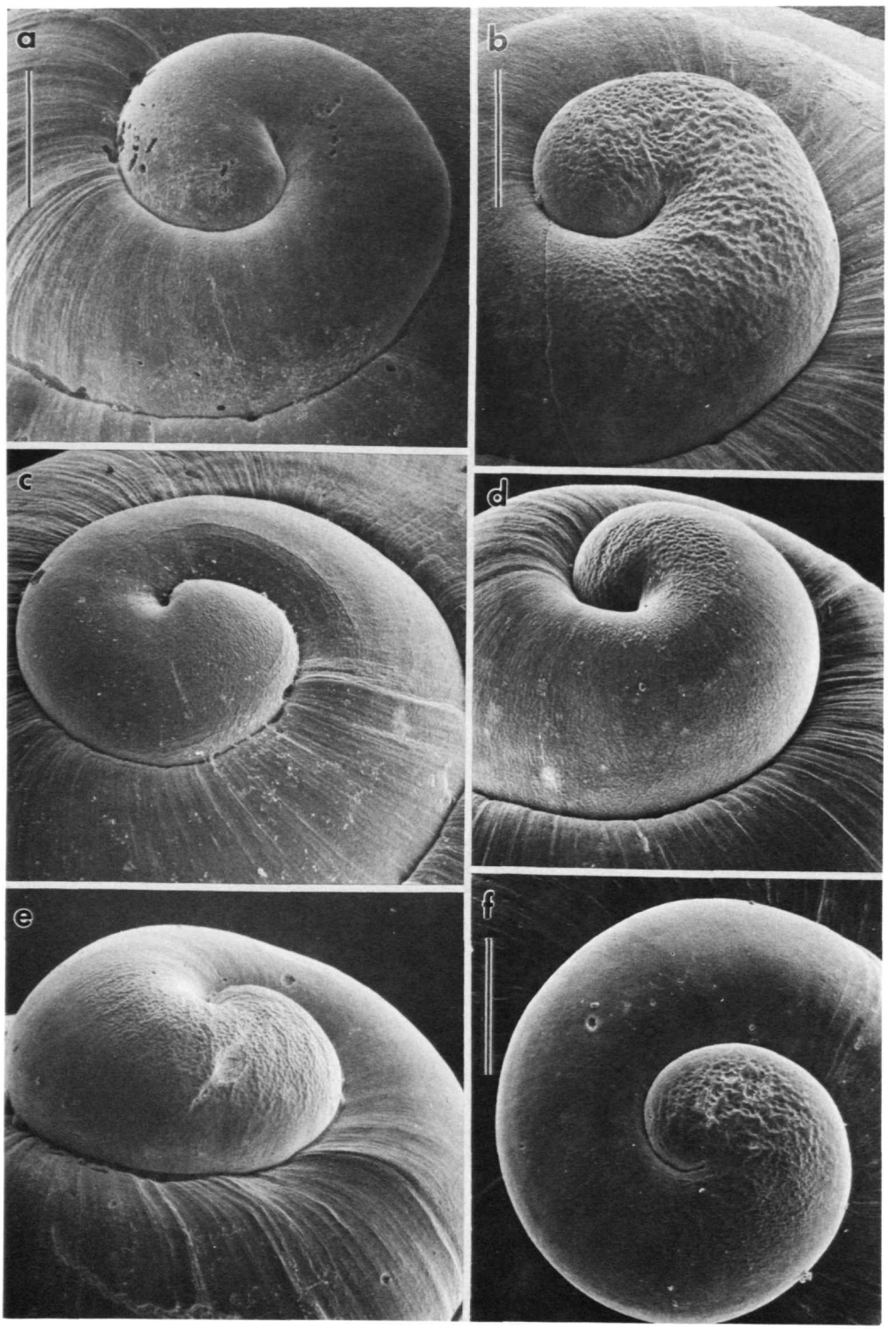


FIGURE 1.—Protoconchs: *a*, *Pyrgulopsis avernalis*, USNM 874533 (bar = 100 μm); *b*, *P. halcyon*, UF 22311 (bar = 86 μm); *c*, *P. fairbanksensis*, USNM 850367 (scale as in *a*); *d*, *P. montezumensis*, USNM 847233 (scale as in *a*); *e*, *P. castor*, UF 22178 (scale as in *a*); *f*, *P. pachyta*, UF 22228 (bar = 120 μm).

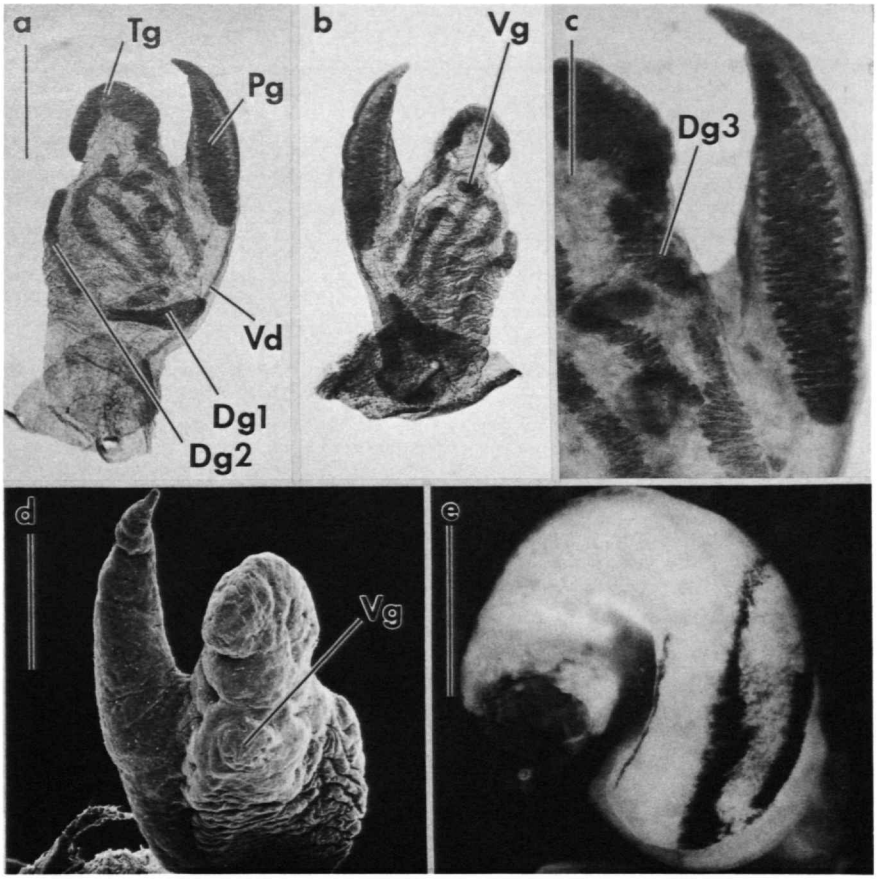


FIGURE 2.—Morphology of *Pyrgulopsis: a,b,* whole mount of penis (dorsal [a], ventral [b] aspects), *P. californiensis*, SBMNH uncat. (bar = 0.5 mm); *c*, close-up of a, showing gland cells (bar = 0.25 mm); *d*, scanning electron micrograph showing ventral aspect of critical point dried penis, ibid. (bar = 0.38 mm); *e*, photograph showing mantle pigmentation pattern, *P. lustrica*, UF 39160 (bar = 1.0 mm). (Dg1 = transverse dorsal gland, Dg2 = dorsal gland along left distal edge, Dg3 = dorsal gland along right edge of lobe, Pg = penial gland, Tg = terminal gland, Vd = vas deferens, Vg = ventral gland.)

right edge, discharging through tip of filament. Penis variably ornamented with one or more glandular units comprised of rows of narrow gland cells; glandular units superficial or borne on low swellings or lobules. Ornament may include a penial gland (rarely multiple)(Pg) covering part or all of dorsal filament; dorsal glands positioned along right edge and/or transversing part or all of width near mid-line (often borne on swelling proximally)(Dg1), along left distal edge (Dg2), and along right edge of lobe (often borne on swelling or lobule) (Dg3); terminal gland (Tg) positioned along or near edge of distal lobe, often fragmented into several units; and ventral gland(Vg), usually positioned proximal to base of filament and usually borne on swelling. Additional dorsal and ventral glands also sometimes present. Penis weakly ciliated. Filament often darkly pigmented.

Females (Figures 4, 5) oviparous; egg capsules simply hemispherical, without coating of sand grains, deposited singly on substrate or shell. Glandular oviduct composed of folded cells. Albumen gland usually with pallial section comprising up to a third of total gland length. Albumen and capsule glands about equal in size. Capsule gland almost always divided into two tissue sections, rarely unipartite. Capsule gland with well-developed ventral channel. Genital aperture a terminal or subterminal slit often opening to a short anterior gutter. Coiled oviduct of one or few loops on left side of albumen gland. Oviduct and bursal duct usually join slightly behind pallial wall, but sometimes well behind or slightly in front of wall. Sperm pouches pressed against left side of albumen gland; bursa copulatrix usually considerably larger than seminal receptacle. Bursa copulatrix sac-like to broadly ovate, sometimes with blunt anterior end ("pyriform"), usually moderate in length relative to albumen gland, positioned on posterior albumen gland (often extending behind gland). Bursal duct short-elongate, narrow to near width of bursa copulatrix,

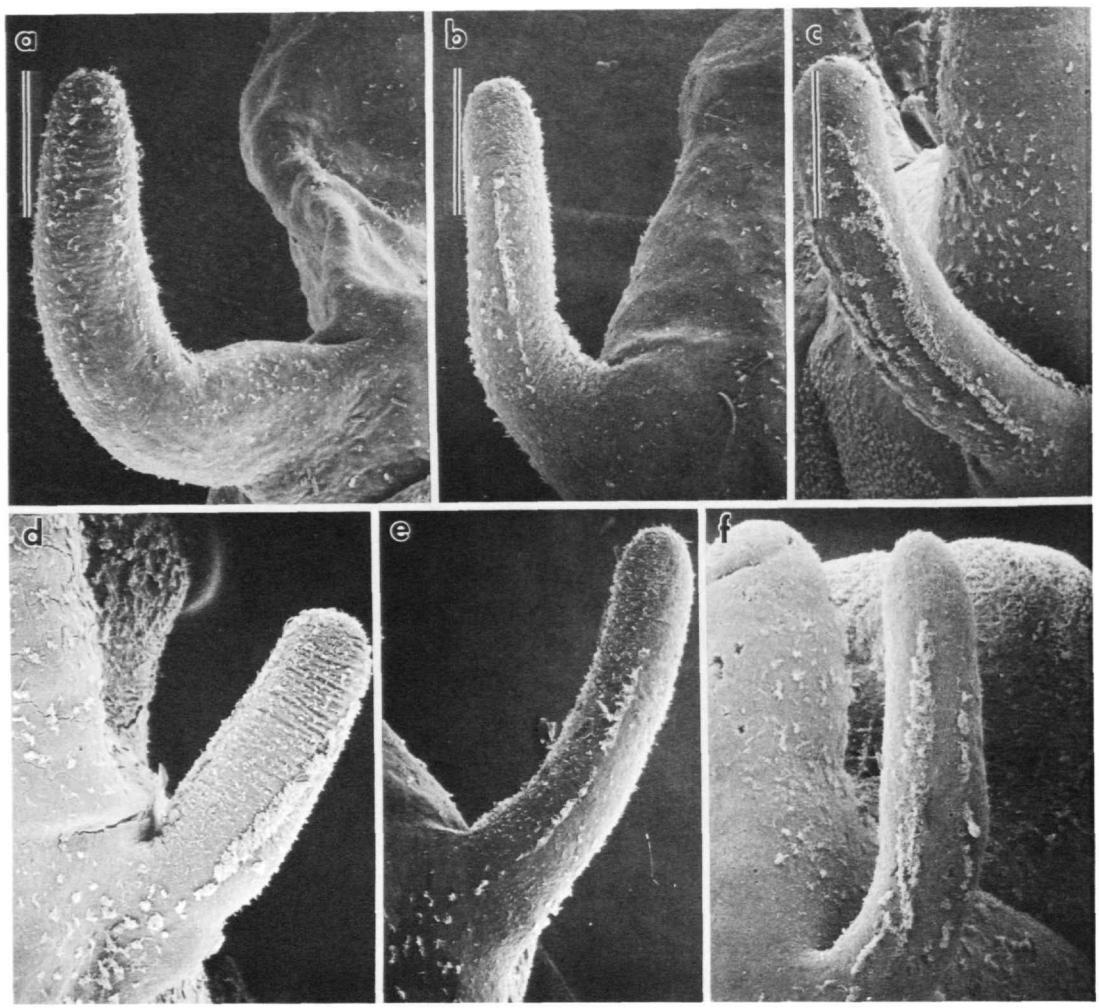


FIGURE 3.—Scanning electron micrographs of dorsal cephalic tentacles showing ciliation: *a, Pyrgulopsis arizonae*, USNM 847226 (bar = 100 μm); *b, P. micrococcus*, USNM 847246 (bar = 176 μm); *c, P. lustrica*, UF 22227 (bar = 200 μm); *d, P. californiensis*, SBMNH uncat. (scale as in *b*); *e, P. micrococcus*, ibid. (scale as in *b*); *f, P. lustrica*, ibid. (scale as in *b*).

positioned on posterior albumen gland, sometimes embedded in albumen gland for part of or entire length. Seminal receptacle ovate to elongate, often folded; usually positioned posterior to coiled oviduct, along mid-line to near ventral side of albumen gland, overlapping anterior bursa copulatrix and/or proximal bursal duct. Seminal receptacle duct usually short, narrow.

DISTRIBUTION.—Western North America, including Snake River basin, Great Basin, California coastal drainages, Baja California, Colorado River basin, Rio Grande basin, Pecos River basin, and internal drainages of Northern Mexico; Eastern North America, including Mississippi River basin, Great Lakes drainage, Tennessee River basin, and coastal drainages of Georgia (Figure 6).

FOSSIL RECORD.—*Pyrgulopsis* appears to date from the late Tertiary of the western United States (Taylor, 1985, table 2), although assignment of fossil forms to the genus is largely conjectural.

REMARKS.—North American workers generally have maintained *Pyrgulopsis* as a distinct genus, while Wenz (1926) and Thiele (1929) treated it as a subgenus within *Tryonia* and *Hydrobia*, respectively. *Pyrgulopsis* early was placed in the subfamily Hydrobiinae (Thiele, 1929; Wenz, 1939; Taylor, 1966b) while Starobogatov (1970) later allocated the genus to the Nymphophilinae, although without explanation. Thompson (1979), in an important paper redefining the Nymphophilinae, similarly (and apparently independently) suggested this placement, although on a tentative basis given that he had not

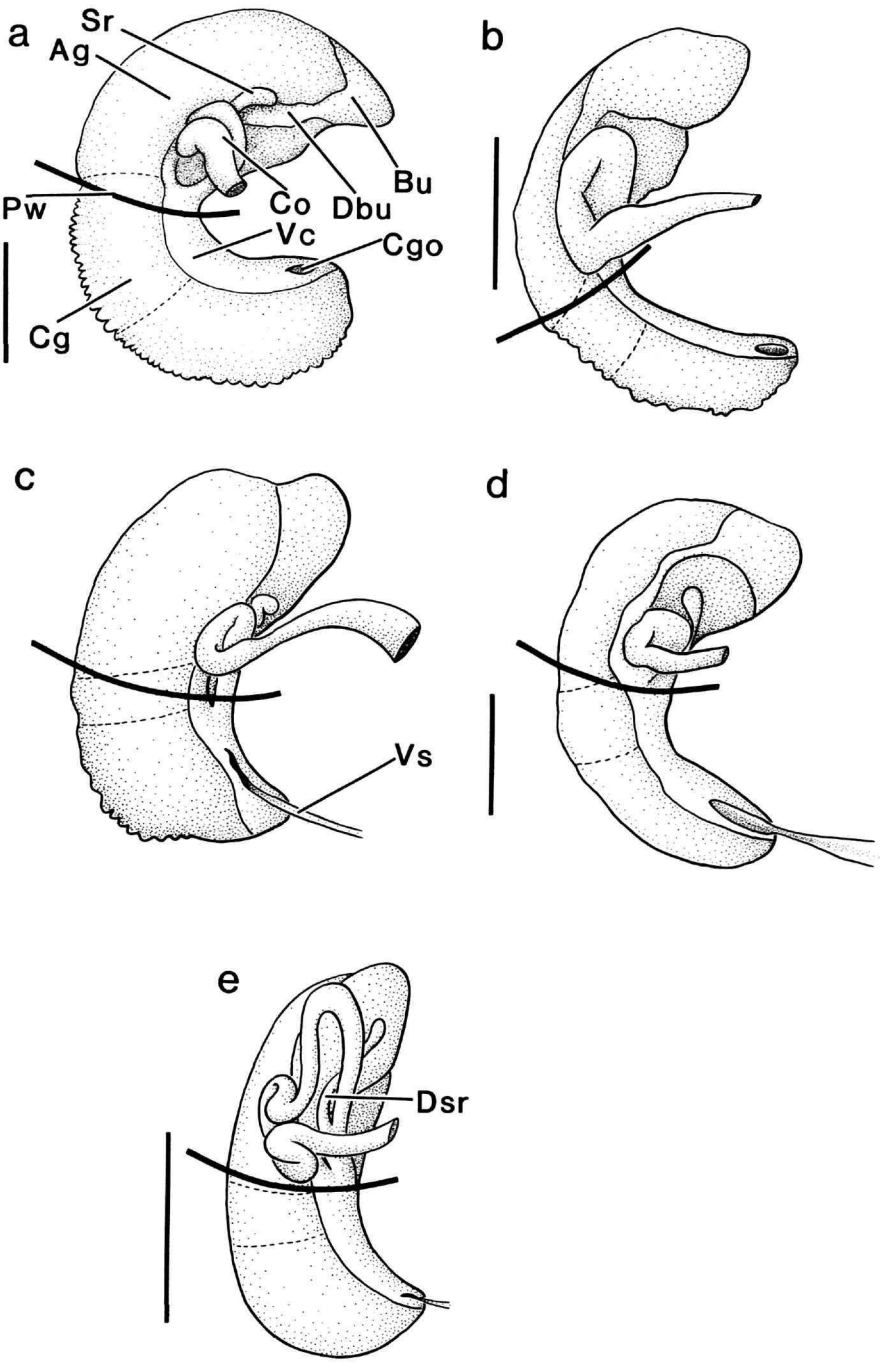


FIGURE 4.—Distal female genitalia (left side): *a*, *P. archimedis*, USNM 874342 (bar = 0.5 mm); *b*, *P. arizonae*, USNM 847226 (bar = 0.5 mm), *c*, *P. avernalis*, USNM 874000 (scale as in *b*); *d*, *P. bernardina*, USNM 847218 (bar = 0.25 mm); *e*, *P. brandi*, UMMZ uncat. (bar = 0.5 mm). Ag = albumen gland, Bu = bursa copulatrix, Co = coiled oviduct, Cg = capsule gland, Cgo = capsule gland opening, Dbu = bursal duct, Dsr = seminal receptacle duct, Pw = pallial wall, Sr = seminal receptacle, Vc = ventral channel, Vs = vestibule.

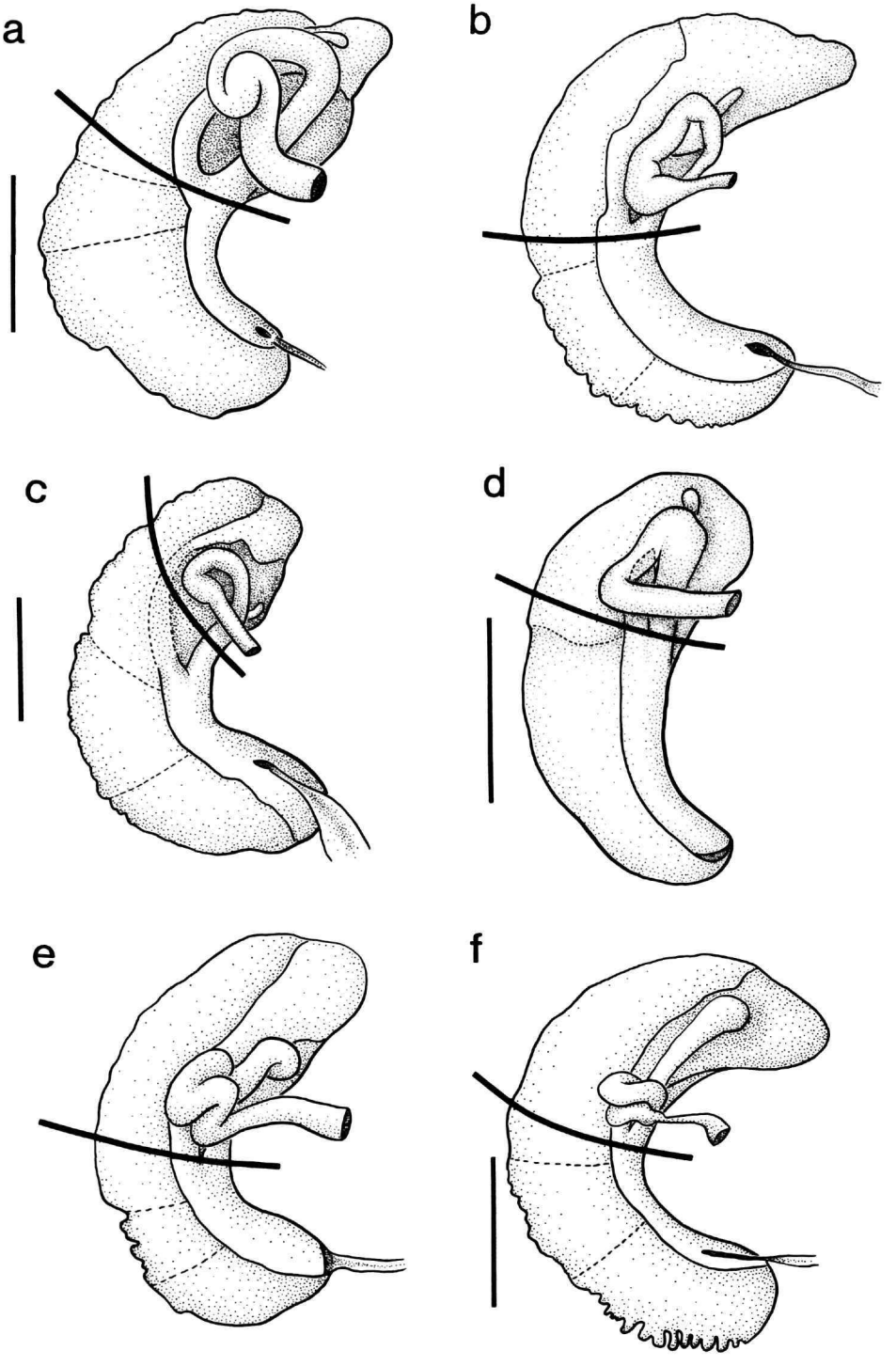


FIGURE 5.—Distal female genitalia (left side): *a*, *P. bruneauensis*, USNM 860508 (bar = 0.5 mm); *b*, *P. californiensis*, SBMNH uncat. (scale as in *a*); *c*, *P. lustrica*, UF 22227 (bar = 0.5 mm); *d*, *P. manantiali*, ANSP A98880 (bar = 0.25 mm); *e*, *P. micrococcus*, USNM 847246 (scale as in *a*); *f*, *P. robusta*, USNM 874185 (bar = 1.0 mm).

studied the anatomy of our genus. Hershler and Thompson (1987) supported this allocation after determining that members of the genus have the glandular, distally bifurcate penis, and female capsule gland with enclosed ventral channel characteristic of the subfamily.

The Nymphopilinae are comprised of eight North American genera: *Birgella, Cincinnatia, Notogillia, Nymphophilus, Pyrgulopsis, Rhapinema, Spilochlamys,* and *Stiobia.* Thompson (1979) also referred six European genera (subfamily Orientalininae (= Orientaliinae)) to the Nymphophilinae, but additional study of these and comparison with North American forms is necessary to corroborate these allocations[1]. Phylogenetic relationships among the nymphophiline genera are not known and although the anatomy of each has been studied to a certain extent (notably by Thompson, 1968, 1969, 1979, 1984; Thompson and McCaleb, 1978), important details such as morphology of the distal female genitalia are lacking for some of them. (The author currently is reviewing these taxa in order to obtain a complete morphological data set and prepare a phylogenetic analysis.)

Birgella, Rhapinema, and *Nymphophilus* share with *Pyrgulopsis* a relatively simple penis with few glands and accessory lobes, but differ in their larger, thicker, broader shells. Based on my limited study of these genera, *Nymphophilus,* locally endemic in northern Mexico, appears to be closest to *Pyrgulopsis* as these taxa share several other possibly derived features such as shell with wrinkled or punctate protoconch and basal keel (the latter present in only some species of *Pyrgulopsis*)[2].

Apart from shell, *Pyrgulopsis* differs from *Nymphophilus* in its more densely punctate protoconch, paucispiral (versus multispiral) operculum, relatively larger attachment region on ventral operculum, narrower central radular tooth, narrower basal process of central tooth, more developed lateral angles of central tooth, narrower central cusps on central and lateral radular teeth, simpler gonadal morphology, generally horizontal (as opposed to transverse) bursa copulatrix, and simple anterior vas deferens (not comprising a raised ridge on neck)(data for *Nymphophilus* from Taylor, 1966b; Thompson, 1979; Hershler, 1985; pers. obs.).

I continue to embrace the broad concept of *Pyrgulopsis* proposed by Hershler and Thompson (1987). The earlier separation of *Pyrgulopsis* from other nymphophilines now considered junior synonyms may be attributable to the scant attention paid to hydrobiid snail anatomy by North American workers until recently [3], and undue significance attached to the presence of a basal keel on the shell of *Pyrgulopsis* (sensu lato). It is of interest to note, with regard to the latter, that western and eastern carinate forms do not comprise a clade within the genus and may represent convergent shell forms (see "Cladistic Analysis"). Anatomical comparisons also were historically hampered by the fact that the type species of our genus, *P. nevadensis,* probably has been extinct for much of this century. The discovery (from resuscitated dried material; Hershler and Thompson, 1987) that the penis of this species is similar in form and glandular endowment to other North American genera paved the way for the revised concept of *Pyrgulopsis* used herein.

The following remarks on taxa placed in synonymy with *Pyrgulopsis* are intended as supplemental to the brief comments provided by Hershler and Thompson (1987).

Baker (1926) erected *Marstonia* as a subgenus of *Amnicola,* distinguished from *Amnicola* s.s. by its small nuclear whorl and longer, sharper radular cusps, and placed six eastern species in this group. Baker (1928) later added additional, principally northern lacustrine taxa to the group. Taylor (1960b) first treated *Marstonia* as a separate genus, although justification for such was not provided. Thompson (1977) reviewed the genus (recognizing eight species), demonstrated that it belonged in the Nymphophilinae, and suggested that some eastern species described as *Pyrgulopsis* may belong to *Marstonia.* While there are no features consistently separating species assigned to *Marstonia* by Thompson from other members of our genus, it is clear that eastern *Pyrgulopsis,* including the above plus carinate forms, comprise a species group distinct from western forms (see "Cladistic Analysis").

Gregg and Taylor (1965) described *Fontelicella,* comprised of three subgenera and twelve western American species. They

[1] Based on published illustrations, only two of these genera (see below) have penial glands, while the others resemble nymphophilines only to the extent that their penes are distally bifurcate. The Orientalininae, which Thompson (1979) placed in synonymy with the Nymphophilinae, is a very large group comprising many more than the six genera listed by Thompson (see Radoman, 1983): it is not clear whether any of these other taxa can plausibly be referred to the Nymphophilinae.

[2] Although most species of *Pyrgulopsis* have the simple penis described above, variation within the group is high, further complicating recognition of its sister-group. However, the more elaborately ornamented penis of species such as *P. californiensis* and *P. wongi* only partly achieves the complexity of glands and accessory lobes typical of other nymphophiline genera such as *Cincinnatia,* and thus I suspect that such a sister group relationship (previously postulated by Hershler and Thompson, 1987) is less likely than that advocated above. Regrettably, the intriguing possibility that *Pyrgulopsis* instead is more closely related to either of two European genera (*Avenionia, Litthabitella*) also endowed with penial glands (see Boeters, 1970, fig. 1; 1974, figs. 6, 7; Boeters and Winter, 1983, figs. 1–9) cannot be meaningfully explored at this time.

[3] An exception being the fine early anatomical work of Berry (1943), which included illustrations of the penis of eastern *Pyrgulopsis letsoni* showing a distal lobe endowed with a single gland. Unfortunately this observation went unnoticed by later workers who described new genera for animals with similar penes.

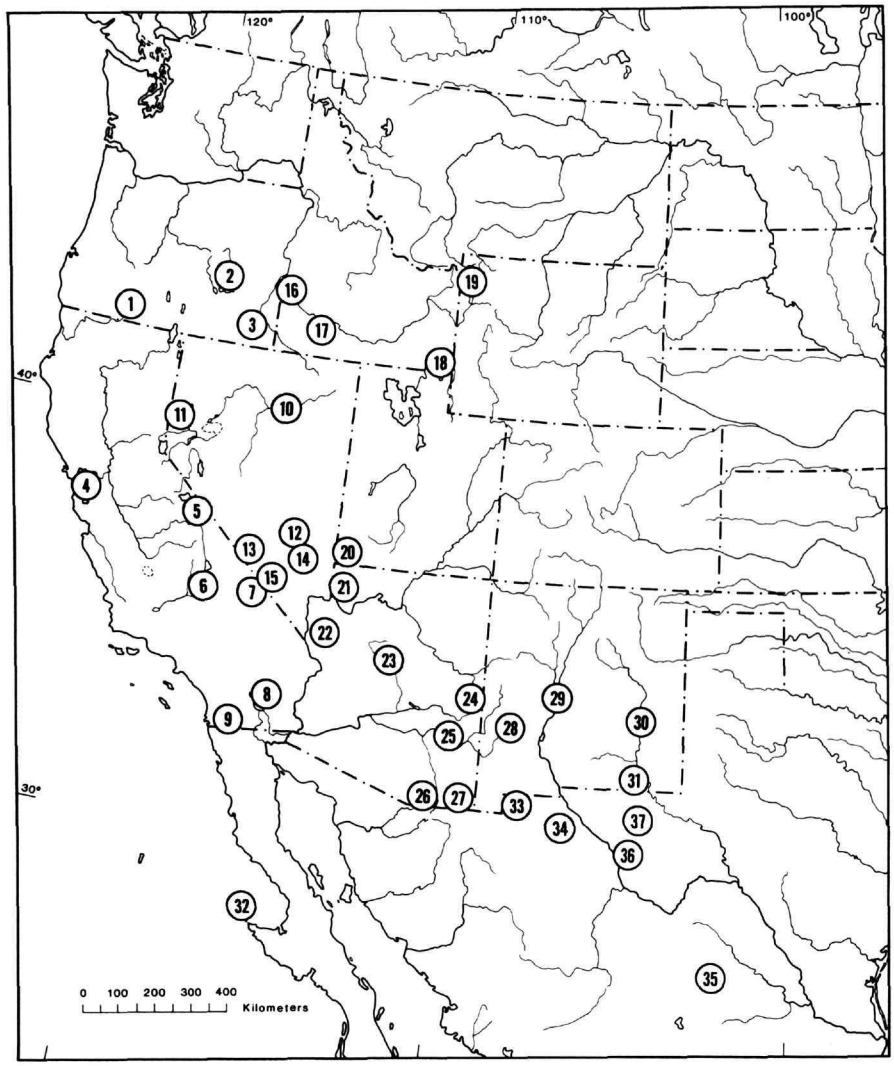
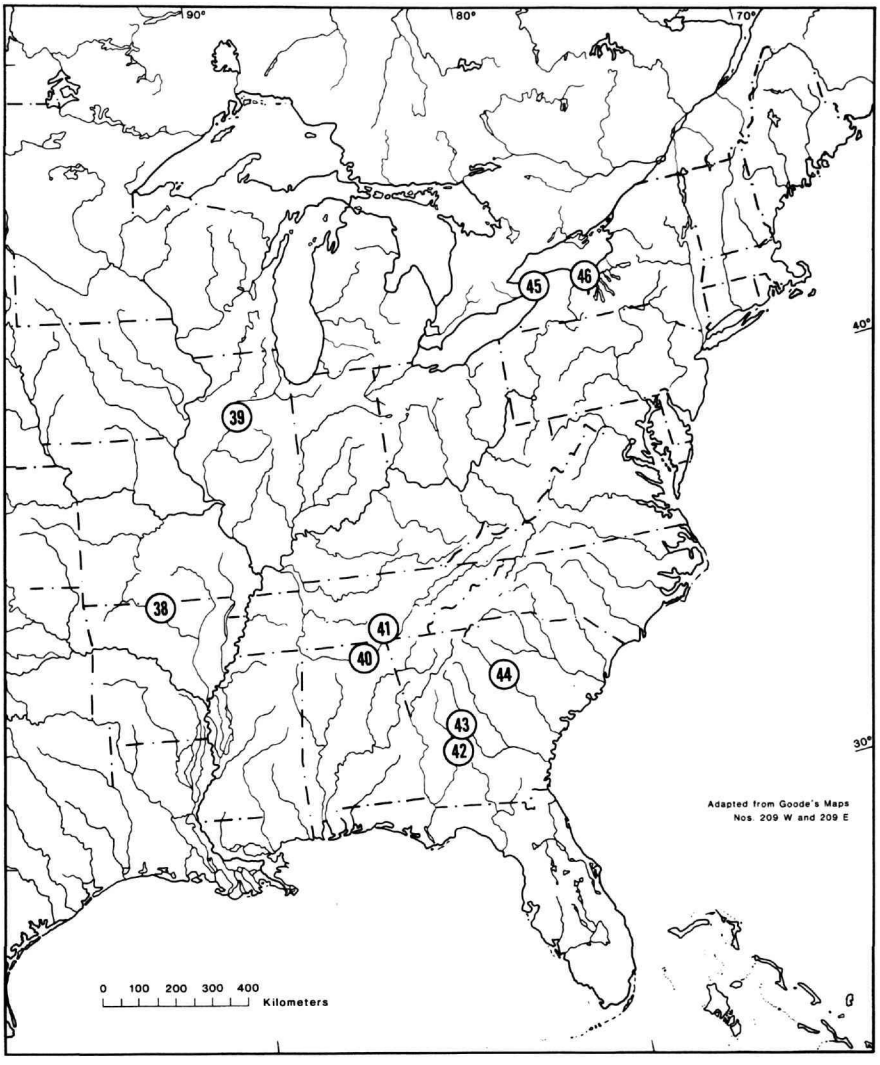


FIGURE 6.—Type locality areas for *Pyrgulopsis* species: 1, Klamath Lake basin, Oregon (*archimedis*); 2, Malheur Lake basin, Oregon (*hendersoni*); 3, Owyhee River drainage, Oregon (*intermedia*); 4, Sacramento-San Joaquin River system, California (*stearnsiana*); 5, Owens River drainage (*aardahli, owensensis, perturbata, wongi*); 6, Indian Wells Valley, California (*giulianii*); 7, Amargosa River drainage, California (*amargosae*); 8, Colorado River drainage, California (*longinqua*); 9, south coastal drainage, California (*californiensis*); 10, Humboldt River drainage, Nevada (*bryantwalkeri*); 11, Pyramid Lake basin, Nevada (*nevadensis*); 12, Pahranagat Valley, Nevada (*merriami*); 13, Amargosa River drainage, Nevada (*micrococcus*); 14, Moapa River drainage, Nevada (*avernalis, carinifera*); 15, Ash Meadows, Nevada (*crystalis, erythropoma, fairbankesensis, isolata, nanus, pisteri*); Snake River drainage, Idaho (16, *idahoensis;* 17, *bruneauensis*); 18, Bear Lake basin, Idaho (*pilsbryana*); 19, Jackson Lake basin, Wyoming (*robusta*); 20, Virgin River drainage, Utah (*deserta, kolobensis*); Colorado River drainage, Arizona (21, *bacchus;* 22, *conica*); 23, Verde River drainage, Arizona (*glandulosa, montezumensis, morrisoni, simplex, sola*); Gila River drainage, Arizona (24, *trivialis;* 25, *arizonae;* 26, *thompsoni*); 27, Rio Yaqui drainage, Arizona (*bernardina*); 28, Gila River drainage, New Mexico (*gilae, thermalis*); 29, Rio Grande drainage, New Mexico (*chupaderae, neomexicana*); Pecos River drainage, New Mexico (30, *roswellensis;* 31, *pecosensis*); 32, Cedros Island, Baja California (*cedrosensis*); 33, Guzmán complex, Chihuahua (*brandi, palomasensis*); 34, Rio del Carmen, Chihuahua (*chihuahua*); 35, Cuatro Ciénegas basin, Coahuila (*manantiali*); 36, Rio Grande drainage, Texas (*metcalfi*); 37, Pecos River drainage, Texas (*davisi*); 38, White River drainage, Arkansas (*ozarkensis*); 39, Illinois River drainage, Illinois (*scalariformis*); 40, Tennessee River drainage, Alabama (*arga, olivacea, pachyta*); 41, Tennessee River drainage, Tennessee (*ogmorphaphe*); 42, Flint River drainage, Georgia (*castor*); 43, Ocmulgee River drainage, Georgia (*agarhecta*); 44, Ogeechee River drainage, Georgia (*halcyon*); Great Lakes drainage, New York (45, *letsoni;* 46, *lustrica*).



contrasted the genus with *Cincinnatia* based on shell, headfoot, body pigmentation, penis, and radula. Taylor (1987) later described 10 new western American species as *Fontelicella*. Species described as or allocated to *Fontelicella* span the entire spectrum of penial morphology found in *Pyrgulopsis* and these taxa are entirely equivalent except for the exclusion of carinate forms in the former.

Mexistiobia Hershler, 1985, a monotypic genus from northern Mexico, is unusual in several features, but these are interpreted as a consequence of its minute size and globose shell: otherwise the animal clearly conforms to *Pyrgulopsis* in all respects.

Taylor (1987) described *Apachecoccus* and *Yaquicoccus*, both monotypic genera from Arizona. Although these are well differentiated from other western species, allocation to *Pyrgulopsis* is suggested by the fact that most if not all of their distinctive features occur in or intergrade to other members of the genus, the exception being the absence of seminal receptacle in *Apachecoccus*. The author described both of these animals as members of *Pyrgulopsis* in a paper (Hershler and Landye, 1988) published shortly after that of Taylor (1987).

Savaginius, erected by Taylor (1966a) for various Pliocene-Pleistocene species from the West (and one Recent species; Taylor, 1981), herein is placed in synonymy with *Pyrgulopsis*, as it is found entirely within the geographic range of Recent members of the genus and is virtually identical in shell shape, although Taylor suggested that *Savaginius* has a more acute protoconch.

ETYMOLOGY.—Genus name feminine, referring to conchological similarity between this group and European *Pyrgula*.

SPECIES OF QUESTIONABLE STATUS.—*Hoyia sheldoni*, from Lake Michigan, also may belong in *Pyrgulopsis* as its shell is closely similar to eastern members of this genus. Unfortunately, only dry shells, albeit live-collected, were available for this species and details discernable from resuscitated animals were not sufficient to confidently assess the status of this taxon. I also have been unable to obtain material for assessment of generic identity of *Amnicola yatesiana*, which may have lived in the San Joaquin Valley, California, during recent times (Taylor, 1981) and which has been allocated to *Savaginius* (see Appendix 2).

Western American Species

Pyrgulopsis aardahli Hershler, 1989

Pyrgulopsis aardahli Hershler, 1989:179, figs. 10–14.

DIAGNOSIS.—Shell ovate to broadly conical, medium-sized, umbilicate. Penial filament short, lobe very small. Penial ornament a weak, dot-like Dg1; small, circular terminal gland; and stalked ventral gland.

DESCRIPTION.—Shell (Figure 7*a*) ovate to broadly conical; height, 2.6–3.4 mm; whorls, 4. Protoconch very weakly punctate. Teleoconch whorls convex, slightly shouldered; sculpture of faint growth lines. Aperture ovate, narrowly adnate to or slightly separated from body whorl. Inner lip complete, medium thickness; columellar lip very slightly reflected. Outer lip slightly prosocline. Umbilicus rimate to open. Periostracum light brown.

Operculum (Figure 7*b,c*) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface strongly frilled. Attachment scar margin well thickened all around (broadly so along most of perimeter). Callus well developed.

Central radular tooth (Figure 32*a*) with moderately indented dorsal edge; lateral cusps, 5; central cusp rounded, considerably broader and slightly longer than laterals; basal cusps, 1, short, narrowly triangular, with moderate dorsal support. Basal process broad; basal sockets deep. Lateral margins thickened; neck weak.

Snout dark gray-black; neck variably pigmented. Cephalic tentacles pale other than a light gray patch proximal to eyespots. Pigment sometimes concentrated along anterior edge of foot and margins of opercular lobe. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 23, tall, broad. Osphradium elongate (33%), centered well posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum finger-like.

Testis, 1.5 whorls, overlapping stomach to edge of style sac. Prostate gland bean-shaped to near-circular; pallial section short. Pallial vas deferens weakly kinked proximally. Penis (Figure 43*a*) large, extending slightly beyond mantle edge; filament short, narrow, tapering; lobe short, narrow (sometimes absent). Dg1 dot-like, sometimes absent, positioned near mid-line. Terminal gland small, circular-transverse, borne on ventral surface distally (sometimes absent). Ventral gland large, elongate, borne on prominent swelling. Proximal penial filament with dark internal pigment.

Ovary, 1 whorl, overlapping posterior stomach. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture a broad terminal slit with very short vestibule. Coiled oviduct a short horizontal twist overlapping a near circular loop. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with about 50% of length posterior to albumen gland. Bursal duct narrow, slightly shorter than bursa copulatrix, partly embedded in albumen gland anteriorly. Seminal receptacle finger-like, usually folded, short, overlapping bursal duct.

TYPE LOCALITY.—Spring, Bramlette Ranch, Benton Valley, Mono County, California (T 1S, R 32E, SW1/4 sec. 6). Holotype, USNM 860406; paratypes, USNM 857951.

DISTRIBUTION.—Known only from type locality, upper Owens River drainage.

REMARKS.—Amongst members of the group of closely similar species living in Owens Valley, California, this snail resembles *P. giulianii* in having a penis with highly reduced lobe and small, circular terminal gland. It differs in having a kinked pallial vas deferens and seminal receptacle positioned lateral to the ventral edge of the albumen gland.

MATERIAL EXAMINED.—USNM 857951 (paratypes).

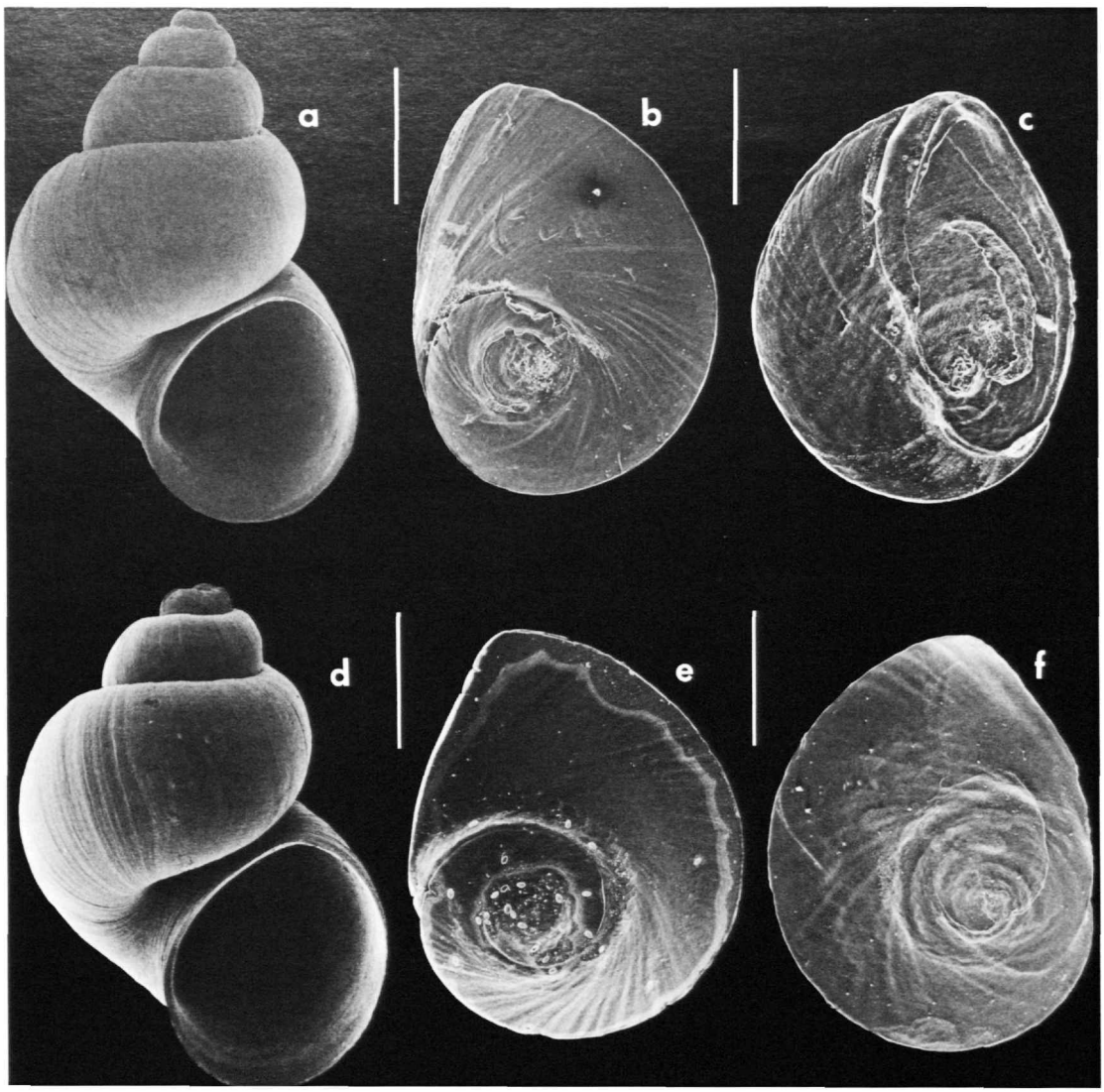


FIGURE 7.—Western *Pyrgulopsis: a–c, P. aardahli (a,* holotype, USNM 860406, 3.3 mm; *b, c,* opercula, USNM 857951, bars = 0.45 mm, 0.42 mm); *d–f, P. amargosae (d,* holotype, USNM 860401, 2.3 mm; *e,f,* opercula, USNM 857972, bars = 0.29 mm, 0.3 mm).

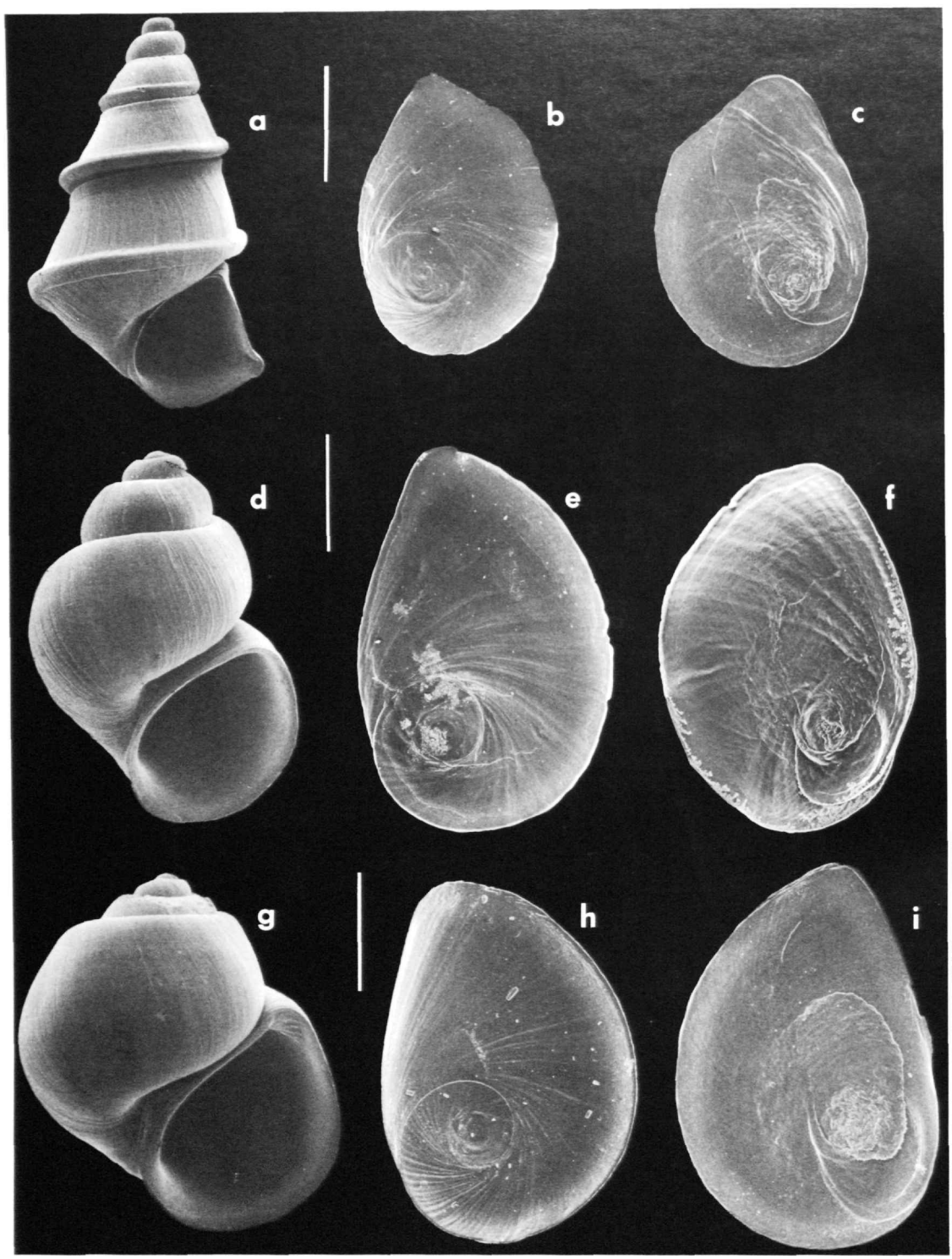


FIGURE 8.—Western *Pyrgulopsis: a–c, P. archimedis* (*a*, paratype, USNM 613965, 3.8 mm; *b*, *c*, opercula, USNM 874190, bar = 0.6 mm); *d–f, P. arizonae*, USNM 847226 (*d*, shell, 1.7 mm; *e*,*f*, opercula, bar = 0.29 mm); *g–i, P. avernalis*, USNM 874003 (*a*, shell, 3.0 mm; *h*, *i*, opercula, bar = 0.5 mm).

Pyrgulopsis amargosae Hershler, 1989

Pyrgulopsis micrococcus.—Hershler and Sada, 1987:788 [in part].
Pyrgulopsis amargosae Hershler, 1989:181, figs. 15, 16, 17a, 18, 19.

DIAGNOSIS.—Shell globose to low-conical, small-medium sized, weakly umbilicate. Penial filament elongate, lobe short. Penial ornament a small terminal glandular patch.

DESCRIPTION.—Shell (Figure 7*d*) globose to low-conical; height, 1.5–2.7 mm; whorls, 4. Protoconch finely punctate, often eroded. Teleoconch whorls convex, shouldered; sculpture of moderate growth lines. Aperture ovate, large, narrowly adnate or slightly separated from body whorl. Inner lip complete, medium thickness; columellar lip very slightly reflected. Outer lip slightly prosocline. Umbilicus rimate to narrowly perforate. Periostracum light brown.

Operculum (Figure 7*e,f*) broadly ovate, very light amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin smooth other than slight thickening between nucleus and inner edge; callus very weak.

Central radular tooth (Figure 32*b*) with highly indented dorsal edge; lateral cusps, 5–6; central cusp pointed, considerably broader and longer than laterals; basal cusps, 1, short, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck pronounced.

Snout dark gray-brown; cephalic tentacles unpigmented to light brown-gray; neck unpigmented to dark gray. Foot variably pigmented, typically dark brown along anterior edge and near posterior tip; opercular lobe dark along anterior edge. Black pigment well developed on pallial roof and visceral coil.

Ctenidial filaments, 25, tall, broad. Osphradium centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum small.

Testis, 1 whorl, slightly overlapping posterior stomach. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 43*b*) large, extending well beyond mantle edge; filament as long as base, thickened, with pointed tip; lobe short, narrow, folded. Terminal gland of 1–2 small patches (sometimes absent). Filament very darkly pigmented internally, pigment moderate near base of filament.

Ovary, 1 whorl, overlapping posterior stomach. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture short, terminal, without vestibule. Coiled oviduct a slight horizontal twist overlapping a broad horizontal loop. Oviduct and bursal duct join beneath oviduct coil behind pallial wall. Bursa copulatrix ovoid, slightly oblique, short and narrow, with about 50% of length posterior to albumen gland. Bursal duct medium width, slightly shorter than bursa copulatrix. Seminal receptacle slender, short, overlapping bursal duct.

TYPE LOCALITY.—Saratoga Spring, Death Valley, San Bernardino County, California (T 18N, R 5E, NW1/4 sec. 2). Holotype, USNM 860401; paratypes, USNM 853515.

DISTRIBUTION.—Lower Amargosa River drainage, California.

REMARKS.—This snail resembles *P. brandi* and *P. bruneauensis* in having an elongate penial filament and single, terminal gland; but differs in its more elongate shell, weaker operculum attachment scar, simple oviduct coil, and several other features of female genitalia.

MATERIAL EXAMINED.—USNM 857972 (topotypes).

Pyrgulopsis archimedis Berry, 1947

Pyrgulopsis nevadensis.—Henderson, 1928:141; 1929:170, fig. 182.—Hanna, 1930:108.—Clench, 1940:137.
Pyrgulifera nevadensis.—Henderson, 1936b:277.
Pyrgulopsis archimedis Berry, 1947:76, pl. 7: fig. 6.—Taylor, 1960a:326; 1975:37; 1981:152–153.—Burch, 1982:27, 110, fig. 274.—Hershler and Thompson, 1987:29, fig. 35.—Turgeon et al., 1988:62.

DIAGNOSIS.—Shell conical, basally carinate, large, weakly umbilicate. Penial filament and lobe medium length. Penial ornament a short, transverse penial gland; short, transverse terminal gland; and stalked ventral gland.

DESCRIPTION.—Shell (Figure 8*a*) conical; height, 4–6 mm; whorls, 5–6. Earliest protoconch weakly punctate, otherwise near smooth. Protoconch and early teleoconch with moderately convex whorls. Later whorls near-vertical or slightly concave just below suture, slightly convex in rest of outline, ornamented below with strong, rounded peripheral keel. Teleoconch growth lines faint. Aperture small, near pyriform above, broadly adnate to body whorl. Parietal lip very thin; columellar lip slightly thicker, very slightly reflected. Outer lip slightly prosocline. Umbilicus rimate. Periostracum brown.

Operculum (Figure 8*b,c*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin moderately thickened all around, especially along outer edge; callus broad, moderately thickened.

Central radular tooth (Figure 32*c*) with moderately indented dorsal edge; lateral cusps, 5–6; central cusp rounded, slightly broader and considerably longer than laterals; basal cusps, 1, moderately long, with strong dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck very weak-absent.

Head-foot unpigmented other than internal patches of gray granules in side of neck, cephalic tentacle above eyespot, and anterior edge of opercular lobe. Pallial roof, visceral coil black.

Ctenidial filaments, 35, tall, broad. Osphradium narrow, elongate (30%), centered well posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum large, broadly triangular.

Testis, 2.25 whorls, overlapping stomach to edge of style sac. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 43*c*) medium-sized, extending only slightly beyond mantle edge; filament slightly shorter than base, tapering; lobe almost as long as filament, rectangular. Penial gland covering proximal half of filament, narrow. Terminal gland medium length, usually transverse, positioned along distal edge (largely ventral). Ventral gland large, central, borne on short stalk. Filament with dark internal

pigment along most of length.

Female genitalia shown in Figure 4*a*. Ovary, 1.25 whorls, slightly overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland slightly longer than albumen gland. Genital aperture terminal, short; vestibule very weakly developed or absent. Coiled oviduct a very weak twist followed by broad, horizontal loop. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, sometimes with strongly angled posterior end, short, medium width, with most of length (80%) posterior to albumen gland. Bursal duct narrow, about as long as bursa copulatrix, partly enveloped in albumen gland posteriorly. Seminal receptacle finger-like, sometimes folded, large (65%), overlapping proximal bursal duct.

TYPE LOCALITY.—Upper Klamath Lake near Algoma, Klamath County, Oregon. Holotype, USNM 739417. Paratypes, USNM 613965.

DISTRIBUTION.—Upper Klamath Lake and uppermost portion of its outflow (Link River).

REMARKS.—Among the western fauna, only this species and *P. nevadensis* have a conical shell with strong basal carina. Although data for the latter, possibly extinct species, are limited, *P. archimedis* appears to differ in having a stronger operculum attachment scar and well-defined penial gland. This snail shares with several other species *(P. chihuahua, P. deserta, P. intermedia, P. kolobensis)* a penis ornamented only with terminal, penial, and ventral glands, but differs in having a larger caecal chamber of the stomach, and more posterior position of the bursa copulatrix.

Recent (1991) sampling of the outflow of Klamath Lake yielded typical *archimedis*, a similar-sized form (aff. *P. intermedia?*) having smooth shell with rounded whorls, as well as intermediates between these two. The smooth form has a darkly pigmented head-foot, but otherwise closely resembles *archimedis* in anatomical features, and it appears that intergradation of some form may be occurring. Given that this situation requires more study, I have decided, for the time being, to base my description of *archimedis* soley on typical, keeled specimens.

MATERIAL EXAMINED.—USNM 874190, Link River, Klamath County, Oregon, T 38S, R 8E, NW1/4 sec. 32.

Pyrgulopsis arizonae (Taylor, 1987)

Apachecoccus arizonae Taylor, 1987:32, fig. 15.—USDI, 1991b:58818.
Pyrgulopsis sancarlosensis Hershler in Hershler and Landye, 1988:35, figs. 13e, 26e, 31a–g, 32, 33.

DIAGNOSIS.—Shell globose to elongate conic, small to medium-sized, umbilicate. Penial filament medium length, broad; lobe elongate. Penial ornament a large, superficial ventral gland often accompanied by a similar dorsal gland. Seminal receptacle absent.

DESCRIPTION.—Shell (Figure 8*d*) globose to elongate conic; height, 1.1–2.4 mm; whorls, 3–4 whorls. Early protoconch moderately punctate, otherwise smooth except for a few adapical spiral lines on later portion. Teleoconch whorls moderately convex, strongly shouldered; sculpture of faint growth lines. Aperture generally ovate, medium to large-sized, usually widely separated from body whorl. Inner lip complete, moderately thick; columellar lip moderately reflected. Outer lip orthocline to slightly prosocline. Umbilicus narrow to broadly open. Periostracum light brown. Operculum (Figure 8*e,f*) ovate, pale to light yellow; nucleus highly eccentric; dorsal surface frilled. Attachment scar margin broadly thickened between nucleus and inner edge, otherwise faint; callus small.

Central radular tooth (Figure 33*d*) with strongly indented dorsal edge; lateral cusps, 3–5; central cusp pointed, narrow, considerably longer than laterals; basal cusps, 1, medium length, with very weak dorsal support. Basal process moderately broad; basal sockets deep. Lateral margins slightly thickened; neck pronounced.

Snout pale to dark brown. Cephalic tentacles usually pale, sometimes light brown. Neck, foot, opercular lobe usually very light, but varying to dark brown. Pallial roof, visceral coil usually dark brown-black, but sometimes quite light.

Ctenidial filaments, 15–18, medium height and width. Osphradium near centrally positioned along ctenidial axis. Kidney opening white. Stomach caecum very narrow, hemispherical.

Testis, 1 whorl, overlapping posterior stomach. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 43*d*) very large, with filament extending well beyond edge of mantle; filament broad, longer than base, tapering distally; lobe medium length, with broad distal edge. Dorsal lobe often bearing large, oval, superficial gland centrally. Ventral gland similar in size and shape, borne on central portion of ventral lobe, rarely accompanied by smaller adjacent gland. Penis unpigmented or with dark internal pigment in filament.

Female genitalia shown in Figure 4*b*. Ovary, 1 whorl, overlapping stomach to edge of style sac. Pallial albumen gland extremely short or absent. Capsule and albumen glands about equal in length; capsule gland very weakly differentiated into two tissue sections. Genital aperture a short terminal slit without vestibule. Coiled oviduct a weak proximal oblique kink followed by thickened, broad, horizontal loop filling half or more of albumen gland length. Oviduct and bursal duct join beneath central portion of loop well posterior to pallial wall. Bursa copulatrix pyriform, posterior end weakly angled, long (66%), almost as broad as albumen gland (73%), with about 85% of length posterior to gland. Bursal duct narrow, slightly shorter than bursa copulatrix. Seminal receptacle absent.

TYPE LOCALITY.—*Pyrgulopsis arizonae:* Unnamed spring on north side of Gila River about 2 mi (3.2 km) north of Bylas

(in T 3S, R 22E, 25,000 ft (7.6 km) west and 15,500 ft (4.7 km) north of the township line, Graham County, Arizona). Holotype, LACM 2203; paratypes, UTEP 10050, ANSP 376020, FSM 160939, USNM 854090. *Pyrgulopsis sancarlosensis:* Springs west of Tom Niece Springs, Graham County, Arizona (T 4S, R 23E, 0.6 km S, 0.4 km W of SE1/4 sec. 21). Holotype, USNM 859051; paratypes, USNM 859052.

DISTRIBUTION.—Upper Gila River drainage, southeastern Arizona.

REMARKS.—This snail is similar to several Ash Meadows forms in having a penis without terminal gland and with a superficial (not stalked) ventral gland. *Pyrgulopsis arizonae* is the only member of the genus lacking a seminal receptacle, and is further distinguished from the above by its elongate penial filament, well-developed penial lobe, frequent presence of a dorsal gland, simple oviduct coil, and large, pyriform bursa copulatrix that is largely posterior to the albumen gland.

MATERIAL EXAMINED.—USNM 847226 (topotypes, *sancarlosensis*).

Pyrgulopsis avernalis (Pilsbry, 1935), new combination

Fluminicola avernalis Pilsbry, 1935a:92, fig. 1.—Morrison, 1940:124.—Gregg, 1941:117.—Baker, 1964:171.—Taylor, 1965:599.—USDI, 1991b:58819.

"Fluminicola" avernalis.—Taylor, 1975:40; 1983:294.

DIAGNOSIS.—Shell globose-trochoid, medium-sized, umbilicus small-absent. Penial filament very short and narrow, lobe absent. Penial ornament a large, superficial ventral gland.

DESCRIPTION.—Shell (Figure 8*g*) globose-trochoid; height, 2.4–4.3 mm; whorls, 4. Protoconch (Figure 1*a*) very weakly punctate. Teleoconch whorls slightly convex, often shouldered; sutures very shallow; sculpture of strong growth lines. Aperture large, lunate, adnate to body whorl. Inner lip complete, highly thickened; columellar lip often strongly reflected. Outer lip often thick, strongly sinuate in larger specimens, with pronouced adapical notch. Umbilicus absent to small. Periostracum light brown.

Operculum (Figure 8*h,i*) ovate, light amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin thickened thickened almost all around, broadly so between nucleus and inner edge; callus moderate.

Central radular tooth (Figure 32*e*) with highly indented dorsal edge; lateral cusps, 4–5; central cusp pointed, slightly broader and longer than laterals; basal cusps, 1, short, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins slightly thickened; neck pronounced.

Dark internal pigment patch prominent just posterior to base of cephalic tentacle. Cephalic tentacles, snout, foot, opercular lobe, neck otherwise pale or light brown. Pallial roof with prominent dark internal pigment patch on right edge near mantle collar; roof otherwise pale to moderate brown. Gonad brown-black; visceral coil otherwise pale to moderately dark brown.

Ctenidial filaments, 25, tall, broad. Osphradium centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum a small, narrow flap.

Testis, 1 whorl, overlapping posterior stomach. Prostate gland bean-shaped, broadened posteriorly; pallial section large (33%). Vas deferens opening from near anterior end of prostate gland, pallial section gently undulating. Penis (Figure 43*e*) large, extending well beyond mantle edge; base elongate-rectangular, filament very short, extremely narrow, well tapered, with pointed tip; lobe absent. Ventral gland very large, circular, pad-like, borne along left edge near distal tip. Filament pale, base lightly pigmented along right edge.

Female genitalia shown in Figure 4*c*. Ovary, 0.75 whorl, overlapping posterior stomach. Pallial oviduct small, terminating well posterior to mantle edge. Albumen gland without pallial section. Capsule gland about equal to albumen gland in length, highly thickened. Genital aperture a long terminal slit; vestibule well developed. Coiled oviduct a short horizontal twist broadly overlapping a broader horizontal loop. Oviduct and bursal duct anterior to oviduct coil just behind pallial wall. Bursa copulatrix ovoid, slightly oblique, elongate (85%), medium width, positioned near ventral edge of albumen gland, with 30%–40% of length posterior to albumen gland. Bursal duct medium width, slightly shorter than bursa copulatrix, sometimes emerging slightly lateral to anterior tip of bursa copulatrix, partly embedded in albumen gland. Seminal receptacle narrow, folded, short, positioned lateral to anterior bursa copulatrix near ventral edge of albumen gland.

TYPE LOCALITY.—Types are fossil (Late Cenozoic) shells, with type locality given as Colorado Desert. This appears to be an error as there are no other reliable records of similar-shelled hydrobiids from this region. The species was attributed to Pahranagat Valley, Nevada by Morrison (1940) on the basis of its association with *Tryonia clathrata,* but there is no known material of *avernalis* from that valley. Gregg (1941) reported live material from Moapa Valley, Nevada (south of Pahranagat Valley), which probably is the type locality area given that this species appears to be endemic to the valley (also see Pratt, 1977). Lectotype (Baker, 1964:171), ANSP 27784; paralectotypes, ANSP 375737, a mixed lot containing several specimens of *P. carinifera.*

DISTRIBUTION.—Springs in Moapa Valley, southern Nevada, Colorado River drainage.

REMARKS.—This species resembles several Ash Meadows endemics in having a penis without distal lobe, ornamented solely by a large ventral gland. In the other species this gland is superficial, whereas in the case of *P. avernalis* it is stalked. This species is also differentiated by its minute penial filament and ventral position of seminal receptacle.

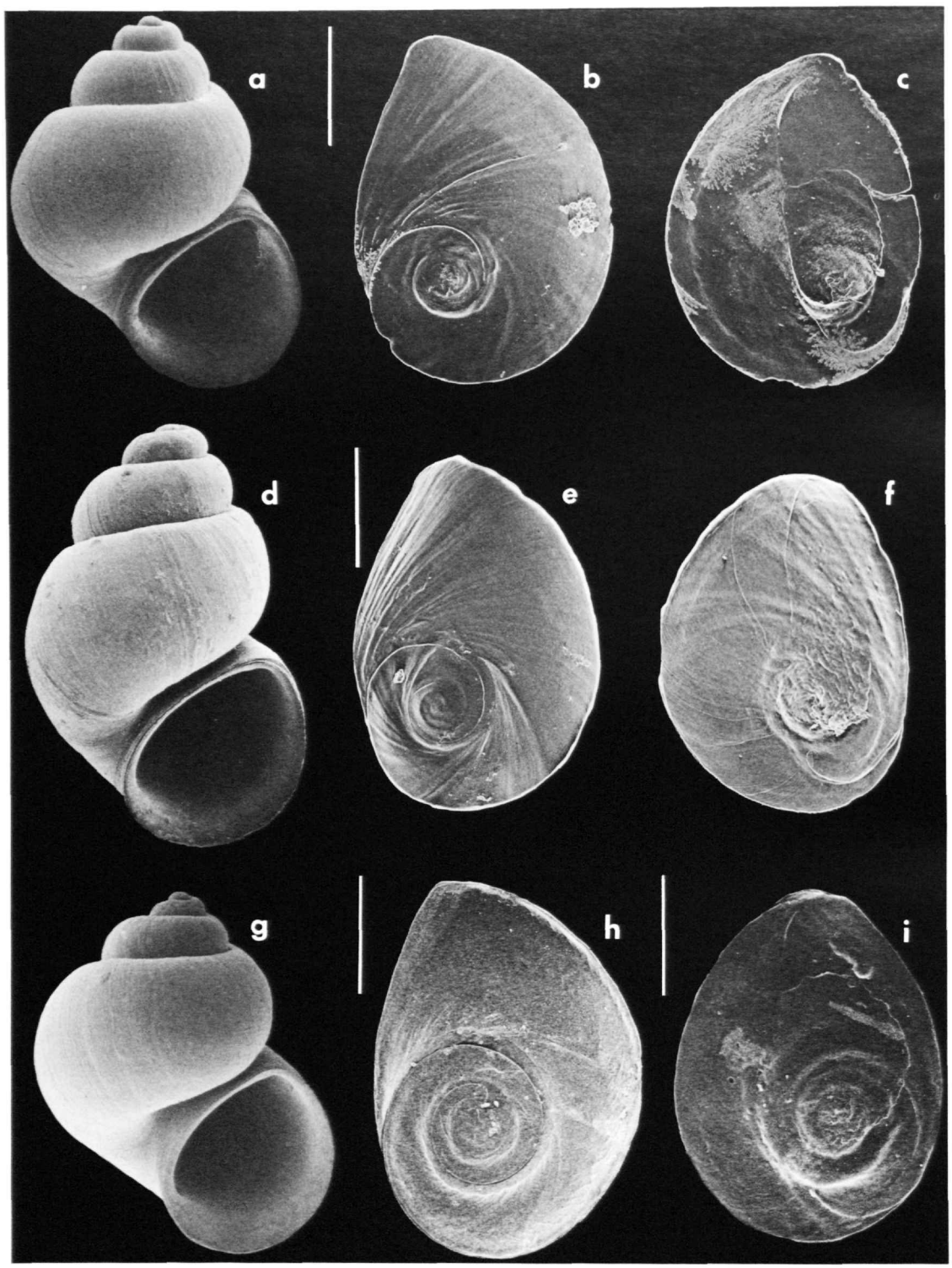


FIGURE 9.—Western *Pyrgulopsis*: *a–c*, *P. bacchus* (*a*, holotype, USNM 859037, 2.3 mm; *b,c*, opercula, USNM 847203, bar = 0.37 mm); *d–f*, *P. bernardina*, USNM 847218 (*d*, shell, 1.5 *e, f*, opercula, bar = 0.2 mm); *g–i*, *P. brandi* (*g*, shell, USNM 600500, 2.3 mm; *h, i*, opercula, USNM 600499, bars = 0.3 mm, 0.27 mm).

Pratt (1977) recorded both *"Fluminicola" avernalis* and an "undescribed species of *Fontelicella*" from Moapa Valley. It is not clear from his abstract which of these two entities corresponds to *avernalis* as recognized herein (no doubt the other referring to *Pyrgulopsis carinifera*).

MATERIAL EXAMINED.—USNM 874000, USNM 874003, Oasis Spring, Moapa Valley, Clark County, Nevada (T 14S, R 65E, sec. 16).

Pyrgulopsis bacchus Hershler, 1988

Pyrgulopsis bacchus Hershler in Hershler and Landye, 1988:21, figs. 10d, 11e–g, 12d–f, 14b, 15.

DIAGNOSIS.—Shell ovate-conic, medium-sized, umbilicate. Penis small; filament medium length; lobe short, sometimes bifurcate. Penial ornament a transverse, often fragmented terminal gland.

DESCRIPTION.—Shell (Figure 9*a*) ovate-conic; height, 2.3–3.1 mm; whorls, 4. Protoconch near smooth. Teleoconch whorls convex, slightly to moderately shouldered; sculpture of pronounced growth lines. Aperture ovate, large, narrowly adnate to slightly separated from body whorl. Inner lip complete, slightly thickened; columellar lip moderately reflected. Outer lip slightly prosocline. Umbilicus perforate. Periostracum light brown. Operculum (Figure 9*b,c*) ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin slightly thickened along outer edge; callus very weak.

Central radular tooth (Figure 32*f*) with strongly indented dorsal edge; lateral cusps, 3–4; central cusp pointed, considerably longer than laterals; basal cusps, 1, short, broadly triangular, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale or with light gray pigment patch distal to eyespots. Snout moderate to dark gray-black. Foot pale or lightly pigmented, with darkest area along anterior edge. Opercular lobe dark along margins; neck usually pale. Pallial roof, visceral coil pigment moderate-dark, often uniformly black.

Ctenidial filaments, 20, tall, medium width. Osphradium centered posterior to middle of ctenidial axis. Kidney with pronounced (50%) bulge into pallial cavity; kidney opening white. Stomach caecum medium-sized.

Testis, 2 whorls, overlapping stomach almost to style sac. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 43*f*) small, stout; base near square; filament slightly shorter than base, broad; lobe short, broader than base, sometimes bifurcate distally. Terminal gland transverse, positioned along distal edge, often fragmented into 2–3 small units, usually with a largely ventral orientation. Filament lightly pigmented.

Ovary, up to 0.5 whorl, very slightly overlapping posterior stomach chamber. Pallial albumen gland short. Capsule and albumen glands about equal in length. Genital aperture a terminal slit without vestibule. Coiled oviduct a short horizontal kink followed by broad horizontal loop. Oviduct and bursal duct join underneath oviduct coil just behind pallial wall. Bursa copulatrix ovoid, medium length and width, positioned near ventral edge of albumen gland, with about 33% of length posterior to gland. Bursal duct narrow, slightly shorter than bursa copulatrix, partly embedded in albumen gland distally. Seminal receptacle finger-like, usually folded, short, overlapping anterior bursa copulatrix or (more commonly) proximal bursal duct, positioned near ventral edge of albumen gland.

TYPE LOCALITY.—Grapevine Spring, Mohave County, Arizona. Holotype, USNM 859037; paratypes, USNM 859038.

DISTRIBUTION.—Several springs in Grand Wash, northwest Arizona, Colorado River drainage.

REMARKS.—This species shares with *P. solus* a penis having a frequently bifurcated lobe ornamented solely by a terminal gland. *Pyrgulopsis bacchus* differs by its stouter penial filament, consistent presence of dorsal gland (sometimes present in *P. arizonae*), absence of an anterior capsule gland vestibule, broader bursa copulatrix, and ventral position of the seminal receptacle.

MATERIAL EXAMINED.—USNM 847203 (topotypes).

Pyrgulopsis bernardina (Taylor, 1987)

Yaquicoccus bernardinus Taylor, 1987:34, fig. 16.—USDI, 1991b:58823.
Pyrgulopsis cochisi Hershler in Hershler and Landye, 1988:41, figs. 25d, 30h–k, 33, 34.

DIAGNOSIS.—Shell narrowly conic, small, weakly umbilicate. Penial filament elongate, lobe absent. Penial ornament of centrally positioned dorsal and ventral glands.

DESCRIPTION.—Shell (Figure 9*d*) narrow-conic; height, 1.3–1.7 mm; whorls, 3.25–4.0. Protoconch weakly punctate, with several weak adapical spiral lines on later portion. Teleoconch whorls convex, shouldered; sculpture of weak-moderately strong growth lines. Aperture ovate, large, very narrowly adnate or slightly separated from body whorl. Inner lip complete, thin; columellar lip slightly reflected. Outer lip near orthocline. Umbilicus usually narrowly rimate. Periostracum light tan.

Operculum (Figure 9*e,f*) ovate, light amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin moderately thickened between inner edge and nucleus and along most of inner edge; callus weak.

Central radular tooth (Figure 33*a*) with strongly indented dorsal edge; tooth face square; lateral cusps, 4–5, elongate; central cusp pointed, slightly longer than laterals; basal cusps, 1, elongate, with modest dorsal support. Basal process medium width; basal sockets deep. Lateral margins slightly thickened; neck moderate.

Cephalic tentacles pale. Snout pale to moderate gray-black. Foot usually pale, sometimes lightly pigmented along anterior edge. Opercular lobe black along inner edge, sometimes dark over entire surface. Neck pale. Pallial roof, visceral coil

moderate-dark brown-black.

Ctenidial filaments, 14, short, narrow. Osphradium centrally positioned along ctenidial axis. Kidney opening slightly thickened. Stomach caecum very small.

Testis, 1.5 whorls, overlapping posterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens without proximal kink. Penis (Figure 44*a*) medium-sized; filament slightly shorter than base, tapering; lobe absent. Dorsal penis bearing large horizontal gland borne on low stalk near distal edge. Ventral gland large, stalked, horizontal, positoned near distal edge of penis. Filament dark.

Female genitalia shown in Figure 4*d*. Ovary, 0.5 whorl, abutting or very slightly overlapping posterior edge of stomach. Pallial albumen gland short. Capsule gland as long as albumen gland. Genital aperture a terminal slit with short vestibule. Coiled oviduct a small, tightly circular loop. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix globular, short, broad, with about half of length posterior to gland. Bursal duct very narrow, elongate (300%), positioned dorsal to coiled oviduct, shallowly embedded in albumen gland. Seminal receptacle finger-like, long (57%), pressed against posterior edge of oviduct lateral to distal bursal duct (well anterior to bursa copulatrix).

TYPE LOCALITY.—*Pyrgulopsis bernardina:* Spring 2,300 ft E, 4,600 ft S of NW corner, sec. 15, T 24S, R 30E, Cochise County, Arizona. Holotype, LACM 2186; paratypes, ANSP 376019, FSM 160934, USNM 854078, USNM 854088. *Pyrgulopsis cochisi:* Spring at San Bernardino Ranch, Cochise County, Arizona. Holotype, USNM 859055; paratypes, USNM 859056.

DISTRIBUTION.—Restricted to type locality area (two springs on San Bernardino Ranch), southeast Arizona, Río Yaqui drainage.

REMARKS.—This species is distinguished from other forms lacking a penial lobe and terminal gland by its smaller ventral gland, continuous transition between penis base and filament, globular bursa copulatrix, and elongate bursal duct.

MATERIAL EXAMINED.—USNM 847218 (topotypes, *cochisi*).

Pyrgulopsis brandi (Drake, 1953), new combination

Amnicola brandi Drake, 1953:27, figs. 1–6.
"Amnicola" brandi.—Taylor, 1975:44.

DIAGNOSIS.—Shell globose-low conic, medium-sized, umbilicate. Penis base small, lobe short, filament highly elongate. Penial ornament a large terminal gland.

DESCRIPTION.—Shell (Figure 9*g*) globose to low-conical; height, about 2.3 mm; whorls, 4. Protoconch invariably eroded (sculpture unknown). Teleoconch whorls moderately convex, slightly shouldered, with shallow sutures; sculpture of moderate growth lines and weak spiral lines. Aperture ovate, very slightly angled above, narrowly adnate or (more often) separated from body whorl. Inner lip complete, medium thickness; columellar lip slightly reflected. Outer lip orthocline or slightly prosocline, sometimes gently sinuate. Umbilicus open. Periostracum tan.

Operculum (Figure 9*h,i*) broadly ovate, very light amber; nucleus slightly eccentric; dorsal surface frilled. Spiral coiling of operculum slightly elevated on ventral surface. Attachment scar margin slightly thickened between nucleus and inner edge, scar faint along outer edge; callus very weak.

Central radular tooth (Figure 33*b*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp pointed, broader and considerably longer than laterals; basal cusps, 1, medium-sized, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins slightly thickened; neck pronounced.

Head-foot, pallial roof, visceral coil dark red-brown. Pigment on pallial roof and visceral coil often darker (near black) on males. Dorsal cephalic tentacles with central unpigmented streak, pigment lighter distally.

Ctenidial filaments, 15, short, broad, flap-like. Osphradium centered posterior to middle of ctenidial axis. Kidney with very short pallial bulge; opening white. Stomach caecum small, hemispherical.

Testis, 1 whorl, overlapping stomach to edge of style sac. Prostate gland with large (50%) pallial section; pallial vas deferens without proximal kink; vas deferens coiled in neck behind penis. Penis (Figure 44*b*) large, elongate, highly coiled, but not extending beyond mantle edge (retracted specimens); base small, square; filament much longer than base, vermiform, with striated surface and pointed tip; lobe about as long as base, with blunt distal edge. Terminal gland a large pad on ventral surface of lobe. Filament darkly pigmented internally.

Female genitalia shown in Figure 4*e*. Ovary, 0.5 whorl, overlapping posterior stomach. Albumen gland without pallial section. Capsule gland as long as albumen gland, highly thickened. Genital aperture a terminal slit; vestibule well developed. Coiled oviduct a posterior oblique twist followed by two broad horizontal loops extending from pallial wall to posterior edge of albumen gland. Oviduct and bursal duct join beneath coil behind pallial wall. Bursa copulatrix ovoid, long (66%), medium width, with 25% of length posterior to albumen gland. Bursal duct narrow, shorter than bursa copulatrix, partly embedded in albumen gland. Seminal receptacle pouch-like, short (about 25%; poorly distinguished from duct), positioned near ventral edge of albumen gland lateral to oviduct coil and overlapping mid-bursa copulatrix. Duct from seminal receptacle elongate.

TYPE LOCALITY.—Springs at Las Palomas, Chihuahua, Mexico. Original specimen labels also indicate that these were thermal (24.4°) waters. Holotype, USNM 601494; paratypes, numerous (Drake, 1953:27–28).

DISTRIBUTION.—This presumably extinct species apparently was endemic to the type locality, which occurs in the portion of northwest Chihuahua known as the "Guzmán complex," comprising the terminus of Ríos Mimbres, Casas Grandes, Santa María, and del Carmen (Miller, 1978, 1981). The springs at Las Palomas dried during the 1970s (Jerry Landye, pers. comm., 1992).

REMARKS.—This snail is united with *P. bruneauensis* by unique synapomorphies of a complex oviduct coil (51-2) and anterior position of seminal receptacle relative to oviduct coil (61-1). *Pyrgulopsis brandi* differs by its stronger operculum attachment scar, larger terminal gland, and elongate seminal receptacle duct.

MATERIAL EXAMINED.—UMMZ uncat. (M50-8), spring-fed pond 3.6 mi. (5.8 km) south of Las Palomas. This is almost certainly the type locality (despite the discrepancy with Drake's data) as only a single spring has been known historically from the area (J. Landye, pers. comm., 1992).

Pyrgulopsis bruneauensis Hershler, 1990

Pyrgulopsis bruneauensis Hershler, 1990:803.—USDI, 1993:5938.
Genus and species undescribed.—USDI, 1991b:58818.

DIAGNOSIS.—Shell globose to broadly conical, medium-sized, umbilicate. Penial filament elongate, lobe very short. Penial ornament a small, weakly developed terminal gland.

DESCRIPTION.—Shell (Figure 10*a*) globose to broadly conical; height, 2.2–2.9 mm; whorls, 3.75–4.25. Early protoconch weakly punctate adapically, otherwise near smooth (often eroded). Teleoconch whorls convex, shouldered; sculpture of moderately pronounced growth lines. Aperture broadly ovate, large, very narrowly adnate or (more commonly) slightly separated from body whorl. Inner lip complete, thick. Outer lip prosocline. Umbilicus rimate to broadly perforate. Periostracum light amber.

Operculum (Figure 10*b,c*) ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar weakly thickened along inner edge near nucleus, very faint otherwise; callus a very weak, narrow thickening near inner edge.

Central radular tooth (Figure 33*c*) with moderately indented dorsal edge; lateral cusps, 4–6; central cusp pointed, slightly broader and considerably longer than laterals; basal cusps, 1, narrowly triangular, with very weak dorsal support. Basal process broad, tongue-like; basal sockets deep. Lateral margins thickened; neck pronounced.

Snout dark brown-black; cephalic tentacles similarly pigmented, although pale around eyespots. Foot pigment moderate-dark, especially along anterior edge. Opercular lobe black along sides, with internal black granules concentrated along inner edge. Neck pigment light-moderate, often with central pale area extending to foot. Pallial roof, visceral coil dark, near-uniformly pigmented.

Ctenidial filaments, 20, tall, narrow. Osphradium centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum very small.

Testis, 1 whorl, overlapping posterior stomach chamber. Prostate gland with large (32%) pallial section; pallial vas deferens proximally kinked. Penis (Figure 44*c*) medium to large-sized; filament elongate (about twice as long as base), muscular, little tapered; lobe very short, slightly tapered distally. Terminal gland small (sometimes very reduced or absent), variably shaped, borne along distal edge, usually in ventral position. Filament very dark (internal pigment).

Female genitalia shown in Figure 5*a*. Ovary, 0.75 whorl, overlapping posterior stomach chamber. Pallial albumen gland large (25%). Capsule gland as long as albumen gland. Genital aperture a subterminal slit (slightly raised and thickened) with vestibule. Coiled oviduct usually of three loops (vertical, posterior oblique, horizontal). Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix ovoid, medium length and width, with about half of length posterior to gland. Bursal duct medium width, about as long as bursa copulatrix. Seminal receptacle stout, short, with short duct pressed against middle loop of coiled oviduct, usually overlapping anterior bursa copulatrix or proximal section of bursal duct.

TYPE LOCALITY.—Spring along west side of Bruneau River, about 100 m downflow from Hot Creek's confluence with the river, Owyhee County, Idaho (T 7S, R 6E, SW1/4 sec. 34). Holotype, USNM 860507; paratypes, USNM 860508.

DISTRIBUTION.—Small springs along Hot Creek and confluent Bruneau River, Owyhee County, Snake-Columbia River basin.

MATERIAL EXAMINED.—USNM 860508 (paratypes).

Pyrgulopsis bryantwalkeri, new name

Fluminicola nevadensis Walker, 1916:6 [unlabeled figure, p. 6 (not *Pyrgula nevadensis* Stearns, 1883)]; 1918:142.—Turgeon et al., 1988:60.
"Fluminicola" nevadensis.—Taylor, 1975:127.

DIAGNOSIS.—Shell globose to ovate-conic, small to medium-sized, umbilicate. Penial filament short, lobe very weak. Penial ornament a weakly developed terminal gland.

DESCRIPTION.—Shell (Figure 10*d*) globose to ovate-conic; height, 1.5–3.2 mm; whorls, 3.5–4.5. Protoconch moderately punctate, although weaker near beginning of teleoconch. Teleoconch whorls moderate to highly convex, shouldered; body whorl sometimes with weak angulation at or near periphery; sculpture of weak to strong growth lines. Aperture broadly ovate, angled above, usually separated (sometimes greatly so) from body whorl. Inner lip complete, thickened; columellar region narrowly excavated. Outer lip prosocline. Umbilicus deeply perforate. Periostracum brown.

Operculum (Figure 10*e,f*) broadly ovate, dark amber;

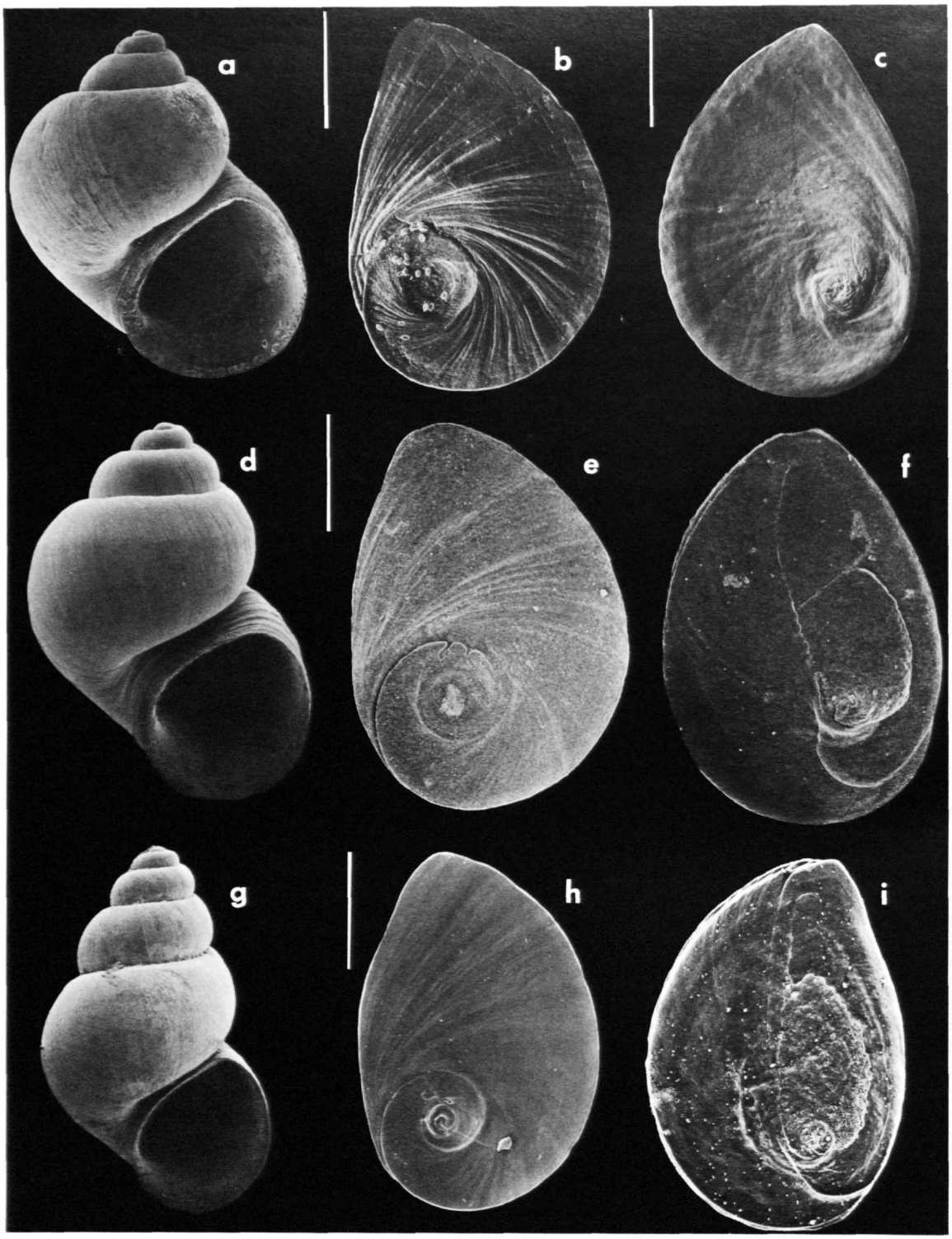


FIGURE 10.—Western *Pyrgulopsis*: *a–c*, *P. bruneauensis* (*a*, holotype, USNM 860507, 2.5 mm; *b,c*, opercula, USNM 860508, bars = 0.35 mm, 0.38 mm); *d–f*, *P. bryantwalkeri*, USNM 874305 (*d*, shell, USNM 874305, 2.4 mm; *e,f*, opercula, USNM 858278, bar = 0.27 mm); *g–i*, *P. californiensis*, SBMNH uncat. (*g*, shell, 3.0 mm; *h,i*, opercula, bar = 0.38 mm).

nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin weakly thickened all around; callus weak.

Central radular tooth (Figure 33*d*) with strongly indented dorsal edge; lateral cusps, 7; central cusp pointed, considerably broader and longer than laterals; basal cusps, 1, medium-sized, with slight dorsal support. Basal process moderately broad; basal sockets deep. Lateral margins unthickened; neck weak.

Cephalic tentacles pale or light brown, with prominent dark internal pigment patch just distal to eyespots. Snout light to dark gray-black. Foot lightly pigmented except for occasional dark cover along anterior and posterior edges. Opercular lobe with dark internal pigment on sides and sometimes a dark patch along anterior edge. Neck pale to with heavy cover of internal black granules. Pallial roof, visceral coil, near-uniform black.

Ctenidial filaments, 18, tall, medium width. Osphradium near centrally positioned along ctenidial axis. Kidney opening white. Stomach with small triangular caecum.

Testis, 1 whorl, overlapping posterior stomach chamber. Prostate gland sub-circular, thin-walled, positioned entirely behind pallial wall. Pallial vas deferens without proximal kink. Penis (Figure 44*d*) medium-sized, narrow; filament short, narrow; lobe very short to virtually absent. Terminal gland small, circular, positioned along distal edge of lobe (often absent). Filament darkly pigmented internally.

Ovary, 1 whorl, overlapping posterior stomach chamber. Pallial albumen gland large (33%). Capsule gland shorter than albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct a broad horizontal loop. Oviduct and bursal duct join anterior to oviduct coil behind pallial wall. Bursa copulatrix ovoid, short (33%), medium width (50%), with only about 20% of length posterior to albumen gland. Bursal duct narrow, shallowly embedded in albumen gland proximally, about as long as bursa copulatrix. Seminal receptacle a very small (20%), bud-like sac overlapping anterior bursa copulatrix, positioned near ventral edge of albumen gland.

TYPE LOCALITY.—A spring in the Cortez foot-hills, Humboldt Valley, Elko County, Nevada. Walker (1916:2) indicated that the general area surveyed was "about the town of Carlin." Neither Walker's account, nor other papers arising from the 1912 Walker-Newcomb Expedition in Northeastern Nevada (Pearse, 1914; Ruthven and Gaige, 1915) permits precise location of the type locality. Note, however, that Warm Spring, a prominent site located just outside of Carlin, harbors a population of snails conforming to type material in shell features and could represent the type locality. Walker (1916) indicated that syntypes were distributed to both the UMMZ and ANSP; UMMZ 118012, labeled "type," and closely conforming to the original description and illustration, is herein selected as the lectotype. Paralectotypes, ANSP 115948, MCZ 31450.

DISTRIBUTION.—Only a single population is known from Humboldt River basin, northeastern Nevada.

REMARKS.—Among the group of species sharing a penis ornamented solely with a terminal gland, *P. bryantwalkeri* is distinguished by its subcentral operculum nucleus, position of testis behind the stomach, simple pallial vas deferens, and short seminal receptacle.

This species is renamed in honor of its describer, Bryant Walker.

MATERIAL EXAMINED.—USNM 858278, Warm Spring, Elko County, Nevada (T 32N, R 52E, SW1/4 sec. 5).

Pyrgulopsis californiensis (Gregg and Taylor, 1965)

Bythinella binneyi.—Orcutt and Dall, 1885:541.
Bythinella intermedia.—Orcutt and Dall, 1885:541.
Paludestrina longinqua.—Pilsbry, 1899:122 [in part].—Stearns, 1901:285 [in part].—Hannibal, 1912a:34 [in part].—Berry, 1922:99 [in part].
Amnicola stearnsiana.—Berry, 1948:59.
Fontelicella californiensis Gregg and Taylor, 1965:109.—Taylor, 1975:50; 1981:152.—Burch, 1982:26, fig. 229.—Turgeon et al., 1988:61.
Pyrgulopsis californiensis.—Hershler and Thompson, 1987, figs. 6, 32, 34.

DIAGNOSIS.—Shell elongate-conic, medium to large-sized. Penial lobe and filament elongate. Penial ornament an elongate penial gland; transverse-elongate Dg1; elongate Dg2; Dg3 borne on weak lobule; large, curved, transverse terminal gland, and several ventral glands. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 10*g*) elongate-conic; height, 3–4 mm; whorls, 4–5. Protoconch weakly punctate, with adapical spiral lines on later portion. Teleoconch whorls moderately convex, shouldered; sculpture of fine growth lines. Aperture ovate, slightly angled above. Inner lip complete, adnate to widely separated from body whorl, medium thickness; columellar lip often reflected. Outer lip thin to moderately thick, often gently sinuate, orthocline to slightly prosocline. Umbilicus rimate to narrowly open. Periostracum brown-black.

Operculum (Figure 10*h,i*) ellipsoidal, light amber; nucleus slightly eccentric; dorsal surface very weakly frilled. Attachment scar margin broadly thickened almost all around; callus weak.

Central radular tooth (Figure 33*e*) with moderately indented dorsal edge; lateral cusps, 4; central cusp rounded, considerably broader and longer than laterals; basal cusps, 1, large, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Snout, foot, neck varying from pale to dark brown-black. Cephalic tentacles usually pale, sometimes with small pigment patches near mid-length. Opercular lobe pale or with dark pigment patch along anterior edge. Pallial roof usually dark; visceral coil moderate-dark, especially dark over gonads.

Ctenidial filaments, 22, medium height and width. Osphradium short, positioned centrally or slightly posterior to ctenidial axis. Kidney opening thickened, sometimes white. Caecal chamber of stomach small, triangular.

Testis, 1.5 whorls, overlapping posterior stomach. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figures 2*a–d*, 44*e*) large, extending well beyond mantle edge; filament slightly shorter than base, broad proximally, strongly tapered distally; lobe slightly shorter than filament, broad, expanded distally. Penial gland extending

almost to filament tip, sometimes fused posteriorly with Dg1. Dg1 crossing entirety of penis width near mid-point, sometimes extending anteriorly along right edge, occasionally fusing with penial gland; Dg2 elongate, positioned along left distal edge, often uniting with Dg1; Dg3 borne on weak lobule along right edge of lobe, sometimes fragmented into several small glands. Dorsal penis also bearing 1–5 elongate, longitudinal-oblique glands distally. Terminal gland elongate, curved, transverse, borne along distal edge (largely ventral surface) of lobe. Ventral gland positioned near base of lobe, borne on low swelling, flanked by smaller, similarly stalked gland(s) on either or both sides. Proximal filament and adjacent area of penis usually darkly pigmented internally.

Female genitalia shown in Figure 5*b*. Ovary, 1 whorl, pressed against edge of or slightly overlapping posterior stomach. Pallial albumen gland short (16%). Capsule gland slightly shorter than albumen gland. Genital aperture a terminal slit, vestibule well developed. Coiled oviduct a broad horizontal loop (sometimes preceeded by slight kink) positioned well behind pallial wall, overlapping much of posterior albumen gland. Oviduct and bursal duct join anterior to coil just behind pallial wall. Bursa copulatrix pyriform, posterior end angled, long, (50%–75%), as broad as albumen gland, with almost entire length (about 90%) posterior to albumen gland. Bursal duct narrow, although sometimes with very wide proximal section, slightly shorter than bursa copulatrix. Seminal receptacle pouch-like, short, overlapping anteriormost bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Campo Creek, San Diego County, California, 0.6 mi. (1.0 km) east of Mountain Empire Dam (W1/2 SW1/4 sec. 19, T 18S, R 5E). Holotype, UMMZ 220000.

DISTRIBUTION.—Pacific coastal and interior drainage, southern California and northern Baja California (Gregg and Taylor, 1965; Taylor, 1981). Record(s) for Baja California require confirmation.

REMARKS.—Among the group of species having a full complement of glands on the penis (i.e., penial gland, Dg1-3, terminal gland, ventral gland), only *P. californiensis* and *P. wongi* have multiple ventral glands and a short seminal receptacle. *Pyrgulopsis californiensis* differs by its elongate shell, albumen gland with pallial portion, shorter and more posteriorly positioned bursa copulatrix, and longer bursal duct.

MATERIAL EXAMINED.—SBMNH uncat. (topotypes).

Pyrgulopsis carinifera (Pilsbry, 1935a), new combination

Fluminicola avernalis carinifera Pilsbry, 1935a:93, fig. 3.—Morrison, 1940:124.—Gregg, 1941:117.
"Fluminicola" carinifera.—Baker, 1964:171.—Taylor, 1975:53.

DIAGNOSIS.—Shell trochoid, basally carinate, medium to large-sized, anomphalous or very weakly umbilicate. Penial lobe and filament medium length; lobe distally bifurcate. Penial ornament a fragmented terminal gland.

DESCRIPTION.—Shell (Figure 11*a*) trochoid; height, 3.8–5.0 mm; whorls, 4–5. Protoconch very weakly punctate. Teleoconch whorls slightly convex, sometimes shouldered. Periphery of body whorl varying from slightly angled to strongly keeled, with keel weakening near aperture; teleoconch sculpture otherwise only of strong growth lines. Aperture ovate, angled above, adnate to body whorl. Inner lip usually complete, columellar lip highly thickened, parietal lip less so. Outer lip medium thickness, strongly prosocline. Umbilicus absent or small, narrowly rimate. Periostracum light brown, very thin.

Operculum (Figure 11*b,c*) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin a faint trace, sometimes only evident between nucleus and inner edge; callus very weak-absent.

Central radular tooth (Figure 33*f*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp pointed, slightly broader and longer than laterals; basal cusps, 1, very short, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck very weak.

Cephalic tentacles usually light brown, with pigment often present only distally. Snout and neck pale to light brown, with black internal patch present posterior to tentacle bases. Foot generally pale, but often dark along anterior and posterior edges; opercular lobe often with pronounced brown streaks on sides. Pallial roof, visceral coil light-moderate brown, with pigment especially dark over gonads.

Ctenidial filaments, 35, broad, tall. Osphradium positioned posterior to center of ctenidial axis. Stomach caecum very small, triangular.

Testis, 0.5 whorl, overlapping posterior stomach. Prostate gland reniform, short, thin-walled, without pallial section; pallial vas deferens without proximal kink. Penis (Figure 44*f*) medium-sized, scarcely extending beyond mantle collar; base elongate, narrowing distally; filament medium length, strongly tapering, with pointed tip; lobe medium length, broad, bifurcating distally. Terminal gland fragmented into two elongate, transverse units borne along distal edges of bifurcated lobe. Filament darkly pigmented internally.

Ovary, 1 whorl, overlapping posterior stomach. Pallial oviduct small, terminating well posterior to edge of pallial cavity. Albumen gland without a pallial section. Capsule gland as long as albumen gland (posterior section very small and behind pallial wall), highly thickened. Genital aperture a terminal slit; vestibule present. Coiled oviduct a small horizontal loop just behind pallial cavity wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length, narrow (33%), positioned along ventral edge of posterior albumen gland with very small or no portion posterior to gland. Bursal duct broad, about as long as bursa copulatrix. Seminal receptacle finger-like, short, overlapping proximal

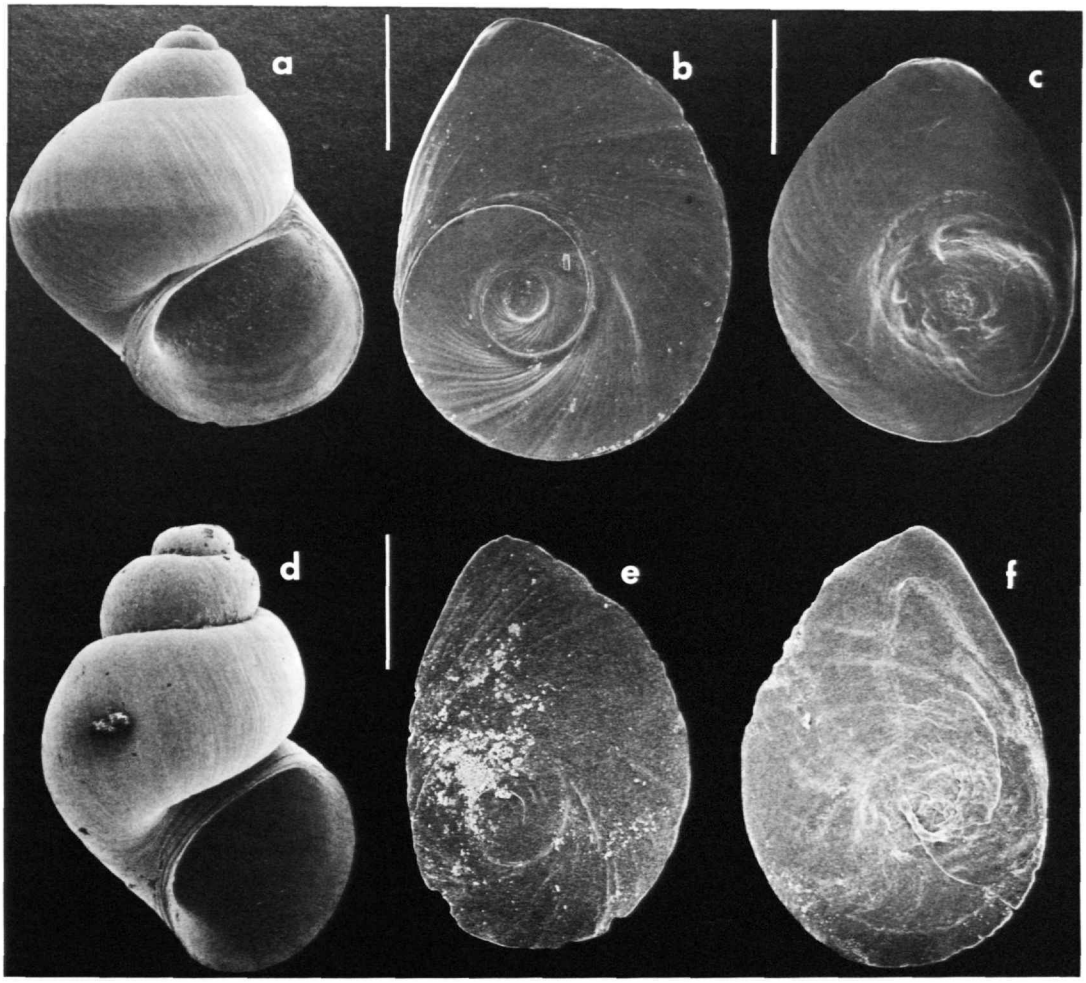


FIGURE 11.—Western *Pyrgulopsis: a–c, P. carinifera (a,* shell, USNM 874099, 2.8 mm; *b,c,* opercula, USNM 874097, bars = 0.5 mm, 0.6 mm); *d–f, P. cedrosensis,* ANSP 141408 (*d,* shell, 1.8 mm; *e,f,* opercula, bar = 0.25 mm).

bursal duct, positioned near ventral edge of albumen gland.

TYPE LOCALITY.—As for *P. avernalis,* this species was described from fossil shells attributed to Colorado Desert, but the type locality almost certainly is from Moapa Valley, southern Nevada. Lectotype (Baker, 1964:171), ANSP 164091; paralectotypes, ANSP 375736.

DISTRIBUTION.—Springs in Moapa Valley, southern Nevada, Colorado River drainage.

REMARKS.—Among the various species sharing a penis solely ornamented by a terminal gland, *P. carinifera* is differentiated by features including a large, strongly bifurcate penial lobe, and narrow bursa copulatrix entirely overlapped by the albumen gland. The affinities of this snail possibly lie with two species from Ash Meadows that also have a globose-trochoid shell, sub-central operculum nucleus, and albumen gland without pallial section.

MATERIAL EXAMINED.—USNM 874001, unnamed spring, Moapa Valley, Clark County, Nevada (T 14S, R 65E, sec. 16).

Pyrgulopsis cedrosensis (Pilsbry, 1927), new combination

Paludestrina cedrosensis Pilsbry, 1927:188, fig. 3.
Fontelicella (Fontelicella) cedrosensis.—Gregg and Taylor, 1965:108.
Fontelicella cedrosensis.—Taylor, 1975:55.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized. Penial lobe, filament medium length. Penial ornament unknown.

DESCRIPTION.—Shell (Figure 11*d*) ovate-conic; height, 1.7–2.3 mm; whorls, 3.5–4.0. Apex near-flat, appearing smooth, but eroded. Teleoconch whorls convex, often shouldered; sculpture of weak growth lines. Aperture large, ovate, usually slightly separated from body whorl. Inner lip complete, slightly thickened. Outer lip orthocline to slightly prosocline. Umbilicus near absent to shallowly perforate. Periostracum very thin, virtually colorless.

Operculum (Figure 11*e,f*) ovate, near-colorless except for light amber nuclear region; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin weak-moderately thickened all around; callus weak.

Central radular tooth (Figure 34*a*) with moderately indented dorsal edge; lateral cusps, 5; central cusp pointed, elongate, slightly broader than laterals; basal cusps, 1, elongate-triangular, with weak dorsal support. Basal process with very narrow distal section; basal sockets deep. Lateral margins slightly thickened; neck weak.

Head-foot, visceral coil dark brown-black.

Penial filament medium length, tapered; lobe about equal to filament in length, broad. Proximal filament with scattered black pigment.

TYPE LOCALITY.—Bernsteins Spring, east side of Cedros Island, Baja California Norte, Mexico. Holotype, CAS 66145; paratypes, CAS 66146, ANSP 141408.

DISTRIBUTION.—Probably was endemic to Cedros Island (one or more springs). The type locality and other springs on this island were visited in 1991 and found to be devoid of hydrobiid snails.

REMARKS.—Although glandular details were not discernable in the resuscitated paratypes, the distally bifurcate penis, with prominent lobe and pigmented filament, suggests that this snail belongs to *Pyrgulopsis*.

Pyrgulopsis chihuahua (Pilsbry, 1928), new combination

Fluminicola chihuahua Pilsbry, 1928:116, fig. 3.—Baker, 1964:171.
Cochliopa chihuahua.—Pilsbry, 1935a:92.
"Cochliopa" chihuahua.—Taylor, 1966b:179; 1967:153; 1975:56.

DIAGNOSIS.—Shell globose, small to medium-sized, umbilicate. Penial lobe short, filament elongate. Penial ornament a penial gland, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 12*a,b*) globose; height, 1.5–2.4 mm; whorls, 3.5. Early protoconch weakly punctate; otherwise smooth except for a few weak adapical spiral lines on later portion. Body whorl moderately convex with strong growth lines. Aperture ovate, large, adnate or very slightly separated from body whorl, gently angled above. Inner lip complete, slightly thickened; columellar lip slightly reflected; columellar region strongly excavated. Outer lip prosocline. Umbilicus narrowly perforate. Periostracum light brown, thin.

Operculum (Figure 12*c,d*) broadly ovate, light amber with darker central region; nucleus slightly eccentric; dorsal surface very weakly frilled. Attachment scar margin well thickened all around, portion between nucleus and inner edge sometimes broadly elevated; callus weak to prominent.

Central radular tooth (Figure 34*b*) with moderately indented dorsal edge; lateral cusps, 5–6; central cusp rounded, considerably broader and longer than laterals; basal cusps, 1, curved, narrow, short, with weak dorsal support. Basal process broad; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale or very light brown. Snout light to dark brown. Anterior and posterior edges of foot, margins of opercular lobe often dark brown; neck generally pale, but with scattered internal black granules. Pallial roof, visceral coil usually very dark brown-black.

Ctenidial filaments, 15, tall, narrow. Osphradium small, positioned posterior to center of ctenidial axis. Kidney opening slightly thickened. Caecum of stomach medium-sized, triangular.

Testis, 0.75 whorl, overlapping posterior stomach. Prostate gland stout; pallial section short (23%); pallial vas deferens simple. Penis (Figure 45*a*) medium-sized, scarcely extending beyond mantle edge; filament about as long as base, broadening distally, tapering to pointed tip; lobe short. Penial gland filling almost entire length of filament. Terminal gland large, transverse, borne on ventral surface near distal end of lobe. Ventral gland large, borne on short stalk, positioned near base of filament, often near continuous with terminal gland. Filament darkly pigmented internally and with scattered cover of black epithelial granules.

Ovary, 0.5 whorl, overlapping posterior stomach. Albumen gland without pallial section. Capsule gland as long as albumen gland. Genital aperture a very small terminal slit; vestibule very small or absent. Coiled oviduct a slight horizontal twist followed by small horizontal loop just behind pallial wall. Oviduct and bursal duct join just anterior to oviduct coil at pallial wall. Bursa copulatrix ovoid, medium length and width, with about half of length posterior to albumen gland. Bursal duct narrow, about as long as bursa copulatrix. Seminal receptacle finger-like, short (36%), overlapping mid bursal duct.

TYPE LOCALITY.—Type material came from a plant in the herbarium of the Academy of Natural Sciences that was collected by G. Thurber in 1852, under the auspices of the first United States and Mexican Boundary Survey, and labeled Chihuahua. Pilsbry attributed the material to Ojo Caliente, Chihuahua. On the basis of historical accounts of the expedition, Taylor (1967) later pinpointed the type locality as Ojo Caliente de Santa Rosa, situated in the north-central part of the state. Lectotype (Baker, 1964:171), ANSP 141266; paralectotypes, ANSP 396957.

DISTRIBUTION.—Type locality, Rio del Carmen drainage, and a few populations from southern Chihuahua, Rio Conchos drainage.

REMARKS.—Among species whose penes are ornamented solely by penial, terminal, and ventral glands, this snail is

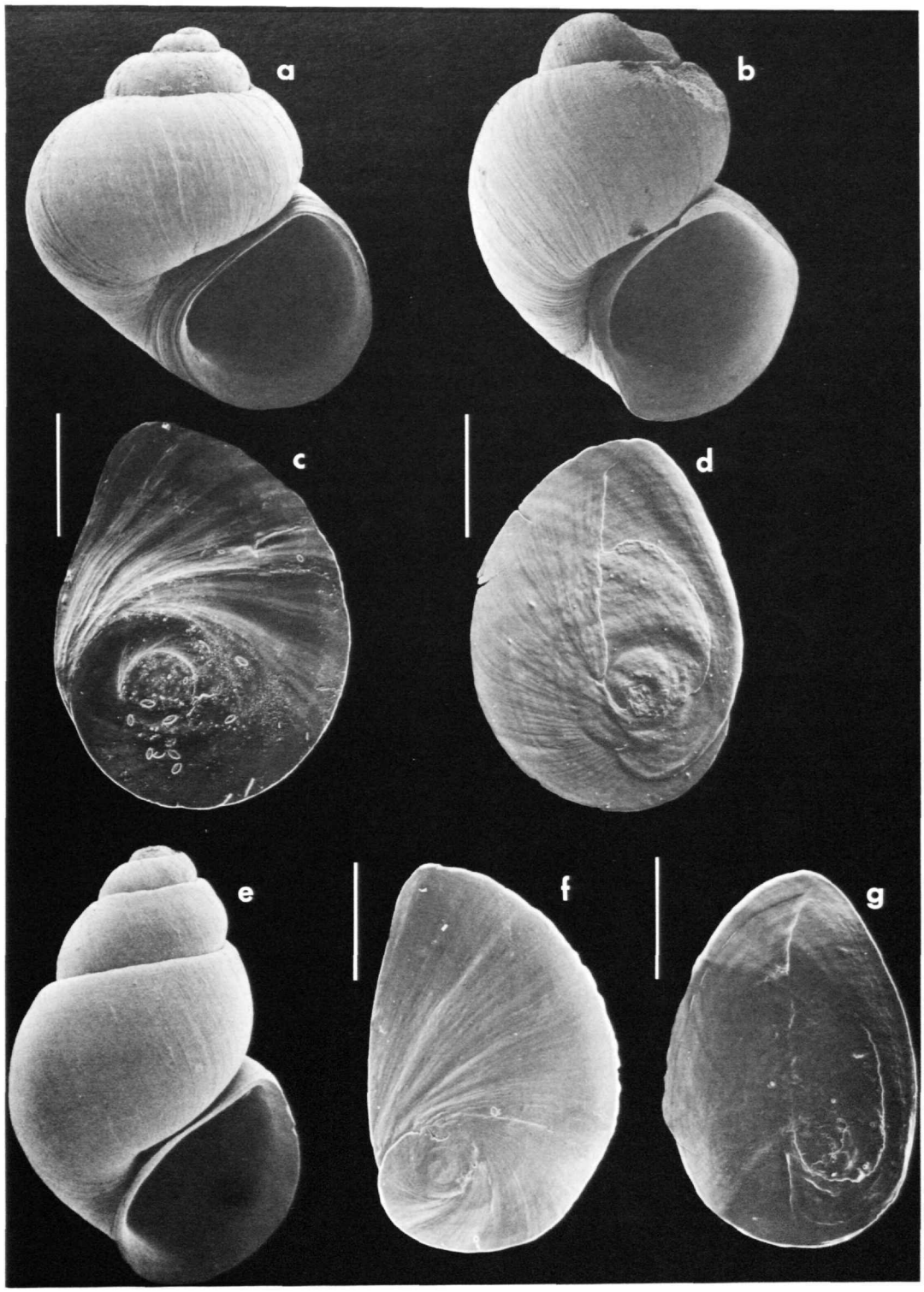


FIGURE 12.—Western *Pyrgulopsis: a–d, P. chihuahua* (*a*, shell, USNM 873291, 1.7 mm; *b*, shell, USNM 873296, 2.0 mm; *c,d*, opercula, bars = 0.31 mm, 0.29 mm); *e–g, P. chupaderae*, USNM 873426 (*e*, shell, 1.7 mm; *f,g*, opercula, bars = 0.26 mm, 0.25 mm).

distinguished by its globose shell and simple pallial vas deferens.

MATERIAL EXAMINED.—USNM 873296 (topotypes); USNM 873291, Ojo Caliente de Rosetilla, east of Delicias, Chihuahua, Mexico.

Pyrgulopsis chupaderae (Taylor, 1987), new combination

Fontelicella chupaderae Taylor, 1987:24, fig. 11.
"Fontelicella" chupaderae.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate- to elongate-conic, small to medium-sized, narrowly umbilicate. Penial lobe and filament medium length. Penial ornament an elongate penial gland, oblique Dg1, short Dg2, Dg3 borne on weak swelling; curved, transverse terminal gland; and ventral gland.

DESCRIPTION.—Shell (Figure 12*e*) ovate- to elongate-conic; height, 1.6–2.8 mm; whorls, 4.0–4.5. Protoconch weakly punctate. Teleoconch whorls slightly to moderately convex, weakly shouldered; sculpture of fine growth lines. Aperture large, narrowly ovate, strongly angled above, adnate or (more commonly) slightly separated from body whorl. Inner lip complete; columellar lip thick, usually broadly reflected. Outer lip near orthocline. Umbilicus narrowly rimate. Periostracum tan to brown.

Operculum (Figure 12*f,g*) narrowly ovate, dark amber; nucleus highly eccentric; dorsal surface frilled. Attachment scar margin thickened all around, broadly elevated between nucleus and inner edge; callus small.

Central radular tooth (Figure 34*c*) with strongly indented dorsal edge; tooth face square; lateral cusps, 5; central cusp pointed, narrow, longer than laterals; basal cusps, 1, medium-sized, with weak dorsal support. Basal process broad; basal sockets deep. Lateral margins slightly thickened; neck very weak.

Cephalic tentacles, snout, anterior and posterior edges of foot, anterior edge of opercular lobe, pallial roof, visceral coil dark gray-black. Neck usually lighter than remaining head-foot, sometimes pale.

Ctenidial filaments, 15, medium height and width. Osphradium centrally positioned along ctenidial axis. Kidney opening white. Stomach caecum small, hemispherical.

Testis, 0.5 whorl, pressed against posterior edge of stomach. Prostate gland elongate bean-shaped; pallial section large (33%); pallial vas deferens proximally kinked. Penis (Figure 45*b*) large, extending well beyond mantle edge; base elongate-rectangular; filament medium length, narrow, strongly tapering; lobe shorter than filament, broad, swollen distally. Penial gland filling most of filament length. Dg1 oblique, filling half or less of penis width, borne on low swelling; Dg2 short, slightly oblique; Dg3 borne on weak swelling along right edge of lobe distally. Terminal gland elongate, curved, transverse, borne along distal edge of lobe (ventral aspect). Ventral gland large, stalked, borne near mid-length, sometimes accompanied by smaller gland anteriorly. Filament moderately pigmented internally.

Ovary, 1 whorl, very slightly overlapping posterior stomach. Pallial albumen gland large (33%). Capsule gland considerably longer than albumen gland. Genital aperture a broad terminal opening without vestibule. Coiled oviduct a small, circular loop abutting pallial wall. Oviduct and bursal duct join at pallial wall. Bursa copulatrix pyriform, posterior end weakly angled-pointed, massive (considerably longer and as broad as albumen gland), with almost entire length posterior to albumen gland. Bursal duct emerges slightly lateral to anterior tip of structure; duct slender, very short, slightly dorsal to coiled oviduct, partially embedded in albumen gland proximally. Seminal receptacle finger-like, short, positioned along ventral edge of bursa copulatrix near mid-length.

TYPE LOCALITY.—Willow Spring, on Cienaga Ranch at south end of Chupadera Mountains, about 5 mi (8 km) west of Bosque del Apache National Wildlife Refuge headquarters, Socorro County, New Mexico. Holotype, LACM 2218; paratypes, UTEP 10052, ANSP 376027, FSM 160938, USNM 854081.

DISTRIBUTION.—Endemic to type locality area, Rio Grande drainage.

REMARKS.—This species differs from closely similar *P. neomexicana* by its single ventral gland on penis, anterior position of ovary, circular oviduct coil, dorsal position of bursal duct, and ventral position of seminal receptacle.

MATERIAL EXAMINED.—USNM 873426 (topotypes).

Pyrgulopsis conica Hershler, 1988

Pyrgulopsis conicus Hershler in Hershler and Landye, 1988:21, figs. 10e, 16a–d, 17, 18.—USDI, 1991b:58821.

DIAGNOSIS.—Shell ovate- to elongate-conic, small to medium-sized, umbilicate. Penial lobe and filament medium length. Penial ornament a near-circular terminal gland.

DESCRIPTION.—Shell (Figure 13*a*) ovate- to elongate-conic; height, 1.8–2.7 mm; whorls, 4. Protoconch near smooth. Teleoconch whorls convex, slightly shouldered; sculpture of moderate growth lines. Aperture adnate or slightly separated from body whorl. Inner lip complete, slightly thickened; columellar lip reflected. Outer lip near orthocline. Umbilicus narrowly rimate to broadly perforate. Periostracum very light amber.

Operculum (Figure 13*b,c*) ovate, very light amber; nucleus highly eccentric; dorsal surface smooth. Attachment scar margin broadly thickened between nucleus and inner edge, and along latter; scar a faint trace along outer edge; callus very small.

Central radular tooth (Figure 34*d*) with moderately indented dorsal edge; lateral cusps, 4–6; central cusp pointed, slightly longer than laterals; basal cusps, 1, short, broadly triangular, with weak to moderate dorsal support. Basal process narrowly

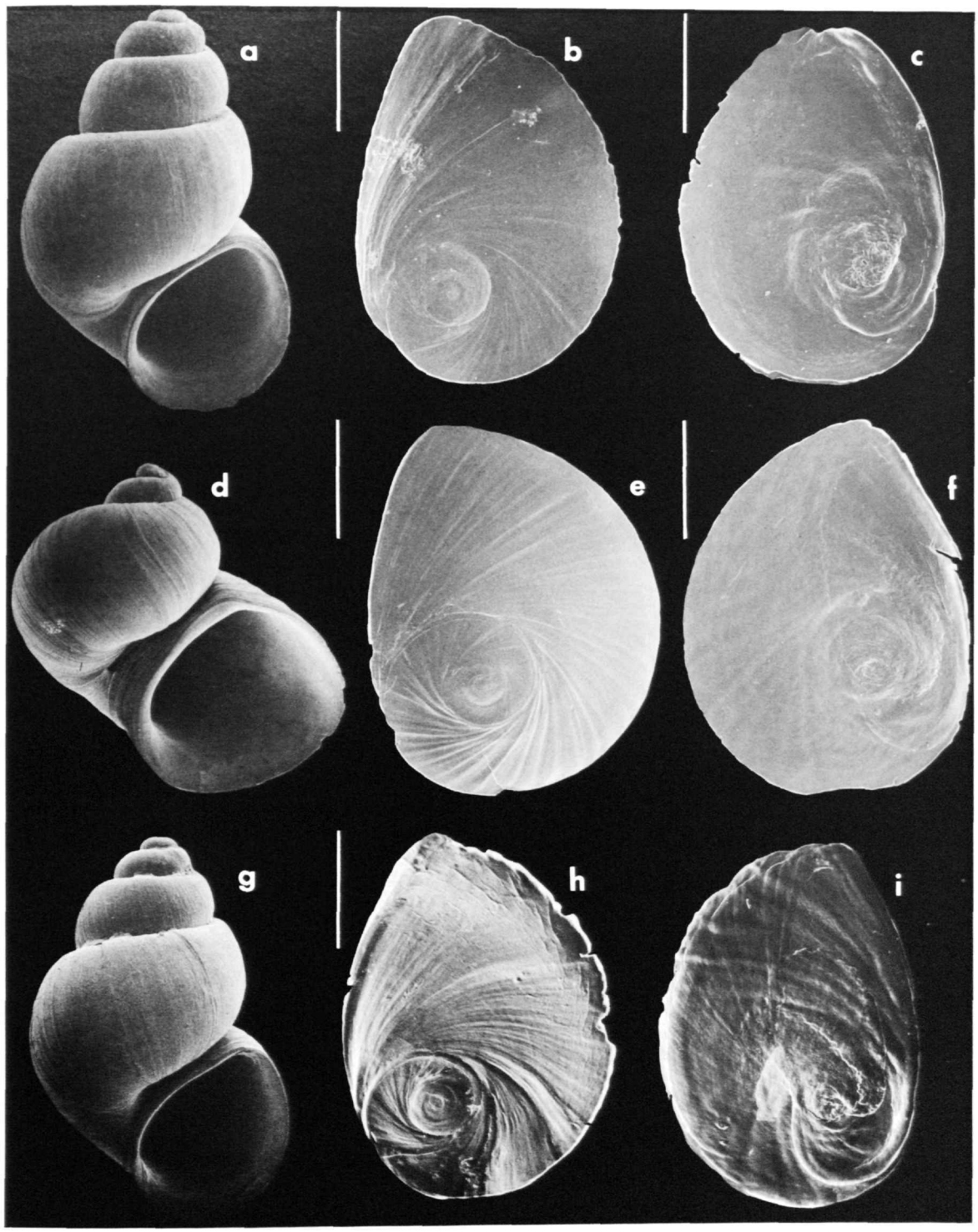


FIGURE 13.—Western *Pyrgulopsis: a–c, P. conica* (*a*, holotype, USNM 859039, 2.5 mm; *b,c*, opercula, USNM 847237, bars = 0.31 mm, 0.30 mm); *d–f, P. crystalis* (*d*, holotype, USNM 859205, 2.3 mm; *e,f*, opercula, USNM 850369, bars = 0.35 mm, 0.31 mm); *g–i, P. davisi*, USNM 873247 (*g*, shell, 2.3 mm; *h, i*, opercula, bars = 0.32 mm, 0.33 mm).

constricted; basal sockets deep. Lateral margins thickened; neck weak.

Head-foot usually pale, although snout sometimes light brown and opercular lobe sometimes dark along inner edge. Pallial roof, visceral coil near pale to dark brown-black.

Ctenidial filaments, 18, medium length, narrow. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum medium-sized, finger-like.

Testis, 1.25 whorls, overlapping posterior and sometimes part of anterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 45*c*) large, elongate; filament medium length, attenuate; lobe slightly shorter than filament, rectangular, slightly oblique. Terminal gland near-circular, positioned along distal edge of lobe (largely on ventral surface). Filament near-pale to dark.

Ovary, 0.5 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture a subterminal pore with short vestibule. Coiled oviduct a broad horizontal loop. Oviduct and bursal duct join just behind pallial wall. Bursal copulatrix ovoid, medium length and width, with about 27% of length posterior to gland. Bursal duct medium width, slightly shorter than bursa copulatrix. Seminal receptacle finger-like, sometimes folded, short, positioned lateral to anterior bursa copulatrix near ventral edge of albumen gland.

TYPE LOCALITY.—Dripping Springs, Mohave County, Arizona (T 19N, R 19W, sec. 4).

DISTRIBUTION.—Sacramento Valley west of Kingman, Mohave County, Arizona, Colorado River basin.

REMARKS.—Among congeners having penis ornamented solely by terminal gland, *P. conica* is distinguished by combination of narrow bursa copulatrix and ventral position of seminal receptacle.

MATERIAL EXAMINED.—USNM 847237 (topotypes).

Pyrgulopsis crystalis Hershler and Sada, 1987

Pyrgulopsis crystalis Hershler and Sada, 1987:797, figs. 8c,f,i, 18c, 23d, 24b, 25, 28.
Pyrgulopsis cristalis [sic].—USDI, 1991b:58821.

DIAGNOSIS.—Shell globose to neritiform, small to medium-sized, umbilicate. Penial lobe absent, filament elongate. Penial ornament a large, superficial ventral gland.

DESCRIPTION.—Shell (Figure 13*d*) globose-neritiform; height, 1.8–2.6 mm; whorls, 3.0–3.5. Protoconch near smooth, sometimes tilted relative to later whorls. Teleoconch whorls convex, without shoulders; sculpture of strong growth lines. Aperture broadly ovate, large, adnate or slightly separated from body whorl. Inner lip complete, broad and highly thickened in mature specimens, very weakly angled above. Outer lip strongly prosocline, weakly sinuate. Umbilicus perforate, excavated. Periostracum light brown.

Operculum (Figure 13*e,f*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin weakly thickened along inner edge (to nucleus) and faint along outer edge; callus a very slight thickening.

Central radular tooth (Figure 34*e*) with moderately indented dorsal edge; lateral cusps, 3–4; central cusp pointed, broader and considerably longer than laterals; basal cusps, 1, short, strongly curved, with weak dorsal support. Basal process medium width; basal sockets moderately deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale or light brown. Snout, foot, neck pale to dark gray-brown. Opercular lobe pale to dark brown along margins. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 18, tall, narrow. Osphradium centered posterior to middle of ctenidial axis. Kidney with very slight bulge (10%) into pallial cavity; opening thickened slightly. Stomach without caecum.

Testis, 0.75 whorl, overlapping stomach to edge of style sac. Prostate gland a fat bean-shape, thickened, without a pallial portion. Pallial vas deferens weakly kinked proximally. Penis (Figure 45*d*) small to medium-sized; filament about as long as base, tapering to pointed tip; lobe absent. Ventral gland large, superficial, positioned slightly distal to mid-line. Filament darkly pigmented internally.

Ovary, 1 whorl, overlapping stomach almost to edge of style sac. Pallial albumen gland short. Capsule gland considerably shorter than albumen gland, highly thickened. Genital aperture a broad terminal pore; vestibule absent. Coiled oviduct a tight vertical coil overlapping a near-circular loop. Oviduct and bursal duct join at pallial wall. Bursa copulatrix ovoid, short (33%), medium width, extending to posterior edge of albumen gland or with up to 30% of length posterior to gland. Bursal duct narrow, longer than bursa copulatrix, partly embedded in albumen gland. Seminal receptacle pouch-like, short, overlapping proximal to mid bursal duct.

TYPE LOCALITY.—Crystal Pool, Ash Meadows, Nye County, Nevada (T 18S, R 50E, NE1/4 sec. 3). Holotype, USNM 859205; paratypes, FSM 93956, USNM 859206.

DISTRIBUTION.—Endemic to type locality, Amargosa River drainage.

REMARKS.—Among the group of species having penes without lobe and terminal gland, this species is distinguished by its broad central radular tooth, absence of caecal chamber of stomach, absence of pallial portion of prostate gland, and anterior position of bursa copulatrix.

MATERIAL EXAMINED.—USNM 850369 (topotypes).

Pyrgulopsis davisi (Taylor, 1987), new combination

Fontelicella davisi Taylor, 1987:10, fig. 4.
"Fontelicella" davisi.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate to narrowly conic, medium-sized, umbilicate. Penial filament and lobe medium length. Penial

ornament an elongate, proximally bifurcate, penial gland; transverse Dg1, short Dg2, Dg3 borne on raised swelling, curved, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 13*g*) ovate- to narrowly conical; height, 2.7–3.9 mm; whorls, 4–4.5. Early protoconch moderately punctate, later portion weakly punctate-smooth, with a few abapical spiral lines. Teleoconch whorls moderately to highly convex, shouldered; sculpture of moderate growth lines. Aperture ovate, angled above, usually separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip near-orthocline. Umbilicus weakly to moderately perforate. Periostracum light tan.

Operculum (Figure 13*h,i*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin broadly thickened between nucleus and inner edge and along most or all of length of latter; scar weaker or faint along outer edge; callus very weak, but broad in extent.

Central radular tooth (Figure 34*f*) with moderately indented dorsal edge; lateral cusps, 4; central cusp rounded, elongate, broader than laterals; basal cusps, 1, short, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins moderately thickened; neck pronounced.

Cephalic tentacles pale or with moderate gray-black pigment proximally. Snout light to dark gray-black. Foot pale or dark along anterior and posterior margins. Opercular lobe with dark internal pigment along sides. Neck generally light, but sometimes with dark internal pigment patch. Pallial roof, visceral coil moderate to dark brown-black. Completely pale individuals rare.

Ctenidial filaments, 20, narrow, short. Osphradium centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum medium-sized.

Testis, 1 whorl, very slightly overlapping posterior stomach. Prostate an elongate bean-shape; pallial section large (>50%); pallial vas deferens undulating along columellar muscle. Penis (Figure 45*e*) large, extending beyond mantle edge; base near square; filament medium length, broad, tapering distally; lobe slightly shorter than filament, narrowing distally. Penial gland elongate, bifurcating proximally. Dg1 crossing about half of penis width, stalked, positioned near mid-penis; Dg2 a narrow strip; Dg3 borne on raised swelling. Dorsal penis sometimes also with 1-2 additional small glands near distal edge. Terminal gland elongate, transverse, slightly curved, borne along distal (largely ventral surface) edge of lobe. Ventral gland prominent, stalked, positioned near distal edge; small glandular dot sometimes present slightly proximally to above. Filament with scattered dark granules.

Ovary, 0.5 whorl, extending to posterior edge of stomach. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture a broad terminal pore with short vestibule. Coiled oviduct a slight kink followed by broad horizontal loop extending to pallial wall. Oviduct and bursal duct join at pallial wall. Bursa copulatrix ovoid, medium length, broad (66%), with most of length (75%) posterior to albumen gland. Bursal duct narrow, about half of length of bursa copulatrix. Seminal receptacle sac-like, short, overlapping anterior bursa copulatrix.

TYPE LOCALITY.—Tributary of Limpia Creek about 5 mi (8 km) northeast of Fort Davis, Jeff Davis County, Texas. Holotype, LACM 2211; paratypes, UTEP 10053, ANSP 376023, FSM 160944, USNM 854085.

DISTRIBUTION.—Thus far known only from the type locality (Pecos River drainage) although dry shell collections suggest that it may also occur at a few other local sites (Taylor, 1987).

REMARKS.—This snail differs from similar *P. metcalfi* by its stronger ventral operculum callus, circular oviduct coil, dorsal position of bursal duct, and ventral position of seminal receptacle.

MATERIAL EXAMINED.—USNM 873427 (topotypes).

Pyrgulopsis deserta (Pilsbry, 1916)

Amnicola deserta Pilsbry, 1916:111, figs. 8, 9.—Walker, 1918:133.—Baker, 1964:172.

"Amnicola" deserta.—Landye, 1981:70.

Fontelicella deserta.—Taylor, 1975:73.—Burch, 1982:26, fig. 237.—Turgeon et al., 1988:61.

Pyrgulopsis deserta.—Hershler and Thompson, 1987:29.—Hershler and Landye, 1988:17, figs. 10c, 11a–d, 12a–c, 13.

DIAGNOSIS.—Shell globose to ovate-conic, small to medium-sized, umbilicate. Penial filament medium length, lobe short. Penial ornament an elongate penial gland, near-circular terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 14*a*) globose to ovate-conic; height, 1.2–2.4 mm; whorls, 3.5–4.25. Early protoconch moderately punctate, otherwise near smooth. Teleoconch whorls very slightly to highly convex, very weakly to strongly shouldered; sculpture of weak growth lines. Aperture angled above, broadly adnate to slightly separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip usually prosocline. Umbilicus narrowly rimate (rarely absent) to broadly perforate. Periostracum light brown. Operculum (Figure 14*b,c*) ovate, light amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin moderately thickened along inner edge (nuclear half) to nucleus; scar faint to absent along outer edge; callus weak-absent.

Central radular tooth (Figure 35*a*) with strongly indented dorsal edge; lateral cusps, 4–6, narrowly elongate; central cusp pointed, considerably longer than laterals; basal cusps, 1, short, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale to moderate brown, sometimes with conspicuous pigment patch just distal to eyespots. Snout pale to dark brown-black; foot similarly pigmented, usually lighter in central region. Opercular lobe pale or with dark streak along inner edge. Neck pale to lightly pigmented. Pallial roof pale to dark; visceral coil moderate-dark, sometimes uniformly black.

Ctenidial filaments, 10, medium height, narrow. Osphra-

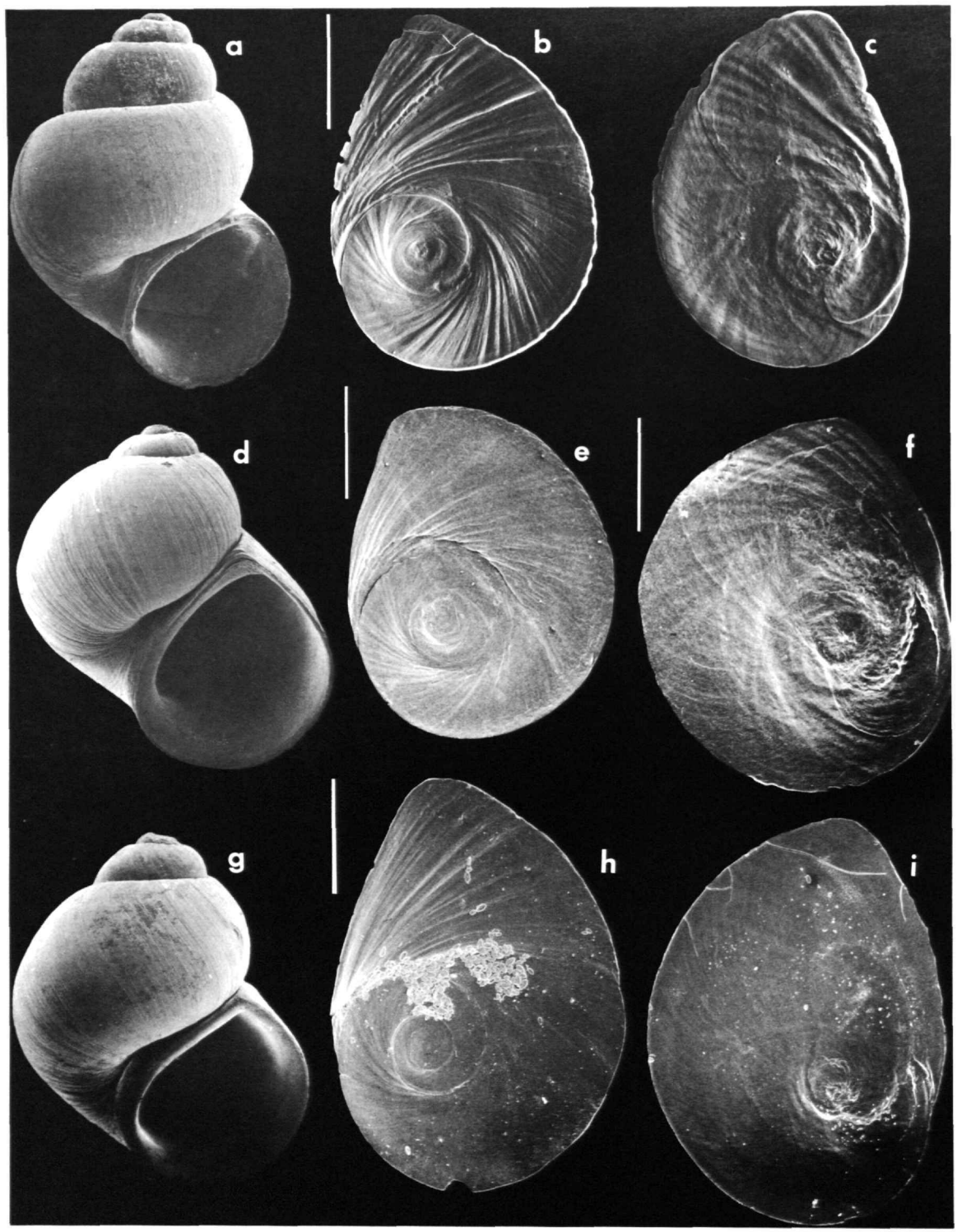


FIGURE 14.—Western *Pyrgulopsis*: *a–c*, *P. deserta* (*a*, shell, USNM 847206, 1.7 mm; *b,c*, opercula, USNM 847202, bar = 0.26 mm); *d–f*, *P. erythropoma*, USNM 857864 (*d*, shell, 2.2 mm; *e,f*, opercula, bars = 0.38 mm, 0.33 mm); *g–i*, bottom row, *P. fairbanksensis* (*g*, holotype, USNM 859203, 2.5 mm; *h*, *i*, opercula, USNM 850367, bar = 0.38 mm).

dium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum medium-sized.

Testis, 0.75–1.0 whorls, abutting or very slightly overlapping posterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 45*f*) large; base square; filament slightly shorter than base, broad; lobe very short, triangular. Penial gland extending almost to tip of filament. Terminal gland variably shaped, borne on distal edge of lobe, usually on ventral side. Ventral gland large, stalked, positioned near base of lobe; second gland sometimes present lateral (inside) to above. Filament pale to moderately pigmented.

Ovary, 0.5–0.75 whorls, abutting or slightly overlapping posterior stomach chamber. Pallial albumen gland large (40%). Capsule gland about equal to albumen gland in length. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a posterior oblique loop well behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursal copulatrix pyriform, posterior end weakly angled, as long or slightly longer and almost as broad as albumen gland, with most of length (90%) posterior to gland. Bursal duct short, narrow, dorsal to coiled oviduct. Seminal receptacle finger-like, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Washington County, Utah (not subsequently restricted). One of two specimens in type lot (per Baker, 1964:172) figured by Pilsbry selected herein as lectotype, ANSP 12112; paralectotypes, ANSP 396958.

DISTRIBUTION.—Virgin River drainage. Consisting of disjunct groups of populations in and near St. George, southwestern Utah; and below the Virgin River Narrows near Littlefield, northwestern Arizona.

REMARKS.—Amongst the group of species whose penis is ornamented by penial, terminal, and ventral glands, this species is strongly differentiated by features including a deeply indented dorsal edge of central radular tooth; simple, circular oviduct coil, enlarged bursa copulatrix, and dorsally positioned bursal duct. *Pyrgulopsis deserta* differs from more advanced members of Clade 5 by its circular terminal gland and absence of dorsal glands on the penis.

The two groups of populations are differentiated, with Arizona snails having smaller, more globose shells.

MATERIAL EXAMINED.—USNM 847202, spring upstream on Virgin River from Littlefield, Mohave County, Arizona (T 40N, R 15W, sec. 3).

Pyrgulopsis erythropoma (Pilsbry, 1899)

Fluminicola fusca var. *minor* Stearns, 1893:282 [nomen nudum].

Fluminicola erythropoma Pilsbry, 1899:125.—Hannibal, 1912b:188.—Walker, 1918:141.—Baker, 1964:172.—Burch, 1982:22.—Turgeon et al., 1988:60.

"Fluminicola" erythropoma.—Taylor, 1975:79.

Pyrgulopsis erythropoma.—Hershler and Sada, 1987:791, figs. 8b,e,h, 17, 18d–i, 19b,c, 20–22, 23a–c, 24a,c, 25.—USDI, 1991b:58821.

DIAGNOSIS.—Shell globose-turbinate, small to medium-sized, umbilicate. Penial filament elongate, lobe absent. Penial ornament a large, superficial ventral gland.

DESCRIPTION.—Shell (Figure 14*d*) globose-turbinate; height, 1.6–2.4 mm; whorls, 3–4. Protoconch weakly punctate, with a few weak adapical spiral lines on later portion. Teleoconch whorls moderately convex, shouldered; sculpture of strong growth lines. Aperture large, broadly ovate, adnate to body whorl. Inner lip complete, thickened. Outer lip prosocline. Umbilicus perforate. Periostracum amber.

Operculum (Figure 14*e,f*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin broadly thickened along inner edge, slightly less thickened between edge and nucleus; scar along outer edge faint; callus moderate.

Central radular tooth (Figure 35*b*) with well-indented dorsal edge; lateral cusps, 7, narrowly elongate; central cusp pointed, considerably longer than laterals; basal cusps, 1, short, broadly triangular, with weak dorsal support. Basal process broad, tongue-like; basal sockets deep. Lateral margins thickened; neck weak.

Cephalic tentacles pale or light-moderate gray. Snout, foot moderate gray. Opercular lobe sometimes black along inner edge (internal) and on sides (epidermal). Neck pale or moderately pigmented. Pallial roof, visceral coil uniformly black.

Ctenidial filaments, 18, tall, medium width. Osphradium small, centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum small, narrow.

Testis, 1 whorl, overlapping stomach to edge of style sac. Prostate gland a fat bean-shape, with large (30%) pallial section; pallial vas deferens with small proximal kink. Penis (Figure 46*a*) medium-sized, blade-like; filament slightly shorter and narrower than base; lobe absent. Ventral gland large, circular, superficial, near-central. Filament dark.

Ovary, 0.5 whorl, overlapping posterior stomach chamber. Albumen usually without a pallial section. Capsule gland as long as albumen gland. Genital aperture a broad, terminal pore, usually without vestibule. Coiled oviduct a weak twist followed by near circular loop. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix globular-ovoid, short (27%), about half as wide as albumen gland, positioned largely (66%–75%) posterior to albumen gland. Bursal duct narrow, about as long as bursa copulatrix. Seminal receptacle finger-like, medium length, positioned lateral to proximal bursal duct.

TYPE LOCALITY.—Ash Meadows, Nye County, Nevada. Original material was collected in 1891 by F. Stephens as member of the Death Valley Exploring Expedition. According to the list of collecting localities of the expedition (Palmer, 1893), the Ash Meadows spring visited by Stephens was, "King Spring or Stone House (altitude about ... 1,160 m), on the eastern side of the valley..." This corresponds to Kings Pool at

Point of Rocks (T 18S, R 51E, SE1/4 sec. 7), which I have considered as the type locality (Hershler and Sada, 1987). Lectotype (Baker, 1964:172), ANSP 73607; paralectotypes, ANSP 396951.

DISTRIBUTION.—Point of Rocks spring complex, Ash Meadows, Amargosa River drainage.

REMARKS.—Distinguished from closely similar *P. pisteri* by its more globose shell, blade-like penis, and absence of anterior capsule gland vestibule.

MATERIAL EXAMINED.—USNM 857861 (topotypes); USNM 857862, Point of Rocks springs.

Pyrgulopsis fairbanksensis Hershler and Sada, 1987

Pyrgulopsis fairbanksensis Hershler and Sada, 1987:796, figs. 8d,g, 18a,b, 19a, 24d, 25–27.—USDI, 1991b:58821.

DIAGNOSIS.—Shell globose-turbinate, medium-sized, umbilicate. Penial filament elongate, lobe short. Penial ornament a small, circular terminal gland.

DESCRIPTION.—Shell (Figure 14*g*) globose-turbinate; height, 2.5–3.4 mm; whorls, 3–4. Early protoconch weakly punctate (Figure 1*c*), later portion near smooth except for faint adapical spiral striae. Teleoconch whorls moderately convex, weakly shouldered; sculpture of strong growth lines. Aperture broadly ovate, adnate or slightly separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip prosocline. Umbilicus rimate to perforate, often eroded. Periostracum light amber.

Operculum (Figure 14*h,i*) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface very weakly frilled. Attachment scar margin smooth except for weak thickening along inner edge near nucleus; callus very small, weak.

Central radular tooth (Figure 35*c*) with weakly indented dorsal edge; lateral cusps, 3–4; central cusp pointed, extremely broad, considerably longer than laterals; basal cusps, 1, small, short, with strong dorsal support. Basal process broad; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale. Snout pale to moderate brown; foot light-moderate brown. Opercular lobe pale or dark along margins, especially anterior and posterior edges. Neck pale-light brown. Pallial roof, visceral coil light-dark brown.

Ctenidial filaments, 18, tall, medium width, extending to mantle edge. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum absent.

Testis, 1.25 whorls, overlapping stomach to posterior edge of style sac. Prostate gland with large (40%) pallial section; pallial vas deferens without proximal kink. Penis (Figure 46*b*) medium-sized, elongate; base elongate-rectangular; filament about as long as and slightly narrower than base; lobe very short, distally blunt. Terminal gland circular, borne along distal edge of lobe, usually on ventral surface. Filament moderate brown; pigment sometimes only present proximally.

Ovary, 0.5 whorl, slightly overlapping anterior stomach chamber. Albumen gland without a pallial section. Capsule gland as long as albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a small, near circular loop (sometimes preceeded and overlapped by weak horizontal twist) slightly posterior to pallial wall. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix sub-globular, medium length, broad (65%), with about 40% of length posterior to albumen gland. Anterior bursa copulatrix usually shallowly embedded in albumen gland.

Bursal duct very narrow, embedded in albumen gland, slightly longer than bursa copulatrix. Seminal receptacle sac-like, short, overlapping proximal bursa duct, sometimes shallowly embedded in albumen gland.

TYPE LOCALITY.—Fairbanks Spring, Ash Meadows, Nye County, Nevada (T 17S, R 50E, NE1/4 sec. 9). Holotype, USNM 859203; paratypes, USNM 859204, FSM 93955.

DISTRIBUTION.—Endemic to type locality, Amargosa River drainage.

REMARKS.—Distinguished from similar *P. isolata* by elongate central radular tooth, absence of caecal chamber of stomach, short penial lobe, circular terminal gland of penis, broad bursa copulatrix, short seminal receptacle.

MATERIAL EXAMINED.—USNM 850367, 850368 (topotypes).

Pyrgulopsis gilae (Taylor, 1987), new combination

Fontelicella gilae Taylor, 1987:16, fig. 7.
"Fontelicella" gilae.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate-conic, medium to large-sized, narrowly umbilicate. Penial filament and lobe medium length. Penial ornament of two elongate penial glands, short Dg2, Dg3 borne on weak swelling, several other small dorsal glands; curved, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 15*a*) ovate-conic; height, 3.1–4.0 mm; whorls, 4.5. Protoconch near smooth. Teleoconch whorls moderately to highly convex, shouldered; sculpture of moderate growth lines. Aperture ovate, adnate or slightly separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip slightly prosocline. Umbilicus narrowly perforate. Periostracum tan.

Operculum (Figure 15*b,c*) ovate, light amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin broadly thickened between nucleus and inner edge, otherwise faint; callus weak.

Central radular tooth (Figure 35*d*) with moderately indented dorsal edge; lateral cusps, 4; central cusp rounded, slightly broader, considerably longer than laterals; basal cusps, 1, medium-sized, slightly curved, with moderate dorsal support. Basal process moderately broad; basal sockets deep. Lateral margins slightly thickened; neck moderate-pronounced.

Head-foot generally pale. Cephalic tentacles with black internal pigment patches distal to eyespots. Snout pale or light brown. Opercular lobe with dark internal pigment along

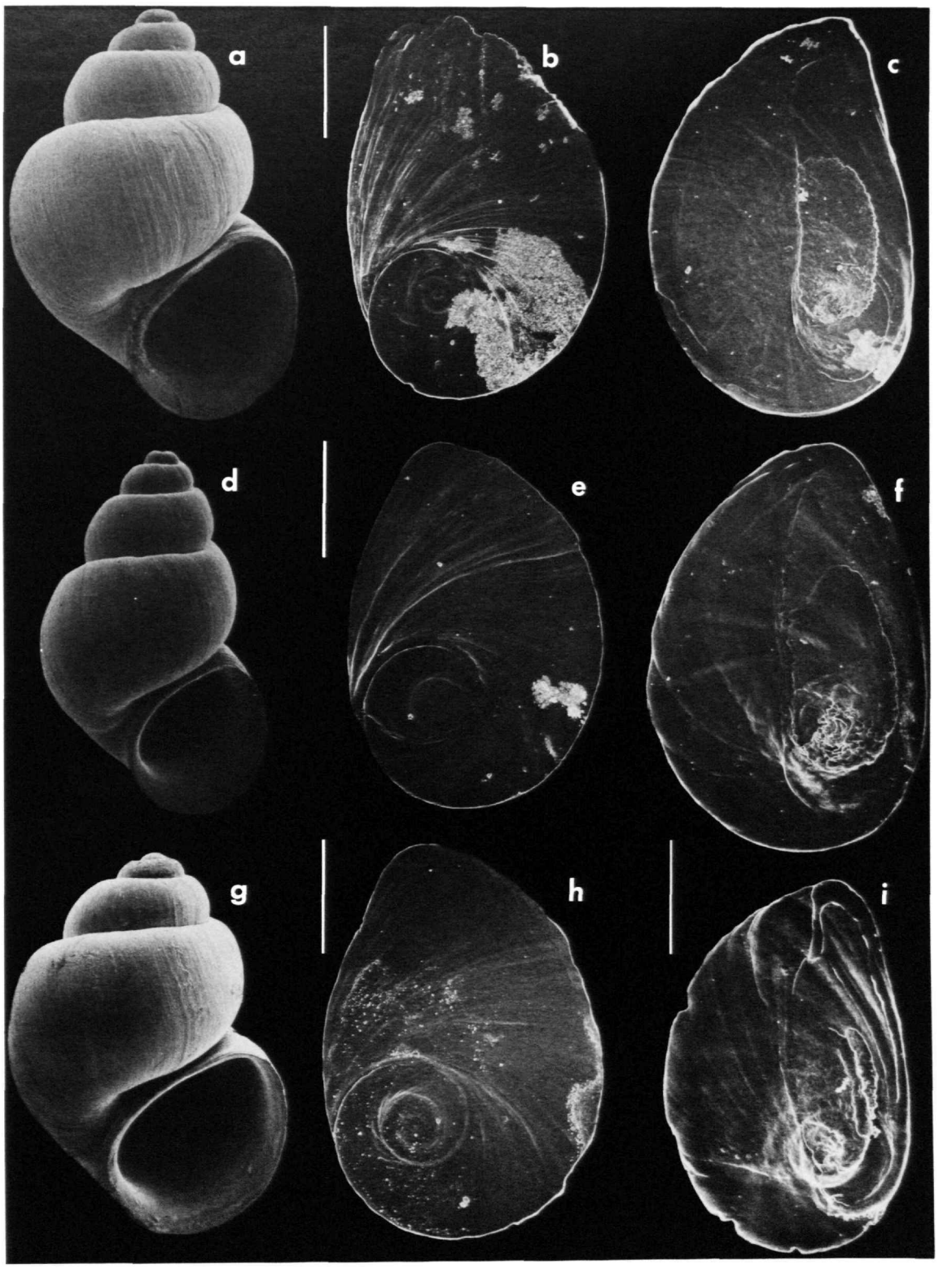


FIGURE 15.—Western *Pyrgulopsis*: *a–c*, *P. gilae*, USNM 873211 (*a*, shell, 2.9 mm; *b,c*, opercula, bar = 0.38 mm); *d–f*, *P. giulianii*, USNM 857954 (*d*, shell, 3.0 mm; *e*, *f*, opercula, bar = 0.33 mm); *g–i*, *P. glandulosa*, USNM 847205 (*g*, shell, 2.4 mm; *h*, *i*, opercula, bars = 0.3 mm, 0.38 mm).

anterior edge and sometimes on sides. Pallial roof, visceral coil light to dark brown-black.

Ctenidial filaments, 20, short, narrow. Osphradium centered slightly posterior of middle of ctenidial axis. Kidney opening white. Stomach caecum medium-sized.

Testis, 1.25 whorls, overlapping stomach to edge of style sac. Prostate gland with short pallial section; pallial vas deferens with thickened proximal coil. Penis (Figure 46*c*) large, extending beyond mantle edge; base near square; filament medium length, gently tapering; lobe slightly shorter than filament, medium width. Penial glands, 2 (sometimes fused distally), filling either edge of filament (that to the right extending slightly onto penis), both extending almost to distal tip of filament. Dg2 short; Dg3 borne on weak swelling. Dorsal penis also bearing medium-sized glands near distal edge (or on proximal lobe), and several smaller scattered glands. Terminal gland transverse, curved, borne along distal edge of lobe (mostly ventrally). Ventral gland stalked, prominent, positioned near distal edge; ventral penis also with 1 or more smaller glands near mid-line. Filament usually with dark internal pigment.

Ovary, 0.5 whorl, slightly overlapping posterior stomach. Pallial albumen gland short. Capsule gland as long as albumen gland, thin. Genital aperture a medium-sized terminal slit with short vestibule. Coiled oviduct of two overlapping horizontal loops slightly posterior to pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix elongate-pyriform, posterior end pointed, about equal to albumen gland in length, broad (80%), almost entirely (90%) posterior to albumen gland. Bursal duct narrow, short. Seminal receptacle sac-like, short, overlapping proximal bursal duct.

TYPE LOCALITY.—Springs on north side of East Fork of Gila River, center of sec. 3, T13S, R 13W, unsurveyed, Grant County, New Mexico. Holotype, LACM 2214; paratypes, UTEP 10054, ANSP 376025, FSM 160936, USNM 854087.

DISTRIBUTION.—Gila River drainage, western New Mexico.

REMARKS.—Amongst members of *Pyrgulopsis*, only this species and *P. merriami* have multiple penial glands. *Pyrgulopsis gilae* differs in its ovate-conic shell, strong ventral operculum attachment scar, presence of Dg2, additional minor dorsal glands, two ventral glands, and short seminal receptacle.

MATERIAL EXAMINED.—USNM 873211, Hot Spring, about 2.5 km below HWY 15 crossing of Gila River, Grant County, New Mexico (T 13S, R 13W, SW1/4 sec. 17).

Pyrgulopsis giulianii Hershler and Pratt, 1990

Pyrgulopsis cf. *stearnsiana*.—Hershler, 1989:194, figs. 37–40.
Pyrgulopsis giulianii Hershler and Pratt, 1990:279, figs. 1–4.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized, umbilicate. Penial filament medium length, lobe very short. Penial ornament a circular Dg1, weakly developed terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 15*d*) ovate-conic; height, 2–4 mm tall; whorls, 4.0–4.5. Early protoconch weakly punctate, later portion near smooth. Teleoconch whorls moderately convex, slightly shouldered; sculpture of weak growth lines. Aperture narrowly adnate or (more commonly) slightly separated from body whorl. Inner lip complete, slightly thickened; columellar lip slightly reflected. Outer lip orthocline to slightly prosocline. Umbilicus narrowly rimate to perforate. Periostracum brown-black, sometimes thick.

Operculum (Figure 15*e,f*) ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin moderately thickened all around; callus pronounced.

Central radular tooth (Figure 35*e*) with slightly indented dorsal edge; lateral cusps, 5–6; central cusp pointed, considerably broader and longer than laterals; basal cusps, 1, small, with strong dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale or light brown proximally. Snout moderate-dark gray. Foot pale to light gray. Opercular lobe moderate to dark gray-black, especially on sides and along anterior edge. Neck pale to lightly pigmented. Pallial roof, visceral coil moderate to (more commonly) dark brown-black.

Ctenidial filaments, 23, tall, medium width. Osphradium centered posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum very small to medium-sized.

Testis, 1.5 whorls, overlapping posterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens simple. Penis (Figure 46*d*) medium-sized (rarely protruding beyond mantle edge); filament shorter than base, narrow; lobe very short, narrow. Dg1 large, circular, centrally positioned. Terminal gland small (sometimes absent), variably shaped, borne along distal edge of lobe, typically on ventral surface. Ventral gland medium-sized, borne on short stalk near distal edge. Filament dark.

Ovary, 0.5–0.75 whorl, usually abutting (rarely slightly overlapping) posterior edge of stomach. Pallial albumen gland short. Capsule gland as long as albumen gland. Genital aperture a broad terminal slit with short vestibule. Coiled oviduct a short vertical twist followed by broad horizontal loop slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, short, about half as wide as albumen gland, with 33%–75% of length posterior to albumen gland. Bursal duct narrow, sometimes partly embedded in albumen gland, medium length. Seminal receptacle a stubby pouch, short, positioned lateral to proximal bursal duct near ventral edge of albumen gland.

TYPE LOCALITY.—Sand Canyon, Kern County, California (T 25S, R 38E, center sec. 7). Holotype, USNM 860444; paratypes, USNM 853519, SBMNH 35140.

DISTRIBUTION.—Springs in southern Sierra Nevada: Death Valley System and Kern River drainage, California.

MATERIAL EXAMINED.—USNM 857974 (paratypes); SBMNH uncat., creek, Grapevine Canyon, 7.2 km west of HWY 6.

Pyrgulopsis glandulosa Hershler, 1988

Pyrgulopsis glandulosus Hershler in Hershler and Landye, 1988:8, figs. 3a–c, 4–9, 10a,b.—USDI, 1991b:58821.

DIAGNOSIS.—Shell broadly to low-conical, medium-sized, umbilicate. Penial filament and lobe short. Penial ornament an elongate Dg1, elongate Dg2, Dg3 borne on weak swelling; elongate, transverse, curved terminal gland and two ventral glands. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 15*g*) broad to low-conical; height, 2.0–2.8 mm; whorls, 3.5–4.0. Protoconch weakly punctate. Teleoconch whorls moderately convex, shouldered; sculpture of strong growth lines. Aperture narrowly adnate or (more commonly) separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip orthocline to slightly prosocline. Umbilicus narrowly rimate to shallowly perforate. Periostracum tan.

Operculum (Figure 15*h,i*) ovate, amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin broadly thickened along inner edge (sometimes all around), thinner to faint along outer edge; callus pronounced.

Central radular tooth (Figure 35*f*) with slightly indented dorsal edge; lateral cusps, 5; central cusp rounded, slightly broader and longer than laterals; basal cusps, 1, medium-sized, curved, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck weak-moderate.

Cephalic tentacles pale, or with moderate internal gray pigment patch just distal to eyespots. Snout pale, rarely light brown. Foot pale. Opercular lobe pale, or with moderate gray-black internal pigment on sides and along inner edge. Neck pale or with central patch of internal black granules. Pallial roof, visceral coil black.

Ctenidial filaments, 21, tall, medium width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum small.

Testis, 1 whorl, overlapping posterior stomach chamber. Prostate gland a fat bean shape, with large (33%) pallial section; pallial vas deferens strongly kinked proximally. Penis (Figure 46*e*) large, extending well beyond mantle edge; filament less than half length of base, narrow; lobe short, distally tapered. Dg1 elongate, usually oblique, extending from right edge (slightly overlapping proximal filament) to mid-penis (but sometimes with sharp posterior bend), posterior portion borne on low swelling; Dg2 elongate, often fused with Dg3; Dg3 borne on weak swelling. Dorsal penis sometimes with several small glandular dots distally. Terminal gland large, transverse, slightly curved, borne on distal edge of lobe, usually on ventral surface. Ventral glands, usually 2, large, stalked, positioned from center to distal edge; proximal gland sometimes absent or broken into several small units.

Ovary, 0.5 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland shorter than albumen gland. Genital aperture a subterminal slit, slightly raised and thickened, with short vestibule. Coiled oviduct a broad horizontal loop well posterior to pallial wall. Oviduct and bursal duct join well behind pallial wall. Bursa copulatrix ovoid, short, medium width, largely (67%) posterior to albumen gland. Bursal duct very narrow, shallowly embedded in albumen gland, about as long as bursa copulatrix. Seminal receptacle pouch-like, medium length, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Nelson Place Spring, Yavapai County, Arizona (T 11N, R 5E, sec. 16). Holotype, USNM 859047; paratypes, USNM 859048.

DISTRIBUTION.—Verde River drainage, central Arizona.

REMARKS.—Distinguished from similar *P. montezumensis* (also from Verde River drainage) by larger penial lobe, presence of Dg3, frequent fusion of dorsal glands, and simple oviduct coil.

MATERIAL EXAMINED.—USNM 847205 (topotypes).

Pyrgulopsis hendersoni (Pilsbry, 1933)

Paludestrina sp.—Henderson, 1929:167.

Amnicola hendersoni Pilsbry, 1933:10, pl. 2: figs. 2, 9, 10.—Henderson, 1936b:276.

Fontelicella (Natricola) hendersoni.—Gregg and Taylor, 1965:109.—Taylor and Smith, 1981:350–351.—Burch, 1982:26, fig. 240.

Fontelicella hendersoni.—Taylor, 1975:94.—Turgeon et al., 1988:61.

Pyrgulopsis hendersoni.—Hershler and Thompson, 1987:29.

DIAGNOSIS.—Shell ovate to low-conical, large, weakly umbilicate. Penial filament short, lobe medium length, broad. Penial ornament an elongate Dg1, short Dg2, Dg3 borne on lobule, elongate, transverse terminal gland, and ventral gland. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 16*a,b*) ovate- to low-conical; height, 4.0–6.5 mm; whorls, 4.5–5.5 whorls. Early protoconch weakly punctate, otherwise nearly smooth. Teleoconch whorls moderately convex, rarely slightly shouldered; sculpture of weak growth lines and faint spiral striae. Aperture ovate, large, broadly adnate to slightly separated from body whorl. Inner lip complete, thin to moderately thick; columellar lip occasionally slightly reflected. Outer lip thin to moderately thick, orthocline to slightly prosocline. Umbilicus narrowly rimate to near absent. Periostracum olive-tan.

Operculum (Figure 16*c,d*) broadly ovate, amber (nuclear region and adjacent inner edge near red); nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin broadly thickened all around, distinctly raised between nucleus and inner edge; callus moderate.

Central radular tooth (Figure 36*a*) with moderately indented dorsal edge; tooth face square; lateral cusps, 3–6; central cusp rounded, broader and slightly longer than laterals; basal cusps, 1, short, curved, with strong dorsal support. Basal process broad; basal sockets shallow. Lateral margins thickened; neck very weak.

Snout dark purple; pigment light to dark on foot, neck. Cephalic tentacles usually dark at least proximally. Opercular lobe with dark internal pigment in anterior half. Pallial roof,

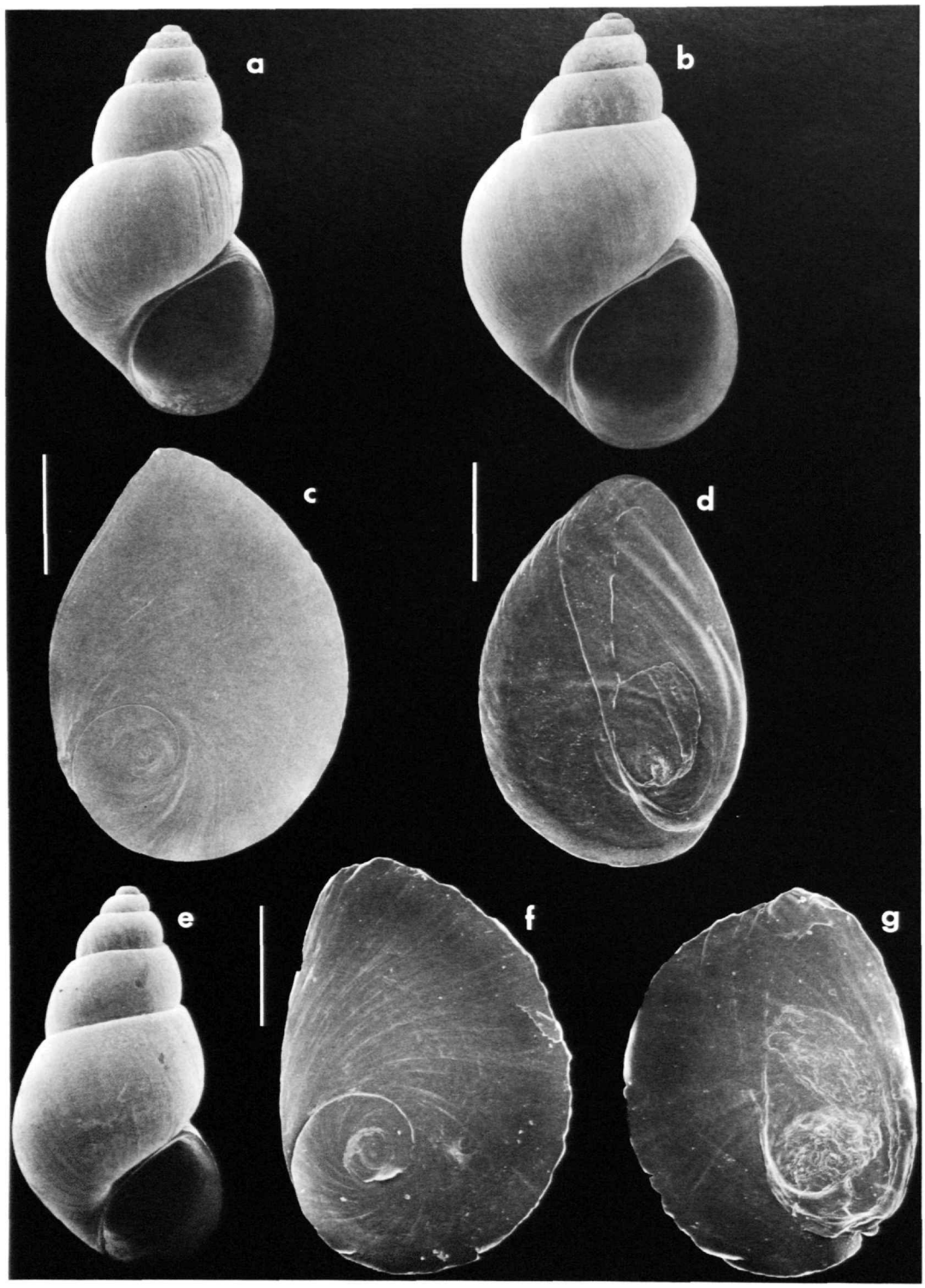


FIGURE 16.—Western *Pyrgulopsis: a–d, P. hendersoni* (*a*, shell, USNM 360805, 4.8 mm; *b*, shell, USNM 874386, 5.3 mm; *c,d*, opercula, USNM 874386, bars = 0.71 mm, 0.67 mm); *e–g, P. idahoensis* (*e*, shell, UCM 20777, 4.9 mm; *f, g*, opercula, USNM 874698, bar = 0.6 mm).

visceral coil black.

Ctenidial filaments, 36, very tall, broad. Osphradium centered posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum prominent, triangular, darkly pigmented.

Testis, 1.5 whorls, overlapping stomach to edge of style sac. Prostate gland very broad posteriorly, thickened, with large pallial section (40%). Pallial vas deferens thickened, with proximal kink. Penis (Figure 46*f*) very large, extending well beyond edge of mantle collar; base elongate-rectangular; filament very short, narrow, tapering; lobe large, broad. Dg1 elongate, extending along right edge (sometimes slightly overlapping proximal filament), to mid-penis; gland curving inward posteriorly where weakly raised; smaller glandular dots sometimes present to left of above. Dg2 usually short, sometimes fused with Dg3, sometimes fragmented into or accompanied by several short strips; Dg3 borne on well-defined lobule. Terminal gland elongate, transverse, straight, borne along distal edge of lobe, usually ventrally. Ventral gland small, stalked, centrally positioned (sometimes absent). Filament darkly pigmented internally.

Ovary, 1.5 whorls, overlapping stomach to edge of style sac. Pallial albumen gland large (30%). Capsule gland longer than albumen gland. Genital aperture a short terminal slit; vestibule very short or absent. Coiled oviduct a horizontal loop (kinked proximally) well behind pallial wall near posterior end of albumen gland. Oviduct and bursal duct join anterior to oviduct coil behind pallial wall. Bursa copulatrix ovoid, about as long and as wide as albumen gland, with most of length (about 70%) posterior to gland. Bursal duct medium width, very short. Seminal receptacle finger-like, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—South of Burns, Oregon. Holotype, ANSP 145951; paratypes, ANSP 396668.

DISTRIBUTION.—Harney Lake basin, Malheur River drainage, Harney County, Oregon (Gregg and Taylor, 1965; Taylor and Smith, 1981).

REMARKS.—Distinguished from similar *P. idahoensis* (from Snake River) by broader shell; simple, circular oviduct coil; consistent presence of ventral penial gland; elongate, ovate bursa copulatrix; dorsal position of bursal duct, and anterior position of seminal receptacle.

Recent field survey by the author (and T. Frest, pers. comm.) indicated that this species is probably extinct in its type locality area. Anatomical data were obtained from material collected from the western Harney Lake basin.

MATERIAL EXAMINED.—USNM 874386, Lower Sizemore Spring, Warm Springs Valley, Harney Lake basin, Harney County, Oregon (T 27S, R 29E, NW1/4 sec. 15).

Pyrgulopsis idahoensis (Pilsbry, 1933)

Amnicola idahoensis Pilsbry, 1933:11, pl. 2: figs. 3, 4, 5.—Henderson, 1936a:137, fig. 6.—Branson et al., 1966:145.

Fontelicella (Natricola) idahoensis.—Gregg and Taylor, 1965:109.—Burch, 1982:26, figs. 241, 242.

Fontelicella idahoensis.—Taylor, 1966a:73; 1975:101.—Turgeon et al., 1988:61.—USDI, 1991b:58819.

Pyrgulopsis idahoensis.—Hershler and Thompson, 1987:29.—Bowler and Frest, 1992:30.—Frest and Bowler, 1992:45.—USDI, 1992:59244.

DIAGNOSIS.—Shell narrow to elongate-conic, large, weakly umbilicate. Penial filament and lobe medium length; lobe broad. Penial ornament an elongate Dg1, short Dg2, Dg3 borne on lobule; elongate, transverse terminal gland, and sometimes a ventral gland. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 16*e*) narrowly- to elongate-conic; height, 5–7.5 mm; whorls, 5–6. Protoconch very weakly punctate near apex, otherwise smooth except for several faint spiral lines on later portion; often eroded, whitish. Teleoconch whorls slightly to moderately convex, often with weak to strong peripheral angulation; sculpture of weak growth lines and numerous, faint spiral lines. Aperture ovate, broadly adnate to or slightly separated from body whorl. Inner lip complete, medium thickness; columellar lip with weak or no reflection. Outer lip prosocline. Umbilicus absent to narrowly rimate. Periostracum olive-tan.

Operculum (Figure 16*f,g*) ovate, generally light amber, but dark red in nuclear region and along inner edge; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin highly thickened all around, broadly so between nucleus and mid-point of inner edge (sometimes slightly raised between nucleus and inner edge); callus moderate.

Central radular tooth (Figure 36*b*) with moderately indented dorsal edge; tooth face square; lateral cusps, 4–5; central cusp rounded, considerably broader, slightly longer than laterals; basal cusps, 1, short, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck very weak-absent.

Cephalic tentacles, snout light-moderate brown. Foot pale or moderate brown along anterior edge. Opercular lobe pale or with dark sides. Neck pale-light. Pallial roof, visceral coil black.

Ctenidial filaments, 35, very tall, broad. Osphradium elongate (35%), centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum broadly triangular, large.

Testis, 2 whorls, overlapping anterior stomach chamber. Prostate gland large, posterior section extremely broad; pallial section large (27%). Pallial vas deferens with strong proximal kink. Penis (Figure 47*a*) large; base broadly rectangular; filament medium length, narrow; lobe about as long as filament, broad. Dg1 crossing penis width at mid-length to outer edge and extending onto base of filament, borne on swelling proximally; small glandular dots sometimes present to left of above. Dg2 usually short, sometimes fused with Dg3; Dg3 large (sometimes fragmented into smaller units), borne on well-defined lobule. Terminal gland transverse, narrowly elongate, straight, positioned along distal edge of lobe, usually largely ventral. Ventral penis with central swelling rarely

bearing small gland; smaller glandular dots also rarely present. Filament dark.

Ovary, 1.0–1.25 whorls, overlapping posterior stomach chamber. Albumen gland without a pallial component. Capsule gland as long as albumen gland. Genital aperture a subterminal slit without vestibule. Coiled oviduct a short kink followed by small circular coil and broad, horizontal loop. Oviduct and bursal duct join well behind pallial wall. Bursa copulatrix pyriform, posterior end angled, almost as long and broad as albumen gland, with about 65% of length posterior to albumen gland. Bursal duct narrow, shallowly embedded in albumen gland proximally, short. Seminal receptacle pouch-like, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—[Snake River at] Homedale, Owyhee County, Idaho. Baker (1964) incorrectly stated that a holotype was selected by Pilsbry. Pilsbry figured two specimens, but did not indicate which if any of these is the type. Herein I designate a lectotype, ANSP 152677, consisting of the first of the two specimens illustrated by Pilsbry. The other specimen is a paralectotype, ANSP 396960.

DISTRIBUTION.—Snake River (main stem), southwestern Idaho.

REMARKS.—Relatively few anatomical specimens were available for this animal. Additional details can be gleaned from the unpublished report of Taylor (1982).

MATERIAL EXAMINED.—USNM 874698, gravel bar just upstream from mouth of Clover Creek, Elmore County, Idaho (T 5S, R 11E, SW1/4 sec 8).

Pyrgulopsis intermedia (Tryon, 1865)

Pomatiopsis intermedia Tryon, 1865:220, pl. 22: fig. 8.—Baker, 1964:173.
Bythinella intermedia.—Tryon, 1870:49, pl. 16: fig. 7.
Fontelicella (s.s.) *intermedia*.—Gregg and Taylor, 1965:108.—Taylor, 1985:309–310.
Fontelicella intermedia.—Taylor, 1975:104.—Burch, 1982:26, fig. 238.—Turgeon et al., 1988:61.
Pyrgulopsis intermedia.—Hershler and Thompson, 1987:29.
Paludestrina longinqua.—Pilsbry, 1899:122 [in part].—Stearns, 1901:284, fig. 2 [in part].—Hannibal, 1912b:186 [in part].—Walker, 1918:138 [in part].

DIAGNOSIS.—Shell ovate-conic, large, narrowly umbilicate. Penial filament and lobe medium length. Penial ornament a penial gland, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 17*a,b*) ovate-conic; height, 4.0–5.5 mm; whorls, 4.5–5.0. Earliest protoconch weakly punctate, otherwise near smooth except for a few spiral lines. Teleoconch whorls highly convex; sculpture of variably pronounced growth lines. Aperture ovate, adnate or slightly separated from body whorl. Inner lip complete, slightly thickened (sometimes greatly in columellar area); columellar lip slightly reflected. Outer lip slightly prosocline. Umbilicus narrowly rimate, sometimes excavated. Periostracum tan-brown.

Operculum (Figure 17*c,d*) ovate, amber with nuclear region especially dark; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin broadly thickened all around, region between nucleus and inner edged raised; callus well developed.

Central radular tooth (Figure 36*c*) with moderately indented dorsal edge; face near square; lateral cusps, 4–5; central cusp rounded, considerably broader, slightly longer than laterals; basal cusps, 1, short, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck weak-absent.

Cephalic tentacles pale except for small black internal pigment patch distal to eyespots. Snout moderate gray. Foot moderate gray, darker along anterior, posterior edges. Opercular lobe dark along sides and anterior edge. Neck lighter than snout, foot. Pallial roof, visceral coil dark, often near-uniform black.

Ctenidial filaments, 25, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney with medium-large bulge into pallial cavity; opening white. Stomach caecum pronounced, triangular.

Testis, 1.75 whorls, overlapping stomach to edge of style sac. Prostate gland with large (25%) pallial section; pallial vas deferens proximally kinked. Penis (Figure 47*b*) medium-sized, extending beyond mantle edge; base near-square, with folds along inside edge; filament medium length, tapering; lobe about as long as filament, broad, with little taper. Penial gland covering about two-thirds of filament. Terminal gland large, usually transverse, borne along distal edge of lobe. Ventral gland stalked, positioned near mid-length. Filament with dark internal pigment.

Ovary, 1 whorl, overlapping anterior stomach chamber. Albumen gland without a pallial section. Capsule gland as long as albumen gland. Genital aperture a terminal slit with short vestibule. Coiled oviduct a short posterior oblique twist followed by near horizontal loop, nearly abutting pallial wall anteriorly. Oviduct and bursal duct join anterior to oviduct coil just behind pallial wall. Bursa copulatrix ovoid-pyriform, medium length and width, with about half of length posterior to albumen gland. Bursal duct slender, shallowly embedded in albumen gland, medium length. Seminal receptacle pouch-like, short, with short duct, positioned lateral to proximal bursal duct near ventral edge of albumen gland.

TYPE LOCALITY.—Owyhee River, southeast Oregon. Type material is labeled Crooked Creek, Owyhee, southeast Oregon. ANSP 27958[a] contained 4 specimens segregated (by Baker) as types, 1 of which was further segregated from the other 3. The latter was broken, and of gerontic appearance, and did not resemble Tryon's figure although the shell measurements were similar to those he gave. I chose another, unbroken, adult shell as lectotype, ANSP 27958; paralectotypes, ANSP 396959.

DISTRIBUTION.—Southern Oregon: Crooked Creek, Owyhee River drainage (Snake basin); Barren Valley (internal drainage), lower Klamath Lake basin; northeast California: Pit River below Fall River (Taylor, 1985:309).

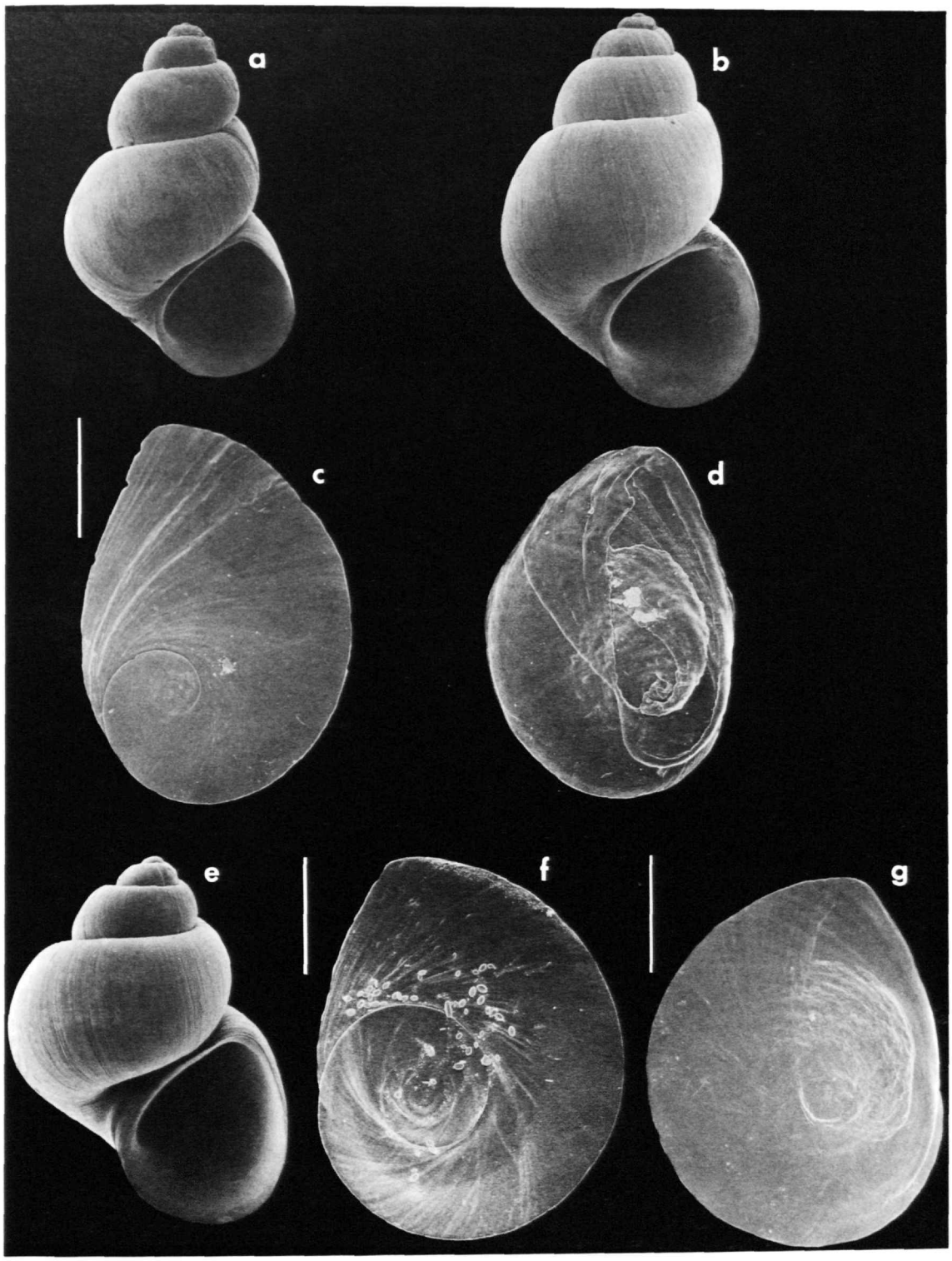


FIGURE 17.—Western *Pyrgulopsis*: *a–d, P. intermedia* (*a*, shell, ANSP 27958, 3.4 mm; *b*, shell, USNM 874195, 4.0 mm; *c,d*, opercula, bar = 0.67 mm); *e–g, P. isolata* (*e*, holotype, USNM 859201, 2.6 mm; *f, g*, opercula, USNM 850366, bars = 0.38 mm, 0.4 mm).

REMARKS.—Amongst the group of species whose penes are ornamented solely by penial, terminal, and ventral glands, this snail is distinguished by the combination of large shell without basal carina, large penis, elongate penial gland, and large caecal chamber of stomach.

I have not confirmed the status of populations aside from near topotypes.

MATERIAL EXAMINED.—USNM 874195, Crooked Creek, at HWY 95 crossing, Malheur County, Oregon (T 33S, R 39E, NE1/4 sec. 24)(presumed near topotypes).

Pyrgulopsis isolata Hershler and Sada, 1987

Pyrgulopsis isolatus Hershler and Sada, 1987:807, figs. 19d, 25, 29c,f, 33d,g, 37, 38.—USDI, 1991b:58821.

DIAGNOSIS.—Shell broadly conical, medium-sized, umbilicate. Penial filament short, lobe very long, broad. Penial ornament a transverse terminal gland.

DESCRIPTION.—Shell (Figure 17*e*) broadly conical (nearly globose); height, 2.6–3.1 mm; whorls, 3.75–4.25. Early protoconch very weakly punctate, nearly smooth otherwise. Teleoconch whorls highly convex, slightly shouldered; sculpture of strong growth lines. Aperture usually slightly separated from body whorl. Inner lip complete, thickened; columellar lip sometimes slightly reflected. Outer lip orthocline to slightly opisthocline. Umbilicus rimate to perforate. Periostracum tan.

Operculum (Figure 17*f,g*) broadly ovate, light amber except for dark, reddish area along inner edge of callus; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin weakly thickened all around (more so between nucleus and mid-point of inner edge); callus weak.

Central radular tooth (Figure 36*d*) with moderately indented dorsal edge; lateral cusps, 3–4; central cusp rounded, about as long as wide, considerably broader, slightly longer than laterals; basal cusps, 1, short, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale or with internal gray-black patch just distal to eyespots. Snout light to dark brown-gray. Foot near pale to dark gray. Opercular lobe light, sometimes with dark internal pigment along inner edge and sides. Neck pale-light. Pallial roof, visceral coil, near uniformly black.

Ctenidial filaments, 21, tall, broad. Osphradium centrally positioned along ctenidial axis. Kidney opening white. Stomach caecum small.

Testis, 1 whorl, broadly overlapping posterior stomach chamber. Prostate gland with large (30%) pallial section; pallial vas deferens simple. Penis (Figure 47*c*) large; base elongate-rectangular; filament short, narrow; lobe elongate-rectangular, about as long as base, without distal taper. Terminal gland transverse, straight, elongate, borne along distal edge of lobe. Filament dark.

Ovary, 1 whorl, overlapping posterior stomach chamber. Albumen gland without a pallial component. Capsule gland longer than albumen gland. Genital aperture an elongate terminal slit with very short vestibule. Coiled oviduct a broad, near-horizontal loop well behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with about 66% of length posterior to gland. Bursal duct narrow, about as long as bursa copulatrix, embedded in albumen gland. Seminal receptacle narrowly sac-like, usually folded, short, overlapping anterior bursa copulatrix.

TYPE LOCALITY.—Spring south of Clay Pits, Ash Meadows, Nye County, Nevada (T 18S, R 50E, NE1/4 sec. 7). Holotype, USNM 859201; paratypes, USNM 859202, FSM 93959.

DISTRIBUTION.—Endemic to type locality, Amargosa River drainage.

MATERIAL EXAMINED.—USNM 850366 (topotypes).

Pyrgulopsis kolobensis (Taylor, 1987), new combination

Fontelicella kolobensis Taylor, 1987:19, fig. 8.
Fontelicella pinetorum Taylor, 1987:20, fig. 9.

DIAGNOSIS.—Shell ovate-conic, medium to large-sized, umbilicate. Penial filament short, lobe medium length. Penial ornament a short penial gland, transverse terminal gland, and usually a ventral gland.

DESCRIPTION.—Shell (Figure 18*a*) ovate-conic; height, 2.8–4.0 mm; whorls, 3.75–4.5. Earliest protoconch very weakly wrinkled, otherwise near smooth. Teleoconch whorls moderately convex, sometimes weakly shouldered; sculpture of faint growth lines. Aperture ovate, narrowly adnate or slightly separated from body whorl. Inner lip complete; columellar lip weakly reflected, sometimes thickened. Outer lip orthocline-slightly prosocline. Umbilicus rimate to perforate. Periostracum tan-brown.

Operculum (Figure 18*b,c*) ovate, light amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin a weak trace along outer edge; callus weak.

Central radular tooth (Figure 36*e*) with well-indented dorsal edge; lateral cusps, 4–5; central cusp rounded, slightly broader and longer than laterals; basal cusps, 1, medium-sized, slightly curved, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Tentacles pale except for small pigment patch either distal to eyespot or near tip. Snout light to dark gray-brown. Foot light gray-brown; sides of opercular lobe with dark internal pigment. Neck pale-moderately pigmented. Pallial roof, visceral coil moderate to dark brown-black.

Ctenidial filaments, 20, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach with medium-sized caecum.

Testis, 1.5–2.0 whorls, overlapping anterior stomach chamber (sometimes to edge of style sac). Prostate gland with short pallial section; pallial vas deferens proximally kinked. Penis (Figure 47*d*) large; filament short, tapering; lobe medium length, near-rectangular. Penial gland weak, covering only base

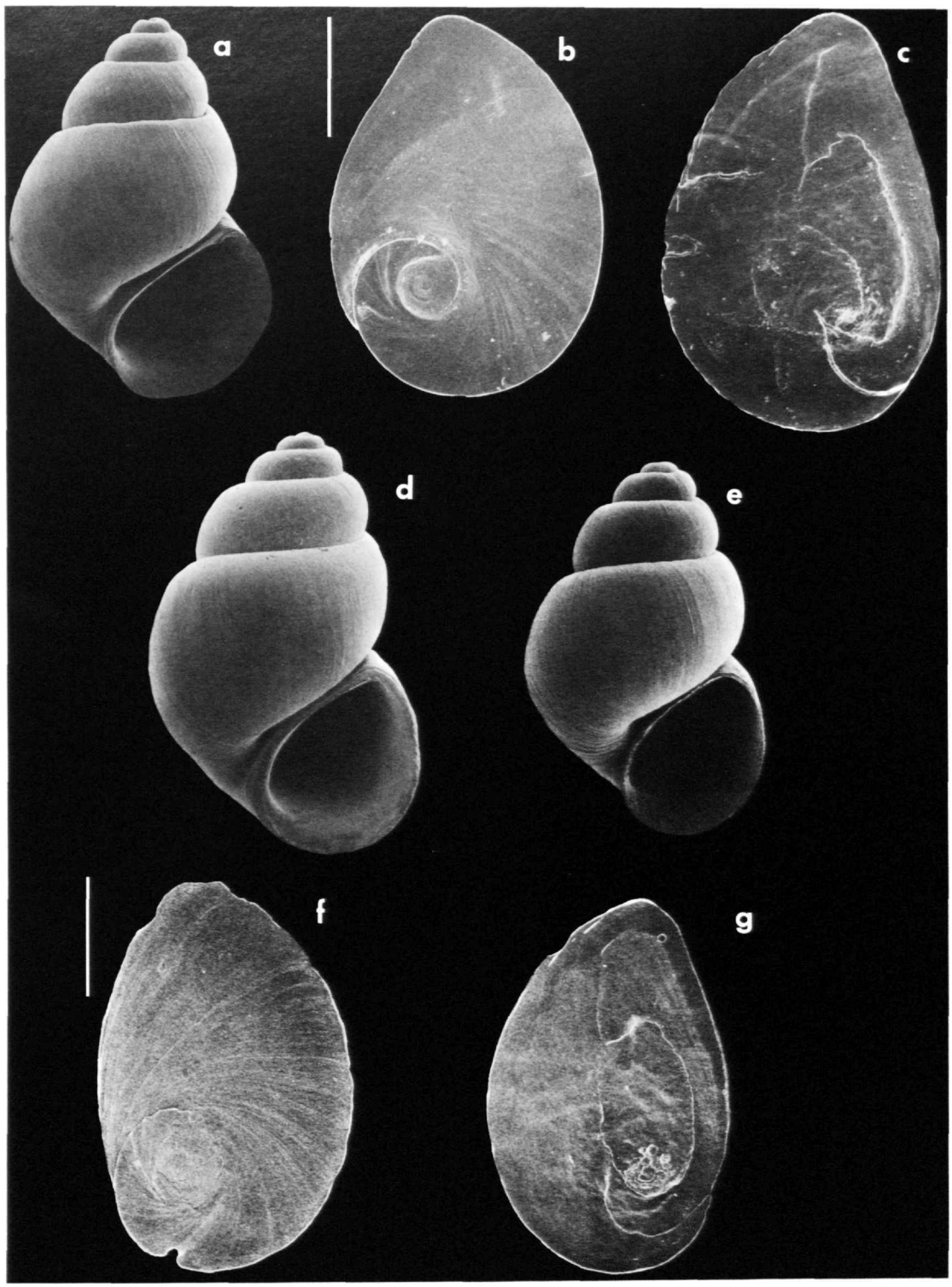


FIGURE 18.—Western *Pyrgulopsis: a–c, P. kolobensis*, USNM 847249 (*a*, shell, 3.2 mm; *b,c*, opercula, bar = 0.43 mm); *d–g, P. longinqua* (*d*, shell (left), USNM 526733, 3.5 mm; *e*, shell (right), USNM 874059, 2.3 mm; *f,g*, opercula, bar = 0.3 mm).

of filament. Terminal gland elongate, straight, transverse (sometimes fragmented into 2–3 units), positioned along distal edge of lobe. Ventral gland usually prominent (sometimes weak or absent), stalked, borne on ventral surface of lobe (glandular dot distal to above also sometimes present). Filament with moderately dark internal pigment.

Ovary, 1 whorl, overlapping posterior stomach. Albumen gland with short pallial section. Capsule gland shorter than albumen gland. Genital aperture a sub-terminal slit with vestibule. Coiled oviduct of two overlapping horizontal loops (proximal loop smaller) positioned slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with much of length (50%–70%) posterior to albumen gland. Bursal duct slender to wide, shallowly embedded in albumen gland, medium length. Seminal receptacle pouch-like, short, slightly overlapping anterior bursa copulatrix or overlapping (or lateral to) proximal bursal duct, usually positioned near ventral edge of albumen gland.

TYPE LOCALITY.—*Pyrgulopsis kolobensis:* Toquerville Springs, sec. 35, T 40S, R 13W, Washington County, Utah. Holotype, LACM 2216. *Pyrgulopsis pinetorum:* Spring tributary to Leeds Creek, 2,400 ft W, 2,300 ft N, sec. 16, T 40S, R 14W, Washington County, Utah. Holotype, LACM 2217.

DISTRIBUTION.—Upper Virgin River drainage, southwestern Utah.

REMARKS.—Study of numerous lots of material from the upper Virgin River drainage revealed extensive variation in features used to separate *kolobensis* and *pinetorum* by Taylor (1987), including the presence/absence of a ventral gland on the penis, thus suggesting that a single species is involved. Amongst the group of species whose penes are ornamented solely by penial, terminal, and ventral glands, this snail is distinguished by its ovate-conic shell and weak ventral operculum callus.

MATERIAL EXAMINED.—USNM 847249 (topotypes, *kolobensis*).

Pyrgulopsis longinqua (Gould, 1855)

Amnicola longinqua Gould, 1855:130; 1856:333, pl. XI: figs. 10, 11.—Binney, 1865:87, fig. 173.—Tryon, 1870:36, pl. 17: fig. 5.—Baily and Baily, 1951:51, pl. 4: fig. 7.

Paludestrina longinqua.—Pilsbry, 1899:122 [in part].—Stearns, 1901:284, fig. 2.—Walker, 1918:138.

Pelidostrema [sic] *longigua* [sic].—Jaeger, 1965:65.

Fontelicella s.s. *longinqua.*—Gregg and Taylor, 1965:108.—Taylor, 1975:114.

Pyrgulopsis longinqua.—Hershler and Thompson, 1987:29.

DIAGNOSIS.—Shell ovate to narrowly-conic, medium-sized, weakly umbilicate. Penial filament and lobe medium length. Penial ornament an elongate penial gland, transverse Dg1, Dg2, Dg3 borne on swelling; elongate, transverse terminal gland, and ventral gland. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 18*d,e*) ovate-narrow conic; height, 2.5–3.8 mm; whorls, 4.5–5.0. Protoconch near smooth except for faint adapical spiral lines on later portion. Teleoconch whorls moderately convex, slightly shouldered; sculpture of strong growth lines. Aperture ovate, small, broadly adnate to very slightly separated from body whorl. Inner lip complete, thin to thick; columellar lip slightly reflected. Outer lip thin to thick, orthocline to slightly prosocline. Umbilicus absent to narrowly rimate or very shallowly perforate. Periostracum light tan.

Operculum (Figure 18*f,g*) narrow-broadly ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened all around; callus moderate.

Central radular tooth (Figure 36*f*) with moderately indented dorsal edge; lateral cusps, 5; central cusp pointed, slightly broader and considerably longer than laterals; basal cusps, 1, short, with moderate dorsal support. Basal process moderately broad; basal sockets deep. Lateral margins slightly thickened; neck pronounced.

Head-foot generally pale. Snout sometimes light gray. Opercular lobe sometimes with moderate internal gray-black patch along anterior edge. Neck sometimes with internal black pigment. Pallial roof, visceral coil usually pale or weakly pigmented (rarely dark).

Ctenidial filaments, 20, medium height and width. Osphradium centered slightly posterior to middle of ctenidium. Kidney opening white. Stomach with prominent caecum.

Testis, 1 whorl, extending to posterior edge of stomach. Prostate gland an elongate bean-shape, with short pallial section; pallial vas deferens with proximal kink. Penis (Figure 47*e*) large, extending well beyond mantle edge; base square-rectangular; filament medium length, broad; lobe equal to or slightly longer than filament, expanded distally. Penial gland filling most of filament, sometimes fused with Dg1. Dg1 crossing at least half of penis width near mid-length; Dg2 short-elongate, sometimes fused with Dg1 and/or Dg3; Dg3 borne on moderately raised swelling. Dorsal penis also with 1–3 additional small glands near distal edge, sometimes fused with Dg2 or Dg3. Terminal gland elongate, transverse, curved, borne along distal edge, largely on ventral surface. Ventral gland small, stalked, positioned near mid-length. Filament pale to with dark internal pigment.

Ovary, 0.5 whorl, pressed against posterior edge of stomach. Pallial albumen gland short. Capsule gland as long as albumen gland. Genital aperture a broad terminal slit with vestibule. Coiled oviduct a broad, open horizontal loop (sometimes preceeded by weak horizontal kink) filling much of albumen gland length. Oviduct and bursal duct join anterior to oviduct coil just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with most of length (77%) posterior to albumen gland. Bursal duct slender, about as long as bursa

copulatrix. Seminal receptacle pouch-like, slender, short, overlapping anterior bursa copulatrix (with small portion of length posterior to albumen gland) near ventral edge of albumen gland, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Colorado Desert (Cienega Grande), subfossil. This and other species described by Gould (with same type locality) based on material collected in conjunction with the Pacific Railroad Survey have been attributed to the Salton Sea area of southeastern California (Henderson, 1936c; Bequaert and Miller, 1973:203). The sole known *Pyrgulopsis* living in this area conforms to Gould's description and illustration of *longinqua* and closely resembles at least some of the Pacific Railroad Survey material originally identified as this species (although extant snails are smaller than the subfossil specimens). The status of type material for this species, however, is unclear. The types referred to by Binney (1865; catalog number 9220) have not been located although I suspect that USNM 121121 (originally a 5 specimen lot from Blake, as was Binney's) could be this lot. A possible holotype (MCZ 189153) referred to by Johnson (1964) in fact is *P. avernalis* (putative paratypes (MCZ 2106) are a mixture of *P. avernalis* and *P. carinifera*), which has a very different shell from that described by Gould and which does not occur in the Colorado Desert although originally incorrectly attributed to the region by Pilsbry.

DISTRIBUTION.—Salton Sea basin, Riverside County, southeastern California. Only a single living population is known, from a small spring in the Salt Creek drainage.

REMARKS.—This species differs from similar *P. thermalis* in its more elongate shell, posterior position of male and female gonad, position of Dg1 posterior to penial filament, and presence of Dg3.

MATERIAL EXAMINED.—USNM 874104, unnamed spring about 1.5 km west-southwest of Hunters Spring, Riverside County, California (T 8S, R 11E, NE1/4 sec. 14).

Pyrgulopsis manantiali (Hershler, 1985)

Hydrobiinae? incertae sedis.—Taylor, 1966b:173, fig. 4.
"Stiobia" n.sp.—Hershler, 1984:67.
Mexistiobia manantiali Hershler, 1985:47, figs. 10–13.
Pyrgulopsis manantiali.—Hershler and Thompson, 1987:29, fig. 8.

DIAGNOSIS.—Shell globose to broadly conical, small, broadly umbilicate. Penial filament elongate, lobe short. Penial ornament a horizontal terminal gland.

DESCRIPTION.—Shell (Figure 19*a*) globose to broadly conical; height, 1.0–1.25 mm; whorls, 3. Protoconch finely punctate, with faint suggestion of a few spiral lines on later portion. Teleoconch whorls moderately convex, sometimes shouldered; sculpture of strong growth lines. Aperture broadly lunate, only very slightly angled above, narrowly adnate or separated (sometimes greatly so) from body whorl. Inner lip complete, moderately thickened. Outer lip slightly thickened, prosocline. Umbilicus broadly perforate. Periostracum light gray, extremely thin.

Operculum (Figure 19*b,c*) broadly ovate, multispiral, light amber; nucleus near central; dorsal surface weakly frilled. Attachment scar margin thickened all around, broadly so between nucleus and mid-point of inner edge. Early opercular whorls elevated above ventral surface (as thickened cords); callus small.

Central radular tooth (Figure 37*a*) with highly indented dorsal edge; lateral cusps, 4–6; central cusp pointed, narrow; basal cusps, 1, elongate, slightly curved, with very weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins moderately expanded; neck pronounced.

Cephalic tentacles, snout, foot, neck light to dark brown-black. Opercular lobe light to moderately pigmented along edges. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 12, tall and broad. Osphradium large (50%), broad, positioned centrally to well posterior to middle of ctenidial axis. Kidney with very small bulge into pallial cavity, opening very slightly thickened. Stomach without caecum.

Testis, 0.5 whorl, very slightly overlapping posterior stomach. Prostate gland ovate, thin-walled, with large (25%) pallial section; pallial vas deferens proximally kinked. Penis (Figure 48*a*) large; filament elongate, medium width, gently tapered; lobe short, strongly tapered distally. Terminal gland small, narrow, horizontal, borne on ventral surface of lobe and extending from near distal tip onto distal penis. Filament darkly pigmented internally.

Female genitalia shown in Figure 5*d*. Ovary, 0.5 whorl, pressed against posterior edge of stomach. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland, thin-walled, of a single tissue section. Genital aperture a terminal, large slit with vestibule. Coiled oviduct a broad horizontal loop occupying much of anterior albumen gland. Oviduct and bursal duct join at pallial wall. Bursa copulatrix finger-like, very short (25%) and narrow (20%), shallowly embedded in albumen gland, positioned immediately posterior to pallial wall (well anterior to posterior edge of gland). Bursal duct extremely short, virtually indistinguishable from bursa. Seminal receptacle finger-like, as long as bursa copulatrix, positioned behind oviduct coil (well behind bursa copulatrix).

TYPE LOCALITY.—Small spring, 100 m south of Rio Mesquites at Tierra Blanca, Cuatro Ciénegas basin, Coahuila, Mexico.

DISTRIBUTION.—Cuatro Ciénegas basin, Coahuila, Mexico.

REMARKS.—Among species having a penis solely ornamented by a terminal gland, this snail is strongly differentiated by its minute size, globose shell, multispiral operculum, elongate osphradium, posterior position of ovary, and unusually small and narrow bursa copulatrix having a uniquely anterior position.

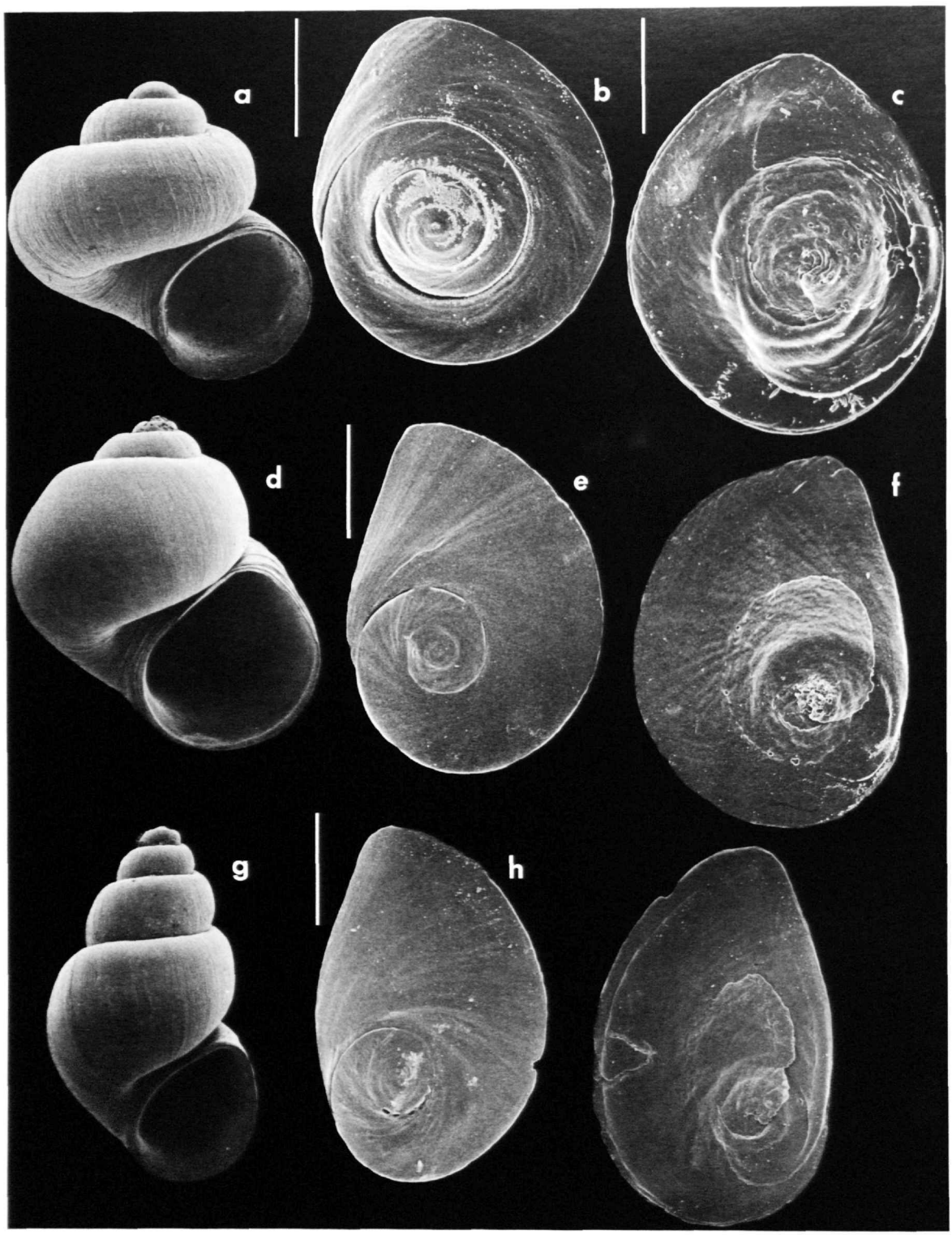


FIGURE 19.—Western *Pyrgulopsis*: *a–c*, *P. manantiali*, ANSP A98881 (*a*, shell, 0.9 mm; *b*, *c*, opercula, bars = 150 µm, 158 µm); *d–f*, *P. merriami*, USNM 873395 (*d*, shell, 2.5 mm; *e,f*, opercula, bar = 0.43 mm); *g–i*, *P. metcalfi*, USNM 873301 (*g*, shell, 3.1 mm; *h,i*, opercula, bar = 0.3 mm).

Pyrgulopsis merriami (Pilsbry and Beecher, 1892), new combination

Fluminicola merriami Pilsbry and Beecher in Pilsbry, 1892:143; 1899:123.—Stearns, 1893:281, fig. 2; 1901:286, fig. 5.—Walker, 1918:142.—Morrison, 1940:124.—Baker, 1964:174.—Burch, 1982:22, fig. 146.—Turgeon et al., 1988:60.—USDI, 1991b:58819.
Fluminicola (Heathilla) merriami.—Hannibal, 1912b:188.
"Fluminicola" merriami.—Taylor, 1975:122.

DIAGNOSIS.—Shell globose, medium-sized, umbilicate. Penial filament short, lobe medium length. Penial ornament of three penial glands, small Dg3 on tubercle; and curved, horizontal terminal gland.

DESCRIPTION.—Shell (Figure 19*d*) globose; height, about 3 mm; whorls, about 4. Early protoconch moderately punctate, sculpture weaker in later portion. Teleoconch whorls moderately convex, distinctly shouldered, with shallow sutures; sculpture of strong growth lines and weak spiral striae. Aperture ovate, large, narrowly adnate to or (rarely) slightly separated from body whorl. Inner lip complete, thickened in columellar region. Outer lip prosocline. Umbilicus deeply perforate. Periostracum light brown.

Operculum (Figure 19*e,f*) broadly ovate, very light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened along inner edge near nucleus, otherwise smooth; callus moderate.

Central radular tooth (Figure 37*b*) with moderately indented dorsal edge; lateral cusps, 5; central cusp pointed, slightly longer than laterals. Basal cusps, 2, very short (outer cusp more so), narrow, with weak dorsal support. Basal process wide; basal sockets deep. Lateral margins thickened; neck very pronounced.

Cephalic tentacles pale except for dark internal pigment patches distal to eyespots. Snout and foot pale to moderate brown. Opercular lobe, neck usually pale. Pallial roof, visceral coil light to dark brown-black.

Ctenidial filaments, about 27, tall, narrow. Osphradium centered posterior to middle of ctenidial axis. Kidney with small bulge into pallial cavity (16%); opening slightly thickened. Stomach with narrow caecum.

Testis, 1.5 whorls, overlapping posterior stomach chamber. Prostate gland a broad bean shape, with short pallial section. Pallial vas deferens with proximal kink. Penis (Figure 48*b*) large; filament short, broad; lobe large, broad. Penial glands consisting of two units covering most of filament (one each on dorsal and ventral surfaces; sometimes fused distally), and much smaller unit between the above along dorsal edge proximally. Dg3 on small raised tubercle, sometimes borne along edge of lobe or slightly onto ventral surface. Terminal gland elongate, curved, usually horizontal, overlapping both dorsal and ventral surfaces. Ventral gland large, sub-terminal, stalked, usually positioned right of mid-line; second, very small gland sometimes present lateral to above. Filament unpigmented.

Ovary, 1 whorl, overlapping posterior stomach chamber. Albumen gland without pallial section. Capsule gland as long as albumen gland. Ventral channel tall; genital aperture a terminal broad pore without vestibule. Coiled oviduct a slight horizontal twist followed by broad horizontal loop filling much of albumen gland (and partly overlapping bursa copulatrix). Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, almost as long and as wide as albumen gland, with most of length (75%) posterior to albumen gland. Bursal duct broad, short. Seminal receptacle pouch-like, fat, short, overlapping anterior bursal copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—A warm spring (temperature 97° F. [36° C.]) in Pahranagat Valley [Lincoln County], Nevada. It is not clear from narrative accounts of the Death Valley Expedition, nor from the map showing the expedition route, which particular spring in Pahranagat Valley was visited. There are several thermal springs in the valley (Garside and Schilling, 1979): Ash Springs (T6S, R60E, NE1/4 sec. 1) harbors a hydrobiid population closely conforming to *merriami* in shell features and probably is the type locality. (Other large thermal springs along the basin floor contain another species that does not closely resembly *merriami.*) Lectotype (Baker, 1964:174), ANSP 67278; paralectotypes, ANSP 27782; USNM 123626.

DISTRIBUTION.—Known only from presumed type locality in Pahranagat Valley, which presumably drained to the Colorado basin in late Cenozoic pluvial periods (Hubbs and Miller, 1948).

MATERIAL EXAMINED.—USNM 873163 (presumed topotypes).

Pyrgulopsis metcalfi (Taylor, 1987), new combination

Fontelicella metcalfi Taylor, 1987:12, fig. 5.
"Fontelicella" metcalfi.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate to narrowly-conic, medium-sized, narrowly umbilicate. Penial filament and lobe medium length. Penial ornament an elongate penial gland, oblique Dg1, oblique Dg2, small Dg3 borne on weak swelling; elongate, slightly curved, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 19*g*) ovate- to narrow-conic; height, 2.0–2.7 mm; whorls, 3.5–4.5. Early protoconch weakly punctate, later portion with weak spiral lines adapically. Teleoconch whorls moderately convex, shouldered; sculpture of moderate growth lines. Aperture ovate, adnate or slightly separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip slightly prosocline, weakly sinuate. Umbilicus narrowly rimate, shallow. Periostracum light tan.

Operculum (Figure 19*h,i*) narrowly ovate, light amber (darker in nuclear region); nucleus slightly eccentric; dorsal surface weakly frilled. Margins of attachment scar moderately thickened between nucleus and mid-point of inner edge. Callus broad, thickened near nucleus.

Central radular tooth (Figure 37*c*) with moderately indented dorsal edge; lateral cusps, 5; central cusp pointed, considerably broader and longer than laterals; basal cusps, 1, (second very

small cusp occasionally present) large, curved, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck moderate.

Tentacles pale except for weak internal pigment patch just distal to eyespots. Snout light to dark gray-black. Foot pale except for gray-black cover along anterior edge. Opercular lobe black along anterior edge and sides. Neck pale. Pallial roof, visceral coil usually black.

Ctenidial filaments, 17, tall, narrow. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach with large triangular caecum.

Testis, 1 whorl, slightly overlapping posterior stomach chamber. Prostate gland an elongate bean-shape; pallial section short. Pallial vas deferens with proximal kink. Penis (Figure 48*c*) large; filament medium length, broad; lobe slightly shorter than filament, broad. Penial gland covering most of filament, weakly bifurcate proximally. Dg1 short, curving from just behind penial gland to near mid-width, borne on swelling; Dg2 strongly oblique (sometimes a series of smaller glands), extending from near Dg1 to near left distal corner of penis; Dg3 small, weakly raised, positioned near inner edge of lobe near base. Dorsal penis also sometimes with several small glandular dots adjacent to Dg1, Dg2. Terminal gland elongate, transverse, slightly curved, positioned largely on ventral side of lobe. Ventral gland prominent, borne on sub-terminal swelling. Filament with moderately dark internal pigment.

Ovary, 1 whorl, abutting posterior edge of stomach. Pallial albumen gland large (25%). Capsule gland as long as albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct a broad horizontal loop well behind pallial wall, covering much of posterior albumen gland. Oviduct and bursal duct join slightly behind pallial wall (anterior to coiled oviduct). Bursa copulatrix elongate-pyriform, posterior end rounded, medium length, as wide as albumen gland, with much of length (65%) posterior to gland. Bursal duct narrow, medium length. Seminal receptacle sac-like, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Naegele Springs, 5.3 mi (8.5 km) north-northwest of Ruidosa, Presidio County, Texas. Holotype, LACM 2212; paratypes, UTEP 10055, ANSP 376024, FSM 160937, USNM 854077.

DISTRIBUTION.—Known only from type locality, Rio Grande basin.

MATERIAL EXAMINED.—USNM 873301 (topotypes).

Pyrgulopsis micrococcus (Pilsbry, 1893)

Amnicola micrococcus Pilsbry in Stearns, 1893:277, fig. 1.—Pilsbry, 1899:121 [in part].—Stearns, 1901:286 [in part; fig. 4].—Hannibal, 1912a:38; 1912b:185.—Walker, 1918:134.—Baker, 1964:174.—Richardson et al., 1991:64.

Fontelicella (Microamnicola) micrococcus.—Gregg and Taylor, 1965:109.—Burch, 1982:26, figs. 231, 244.

Fontelicella micrococcus.—Taylor, 1975:123.—Turgeon et al., 1988:61.

Pyrgulopsis micrococcus.—Hershler and Thompson, 1987:29, figs. 7, 33.—Hershler and Sada, 1987:788, figs. 8a, 9–16).—Hershler, 1989:182, figs. 17c,d, 20–25.—Hershler and Pratt, 1990:285, fig. 5.—USDI, 1991b:58818.

Paludestrina stearnsiana.—Berry, 1909:78.

Amnicola stearnsiana.—Berry, 1948:59.

Paludestrina longinqua.—Hannibal, 1912a:34 [in part].

Hydrobia sp.—Taylor, 1954:69.

Genus and species undescribed [Virile Amargosa Snail].—USDI, 1991b: 58818.

DIAGNOSIS.—Shell globose to ovate-conic, small to medium-sized, umbilicate. Penial filament medium length, lobe short. Penial ornament a variably shaped terminal gland.

DESCRIPTION.—Shell (Figure 20*a*) globose to ovate-conic; height, 1.1–3.1 mm, whorls, 3.25–3.5. Protoconch weakly punctate adapically, becoming smoother toward beginning of teleoconch; later portion with a few weak spiral lines adapically. Teleoconch whorls convex, slightly shouldered; sculpture of moderately strong growth lines. Aperture usually slightly separated from body whorl. Inner lip complete, slightly thickened; columellar lip slightly reflected. Outer lip near orthocline. Umbilicus rimate-perforate. Periostracum light brown.

Operculum (Figure 20*b,c*) ovate, light amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin slightly thickened between nucleus and mid-point of inner edge; callus small.

Central radular tooth (Figure 37*d*) with moderately indented dorsal edge; lateral cusps, 4–7; central cusp pointed, slightly broader and longer than laterals; basal cusps, 1, medium-sized, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale or with small patch of gray-black pigment just distal to eyespots. Snout pale to dark gray-black. Foot pale to black; pigment often especially strong along anterior edge. Opercular lobe pale or black along anterior edge. Neck pale to dark gray-black. Pallial roof, visceral coil moderate to dark gray-black.

Ctenidial filaments, 17, medium height, narrow. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening thickened, sometimes white. Stomach caecum small, broad.

Testis, 1.0–1.5 whorls, overlapping anterior stomach chamber almost to posterior edge of style sac. Prostate gland a fat bean-shape, with medium-large (20%–33%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 48*d*) medium-sized; filament medium length, narrow, tapered; lobe usually short, squat, rounded distally. Terminal gland medium-sized (sometimes reduced-absent), circular-horizontal, borne along ventral surface of distal edge of lobe. Filament dark.

Female genitalia shown in Figure 5*e*. Ovary, 0.5–0.75 whorl, slightly overlapping posterior stomach chamber. Albumen gland without a pallial section. Capsule gland shorter than albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a slight horizontal twist followed by broad horizontal loop (often kinked in middle), positioned well behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with up to half of length posterior to gland. Bursal duct

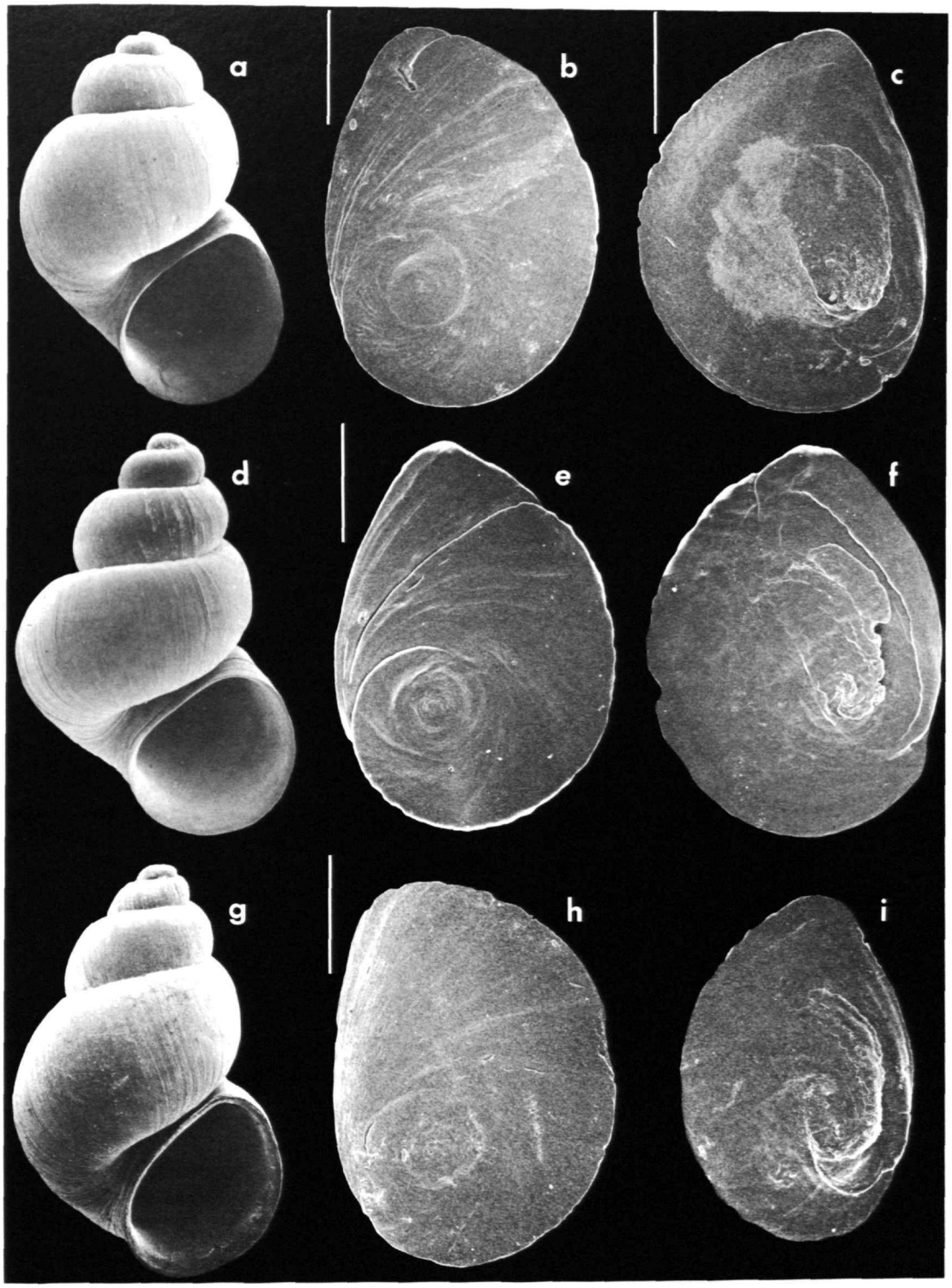


FIGURE 20.—Western *Pyrgulopsis*: *a–c*, *P. micrococcus*, USNM 847246 (*a*, shell, 2.3 mm; *b,c*, opercula, bars = 0.3 mm, 0.33 mm); *d–f*, *P. montezumensis* (*d*, shell, USNM 859043, 2.5 mm; *e,f*, opercula, USNM 847233, bar = 0.27 mm); *g–i*, *P.morrisoni* (*g*, shell, USNM 874453, 3.0 mm; *h, i*, opercula, USNM 847231, bar = 0.3 mm).

moderately broad, medium length. Seminal receptacle pouch-like, short, partly overlapping (or slightly lateral to) anterior bursa copulatrix.

TYPE LOCALITY.—Small spring in Oasis Valley [Nye County], Nevada. Lectotype (Baker, 1964:174), ANSP 67279; paralectotypes, ANSP 368399, USNM 123622.

DISTRIBUTION.—Widespread in southeastern California and southwestern Nevada: Death Valley system, Mohave River drainage, small endorheic basins.

REMARKS.—*Pyrgulopsis micrococcus* is distinguished from closely similar *P. stearnsiana* by its larger penial lobe, weak operculum attachment scar, absence of a pallial section of albumen gland, and position of bursal duct lateral to albumen gland.

MATERIAL EXAMINED.—USNM 847246, unnamed springs comprising headwaters of Amargosa River, Springdale, Nye County, Nevada (T 10S, R 47E, NE1/4 sec. 31).

Pyrgulopsis montezumensis Hershler, 1988

Amnicola palomasensis.—Smith, 1953:9.

Pyrgulopsis montezumensis Hershler in Hershler and Landye, 1988:23, figs. 10g, 13a,d, 21a–c, 22, 23.—USDI, 1991b:58821.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized, umbilicate. Penial filament short, lobe very short. Penial ornament an elongate Dg1, straight terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 20*d*) ovate-conic; height, 1.7–2.7 mm; whorls, 3.5–4.5. Early protoconch (Figure 1*d*) moderately punctate adapically, otherwise weakly punctate. Teleoconch whorls highly convex, shouldered; sculpture of weak growth lines. Aperture broadly adnate to slightly separated from body whorl. Inner lip complete, sometimes very slightly thickened. Outer lip near orthocline. Umbilicus perforate. Periostracum amber.

Operculum (Figure 20*e,f*) ovate, light amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin thickened all around, broadly so along inner edge; callus moderately developed.

Central radular tooth (Figure 37*e*) with moderately indented dorsal edge; lateral cusps, 6–8; central cusp pointed, considerably longer than laterals; basal cusps, 1, small, with moderate dorsal support. Basal process moderately broad; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles, foot, neck pale. Snout near pale to dark purple-black. Opercular lobe pale or lightly pigmented along sides. Pallial roof, visceral coil light to dark.

Ctenidial filaments, 20, tall, medium width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum prominent.

Testis, 1.5 whorls, overlapping posterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens with strong proximal kink. Penis (Figure 48*e*) large; filament short, slender, tapering; lobe very short, broad. Dg1 extending along left edge from near-mid length onto proximal filament (sometimes absent); Dg2 short-elongate, horizontal. Terminal gland medium-sized, often transverse, near straight, borne distally (largely on ventral surface). Ventral gland small, stalked, near distal edge (sometimes reduced-absent). Filament usually unpigmented.

Ovary, 0.5 whorl, very slightly overlapping posterior stomach chamber. Pallial albumen gland large (33%). Capsule gland as long as albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a broad horizontal loop positioned slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length and width, with about half of length posterior to gland. Bursal duct very narrow, shallowly embedded in albumen gland, about as long as buras copulatrix. Seminal receptacle sac-like, narrow, short, overlapping anterior bursa copulatrix.

TYPE LOCALITY.—Montezuma Well, Yavapai County, Arizona (T 15N, R 6E, NW1/4 sec. 31). Holotype, USNM 859043; paratypes, USNM 859044.

DISTRIBUTION.—Endemic to type locality, Verde River drainage.

MATERIAL EXAMINED.—USNM 847233 (topotypes).

Pyrgulopsis morrisoni Hershler, 1988

Pyrgulopsis morrisoni Hershler in Hershler and Landye, 1988:21, figs. 10f, 16e–h, 19, 20.—USDI, 1991b:58821.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized, weakly umbilicate. Penial filament medium length, lobe elongate. Penial ornament a short, straight terminal gland.

DESCRIPTION.—Shell (Figure 20*g*) ovate-conic; height, 1.8–2.9 mm; whorls, 3.74–4.5. Protoconch moderately punctate. Teleoconch whorls moderately convex, often shouldered; sculpture of weak-moderate growth lines. Aperture broadly adnate to body whorl (rarely separated). Inner lip complete, slightly thickened; columellar lip slightly reflected. Outer lip orthocline to slightly prosocline. Umbicilus narrowly rimate (rarely absent) to weakly perforate. Periostracum light amber to brown.

Operculum (Figure 20*h,i*) broadly ovate, very light amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin moderately thickened between nucleus and mid-point of inner edge; callus moderately developed.

Central radular tooth (Figure 37*f*) with moderately indented dorsal edge; lateral cusps, 5–7; central cusp pointed, broader and considerably longer than laterals; basal cusps, 1, large, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale or with dark pigment patch just distal to eyespots. Snout, foot pale-light brown. Opercular lobe pale

or lightly pigmented on sides. Neck pale to with moderate internal brown pigment. Pallial roof, visceral coil moderate-dark brown-black.

Ctenidial filaments, 18, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum very small.

Testis, 1.75 whorls, overlapping anterior stomach chamber almost to posterior edge of style sac. Prostate gland fat, bean-like, with short pallial section; pallial vas deferens with strong proximal kink. Penis (Figure 49*a*) large, rectangular; filament slender, medium length; lobe large, broad. Terminal gland medium-sized, near horizontal, borne along distal edge of lobe, largely in ventral position; lobe rarely bearing a second small gland near distal edge. Filament pale or darkly pigmented.

Ovary, 0.5–0.75 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland shorter than albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a short horizontal twist followed by broad horizontal loop (kinked near mid-length), positioned slightly behind pallial wall. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix ovoid, short (33%), medium width (50%), with about half of length posterior to gland. Bursal duct narrow, partly embedded in albumen gland, almost as long as bursa copulatrix. Seminal receptacle narrow, pouch-like, large (60%), overlapping proximal bursal duct or anterior bursa copulatrix.

TYPE LOCALITY.—Page Springs, Yavapai County, Arizona (T 16N, R 4E, SE1/4 sec. 23). Holotype, USNM 859041; paratypes, USNM 859042.

DISTRIBUTION.—Upper Verde River drainage, Arizona.

REMARKS.—This snail is distinguished from similar *P. simplex* (also from northern Arizona) by its strong ventral operculum attachment scar and callus, broader penial lobe, transverse terminal gland, and kinked oviduct coil.

MATERIAL EXAMINED.—USNM 847231 (topotypes).

Pyrgulopsis nanus Hershler and Sada, 1987

Pyrgulopsis nanus Hershler and Sada, 1987:802, figs. 25, 29a,d, 30–32, 33a,b.—USDI, 1991b:58821.

DIAGNOSIS.—Shell globose, small to medium-sized, umbilicate. Penial filament short; lobe long, broad. Penial ornament a straight, transverse terminal gland.

DESCRIPTION.—Shell (Figure 21*a*) globose; height, 1.5–2.4 mm; whorls, 3–4. Protoconch finely punctate, later portion with a few weak, spiral striae adapically. Teleoconch whorls moderate- highly convex; sculpture of moderate-strong growth lines. Aperture narrowly adnate, rarely separated from body whorl. Inner lip complete, moderately thickened; columellar lip often slightly reflected. Outer lip prosocline. Umbilicus perforate. Periostracum amber.

Operculum (Figure 21*b,c*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin thickened (sometimes broadly so) all around; callus a prominent, highly thickened horizontal bar about half as long as operculum.

Central radular tooth (Figure 38*a*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp pointed, considerably broader, slightly longer than laterals; basal cusps, 1, narrowly triangular, with weak dorsal support. Basal process broad; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale, sometimes with internal brown patch just distal to eyespots. Snout light-dark brown. Foot light-moderately pigmented. Opercular lobe moderate gray-black on sides and (sometimes) along anterior edge. Neck pale-light. Pallial roof, visceral coil dark, near-uniform brown-black.

Ctenidial filaments, 13, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum small to medium-sized.

Testis, 1.5 whorls, overlapping posterior stomach chamber. Prostate gland very broad, with short pallial section; pallial vas deferens with weak proximal kink. Penis (Figure 49*b*) medium-sized; filament short; lobe longer than filament, sometimes as long as base, broad. Terminal gland usually transverse, borne distally along ventral surface of lobe. Filament dark.

Ovary, 0.5 whorl, abutting or very slightly overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland longer than albumen gland. Genital aperture an elongate terminal slit with very short vestibule. Coiled oviduct a small, tight, near circular loop slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, short (30%), narrow (33%), position varying from even with posterior edge of albumen gland to with half of length posterior to gland. Bursal duct narrow, slightly embedded in albumen gland, about as long as bursa copulatrix. Seminal receptacle pouch-like, stubby, short, overlapping proximal bursal duct.

TYPE LOCALITY.—Five Springs, Ash Meadows, Nye County, Nevada (T 17S, R 50E, NE1/4 sec. 22). Holotype, USNM 859191; paratypes, USNM 859192, FSM 93957.

DISTRIBUTION.—Ash Meadows, Amargosa River drainage.

REMARKS.—This snail is similar to two other globose-shelled Ash Meadows species, and shares with one of these, *P. isolata*, an uniquely elongate penial lobe. *Pyrgulopsis nanus* differs by its strong ventral operculum callus, deeply indented dorsal edge of central radular tooth, narrow central cusp of central radular tooth, kinked pallial vas deferens, and presence of a pallial section of albumen gland.

MATERIAL EXAMINED.—USNM 850356, "Mary Scott Spring," Ash Meadows, Nye County, Nevada (T 17S, R 50E, NW1/4 sec. 35).

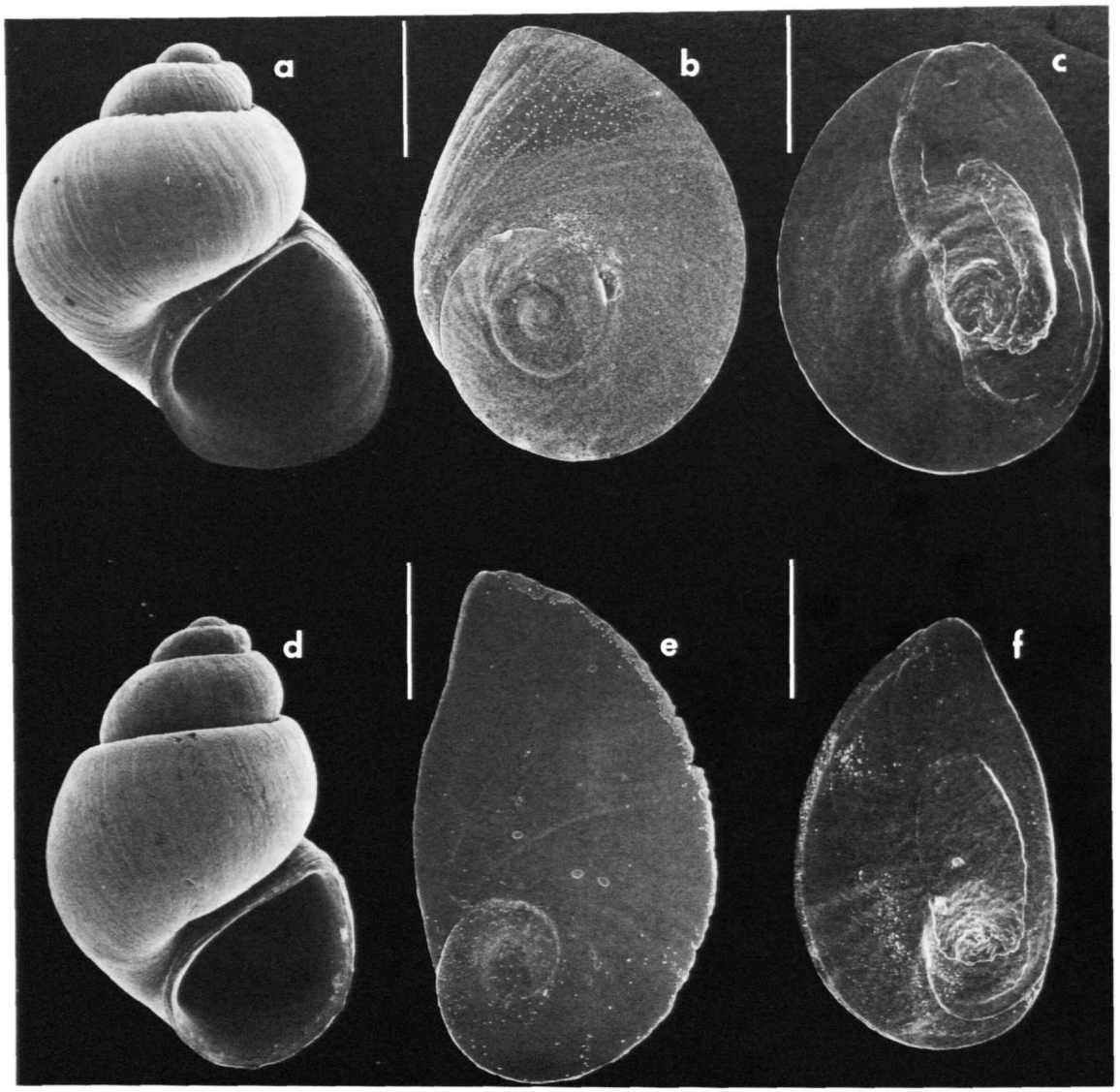


FIGURE 21.—Western *Pyrgulopsis: a–c, P. nanus* (*a*, shell, USNM 859192, 1.7 mm; *b,c*, opercula, USNM 850354, bars = 0.25 mm, 0.27 mm); *d–f, P. neomexicana*, USNM 873227 (*d*, shell, 2.0 mm; *e,f*, opercula, bars = 0.25 mm, 0.3 mm).

Pyrgulopsis neomexicana (Pilsbry, 1916)

Amnicola neomexicana Pilsbry, 1916:111, pl. XXX: fig. 4.—Walker, 1918: 135.—Baker, 1964:174.

"Amnicola" neomexicana.—Taylor, 1975:127.

Fontelicella neomexicana.—Burch, 1982:26 fig. 239.—Taylor, 1987:22, fig. 10.—Turgeon et al., 1988:61.

Pyrgulopsis neomexicana.—Hershler and Thompson, 1987:29, 30.—USDI, 1991a:49646; 1991b:58822.

DIAGNOSIS.—Shell globose to ovate-conic, small to medium-sized, narrowly umbilicate. Penial filament medium length, lobe short, broad. Penial ornament an elongate penial gland, circular-transverse Dg1, short Dg2, Dg3 borne on weak swelling; elongate, curved, transverse terminal gland, and two ventral glands.

DESCRIPTION.—Shell (Figure 21*d*) globose to ovate-conic; height, 1.6–2.3 mm; whorls, 3.5–4.5. Protoconch invariably eroded. Teleoconch whorls slightly convex, strongly shouldered; sculpture of weak growth lines. Aperture ovate, strongly angled above, adnate to or slightly separated from body whorl. Inner lip complete, straight, thickened. Outer lip prosocline, often strongly sinuate. Umbilicus shallow, rimate. Periostracum light brown.

Operculum (Figure 21*e,f*) ellipsoidal, light amber (darker in nuclear region); nucleus highly eccentric; dorsal surface

weakly frilled. Attachment scar margin slightly thickened all around, sometimes more broadly so between nucleus and mid-point of inner edge; callus moderately developed.

Central radular tooth (Figure 38*b*) with strongly indented dorsal edge and highly elongate cusps; lateral cusps, 5; central cusp pointed, considerably longer than laterals; basal cusps, 1, medium-sized, with weak dorsal support. Basal process medium width, highly excavated. Lateral margins very slightly thickened; neck moderate.

Proximal tentacles, snout moderate to dark brown-black. Foot similarly pigmented along anterior and posterior edges. Opercular lobe dark over much of surface. Neck paler than snout. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 20, tall, narrow. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney with pronounced (40%) pallial bulge; opening white. Stomach with small triangular caecum.

Testis, 0.5 whorl, ending slightly posterior to stomach. Prostate gland fat, bean-like, with large pallial section (25%); pallial vas deferens with proximal loop. Penis (Figure 49*c*) large; filament medium length, slender; lobe short, broad. Penial gland filling most of filament length. Dg1 short, circular to diagonal; Dg2 short, oblique (sometimes accompanied by glandular dot); Dg3 on weak swelling along base of lobe near right edge. Terminal gland elongate, transverse, curved, borne along distal edge of lobe (on both surfaces, often split into two fragments). Ventral gland sub-terminal, stalked, usually accompanied by second, smaller gland proximal to above. Filament weakly pigmented.

Ovary, 1 whorl, abutting posterior edge of stomach. Pallial albumen gland large (25%). Capsule gland slightly longer than albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct a broad horizontal loop extending to posterior edge of albumen gland (slightly overlapping bursa copulatrix). Oviduct and bursal duct join anterior to oviduct coil near pallial wall. Bursa copulatrix elongate-pyriform, as long as (or slightly longer than) and as wide as albumen gland, with almost entire length (90%) posterior to gland. Bursa duct narrow, very short, emerging slightly posterior to anterior tip of bursa. Seminal receptacle sac-like, elongate, overlapping bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Socorro [Socorro County], New Mexico, in warm springs. Lectotype (Baker, 1964:174), ANSP 12113; paralectotypes, ANSP 396954.

DISTRIBUTION.—Historically confined to several springs in the Rio Grande drainage of southern New Mexico. Now extinct at type locality area (Taylor, 1987), and represented by only a single living population at Torreon Springs.

MATERIAL EXAMINED.—USNM 873227, Torreon Springs, Socorro County, New Mexico (T 5S, R 2W, NE1/4 sec. 8).

Pyrgulopsis nevadensis (Stearns, 1883)

Pyrgula nevadensis Stearns, 1883:173 [unlabeled figure, p. 173; not *Fluminicola nevadensis* Walker, 1916].—Call, 1884:21.—Call and Beecher, 1884: 851, figs. 1–5.—Baker, 1964:174.

Pyrgulopsis nevadensis.—Call and Pilsbry, 1886:10, pl. II: figs. 1–10.—Ancey, 1888:189.—Pilsbry, 1891c:329; 1899:122.—Hannibal, 1912b:189.—Walker, 1918:30, figs. 101, 102.—Thiele, 1928:378.—Wenz, 1939:558, fig. 1499.—Gregg, 1945:69.—Berry, 1947:77, pl. 7: fig. 7.—Baily and Baily, 1951:52, pl. 4: fig. 9.—Jacobson, 1952a:15.—Taylor, 1960a:327; 1970:33; 1975:127–128.—Burch, 1982:28, figs. 256, 270–272.—Hershler and Thompson, 1987:28, figs. 4, 25–29.—Turgeon et al., 1988:62.

Pyrgalopsis [sic] *nevadensis*.—Brues, 1932:278.

Pyrgulopsis nevadensis var. *ecarinata* Ancey, 1888:189.

Pyrgulopsis nevadensis paiutica Baily and Baily, 1951:52, pl. 4: fig. 10, right figure.—Jacobson, 1952a:16; 1952b:70.—Burch, 1982:28.

Pyrgulopsis paiutica.—Baker, 1964:175.

DIAGNOSIS.—Shell ovate-conic to turriform, usually basally carinate, medium to large-sized, weakly umbilicate. Penial filament medium length, lobe short. Penial ornament a small terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 22*a,b*) ovate-conic to turriform; height, 3.5–5.7 mm; whorls, 4.5–6.0. Protoconch appearing near smooth, but usually eroded. Apical whorls well rounded, late teleoconch whorls much less so, sometimes shouldered; sculpture of strong growth lines. Strong peripheral carina usually present from beginning of third whorl to aperture, but carina development varying to weak cord or very slight angulation. Aperture ovate, broadly adnate to body whorl. Inner lip complete, thin. Outer lip prosocline. Umbilicus absent to narrowly rimate. Periostracum light brown.

Operculum (Figure 22*c,d*) ovate, light amber; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin near smooth, with only faint trace between nucleus and inner edge; central callus weak.

Central radular tooth (Figure 38*c*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp rounded to weakly pointed, considerably broader and longer than laterals; basal cusps, 1 (although occasional weak suggestion of second cusp), elongate, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck absent.

Penis (Figure 49*d*) small (retracted specimens); filament medium length, narrow; lobe shorter than filament. Terminal gland small, borne along distal edge of lobe (on both surfaces). Ventral gland large, positioned near distal edge of penis. Filament pigmented.

TYPE LOCALITY.—*Pyrgulopsis nevadensis:* Walker and Pyramid Lakes, Nevada. Subsequently restricted to Pyramid Lake, Washoe County, Nevada (per Baker, 1964:174). Lectotype, ANSP 27811; paratypes, ANSP 375739. *Pyrgulopsis ecarinata:* Walker and Pyramid Lakes (not restricted subsequently). Location of types not known. *Pyrgulopsis pauitica:* Pyramid Lake, Nevada. Holotype, ANSP 187693; paratypes ANSP 396956.

DISTRIBUTION.—Pyramid Lake (Recent); Walker Lake, Winnemucca Lake (Pleistocene?). The snail persisted in Pyramid Lake at least until the very late 1800s, as evidenced by presence in museum collections of numerous live-collected specimens from this period. Recent dredging hauls from the

FIGURE 22.—Western *Pyrgulopsis: a–d, P. nevadensis* (*a*, shell, USNM 590364, 4.8 mm; *b*, shell, ANSP 187693, 6.1 mm; *c, d*, opercula, USNM 63992, bars = 0.46 mm, 0.43 mm); *e–g, P. owensensis*, USNM 857955 (*e*, shell, 2.3 mm; *f,g*, opercula, bar = 0.3 mm); *h*, shell, *P. palomasensis*, USNM 130016 (2.5 mm).

lake have not yielded live snails (Swain and Meader, 1958; Robertson, 1978; Galat et al., 1981), suggesting that the species now is extinct.

MATERIAL EXAMINED.—USNM 63992, Pyramid Lake, Nevada.

Pyrgulopsis owensensis Hershler, 1989

Pyrgulopsis owensensis Hershler, 1989:187, figs. 26a–d, 27–32.—Hershler and Pratt, 1990:286, fig. 6.

DIAGNOSIS.—Shell near-globose to ovate-conic, small to medium-sized, umbilicate. Penial filament and lobe short. Penial ornament a dot-like Dg1 (sometimes absent); straight, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 22*e*) near-globose to ovate-conic; height, 1.5–2.8 mm; whorls, 3.0–4.25. Early protoconch weakly punctate abapically, other portion smooth. Teleoconch whorls moderately convex, slightly shouldered; sculpture of weak growth lines. Aperture adnate or (more commonly) slightly separated from body whorl. Inner lip complete, slightly to moderately thickened; columellar lip sometimes moderately reflected. Outer lip slightly prosocline. Umbilicus narrowly rimate to perforate. Periostracum light amber.

Operculum (Figure 22*f,g*) ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened almost all around (weak along middle portion of outer edge); callus moderately developed.

Central radular tooth (Figure 38*d*) with moderate-strongly indented dorsal edge; lateral cusps, 4–6; central cusp pointed, narrow, considerably longer than laterals; basal cusps, 1, medium-sized, with moderate dorsal support. Basal process medium width; basal sockets deep. Lateral margins slightly thickened; neck moderate.

Pigment light to moderate gray to brown-black on cephalic tentacles; pigment uniform or concentrated in small patch distal to eyespots. Snout light-dark gray. Foot pigment generally light, heavier along anterior and posterior edges. Opercular lobe moderate-darkly pigmented along sides, sometimes along outer edge as well. Neck pigment pale-moderate, sometimes with internal granules. Pallial roof, visceral coil black.

Ctenidial filaments, 15, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly whitened. Stomach caecum small, narrow.

Testis, 1 whorl, overlapping entire posterior stomach chamber and small portion of anterior chamber. Prostate gland small, with large (25%) pallial section; pallial vas deferens with small proximal kink. Penis (Figure 49*e*) large; filament short, narrow; lobe broad, about equal to filament in length. Dg1 small, dot-like, distally positioned near outer edge, sometimes absent. Terminal gland elongate, transverse, borne along distal edge of lobe. Dorsal penis also sometimes with a small glandular dot on base of lobe (remnant of Dg3?). Ventral gland borne on prominent swelling near base of lobe. Filament dark.

Ovary, 0.5 whorl, abutting or slightly overlapping posterior stomach chamber. Pallial albumen gland large (35%). Capsule gland slightly shorter than albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a slight horizontal twist followed by broad, horizontal loop just behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, medium length, narrow (33%), with 55%–75% of length posterior to gland. Bursal duct narrow, about as long as bursa copulatrix. Seminal receptacle sac-like, narrow, short, usually overlapping proximal bursal duct.

TYPE LOCALITY.—Unnamed spring in canyon south of Piute Creek, Owens Valley, Mono County, California (T 5S, R 33E, NE1/4 sec. 23). Holotype, USNM 860404; paratypes, USNM 857955.

DISTRIBUTION.—Owens River drainage, Owens Valley.

REMARKS.—Amongst the group of similar species in Owens Valley, this species resembles *P. perturbata* in having a medium length penial lobe and transverse terminal gland. It differs in its smaller size, squatter shell, smaller caecal chamber of stomach, and bursa copulatrix positioned entirely lateral to the albumen gland.

Restudy of specimens from Walker River drainage assigned to this species by Hershler and Pratt (1990) indicates that these snails belong to an undescribed, albeit closely similar species.

MATERIAL EXAMINED.—USNM 857955 (paratypes).

Pyrgulopsis palomasensis (Pilsbry, 1895), new combination

Bythinella palomasensis Pilsbry, 1895b:68; 1916:111.—Dall, 1897:369, pl. XXXI: fig. 9.—Drake, 1953:27; 1956:46.—Taylor, 1967:156.
Amnicola palomasensis.—Martens, 1890–1901:434.
Fontelicella palomasensis.—Taylor, 1975:141.

DIAGNOSIS.—Shell ovate, medium-sized, narrowly umbilicate. Animal unknown.

DESCRIPTION.—Shell (Figure 22*h*) ovate; height, about 2.8 mm; whorls, 4.25. Protoconch blunt, smooth (possibly due to wear). Teleoconch whorls highly convex, shouldered; sculpture of strong growth lines and faint spiral striae. Aperture ovate, narrowly adnate to well separated from body whorl. Inner lip complete, thin; columellar lip slightly reflected. Outer lip orthocline. Umbilicus narrowly perforate.

TYPE LOCALITY.—Lake Palomas, northeastern Mexico (subfossil). Taylor (1967) identified this material, collected by E.A. Mearns, as from Station Number 8 of the second United States and Mexico Boundary Survey, allowing a more precise definition of the locality (from Mearns, 1907) as Palomas Lakes, Mimbres Valley, Chihuahua, 1 mile (1.61 km) south of Monument Number 21. Pilsbry's types (USNM 130016) consisted of two specimens: I have selected the specimen figured by Dall (1897) as the lectotype; the other, broken shell, is a paralectotype, USNM 860580.

DISTRIBUTION.—Known only from type locality.

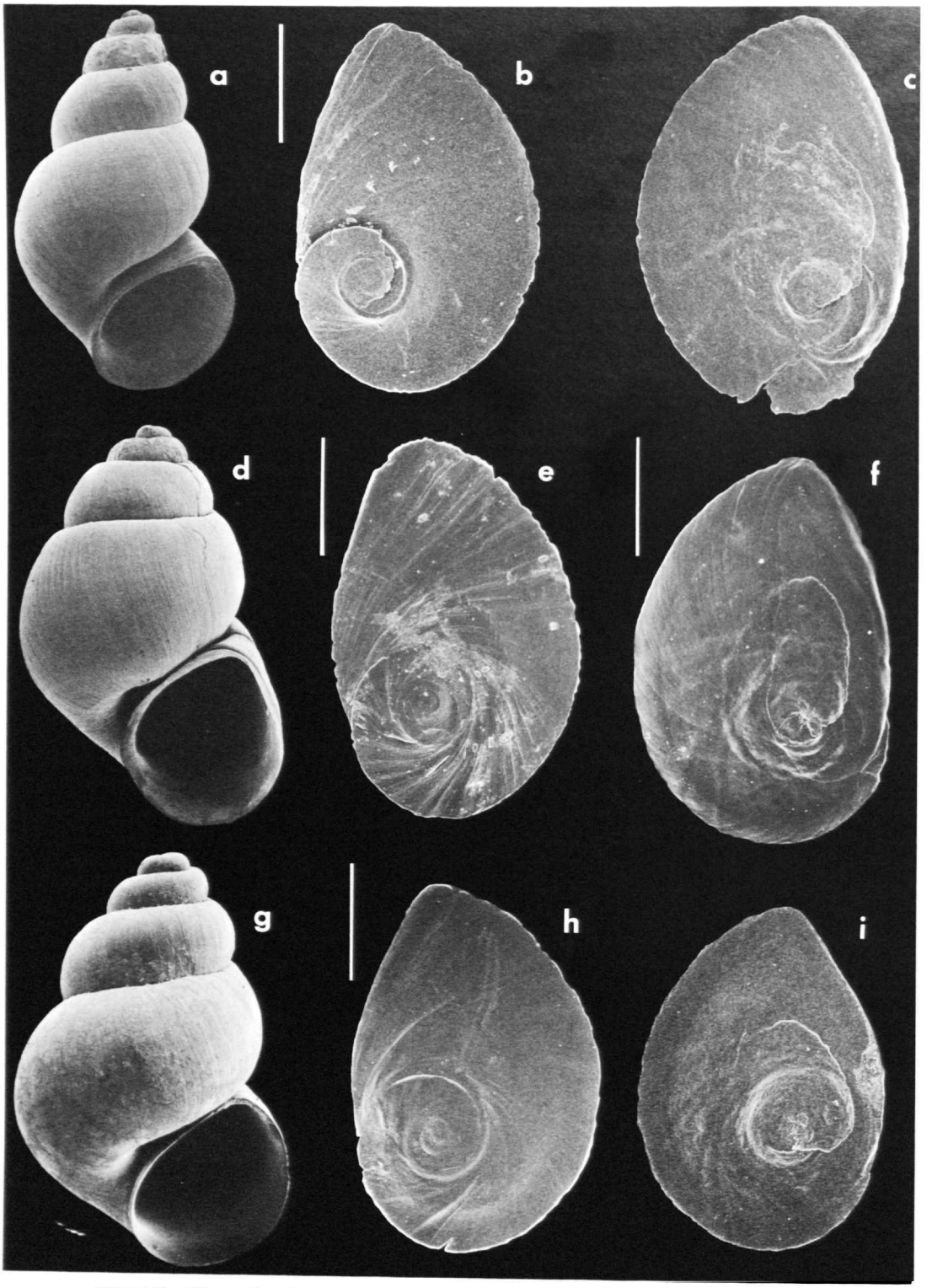


FIGURE 23.—Western *Pyrgulopsis*: *a–c*, *P. pecosensis*, USNM 873131 (*a*, shell, 3.2 mm; *b,c*, opercula, bar = 0.38 mm); *d–f*, *P. perturbata* (*d*, holotype, USNM 860407, 3.4 mm; *e, f*, opercula, USNM 857990, bars = 0.43 mm, 0.38 mm); *g–i*, *P. pilsbryana*, USNM 858279 (*g*, shell, 2.6 mm; *h,i*, opercula, bar = 0.33 mm).

REMARKS.—The small size and ovate shape of these empty western shells suggest membership in *Pyrgulopsis*. This species is distinguished from *Pyrgulopsis brandi*, which was described from extant populations occurring in the same region, by its squatter shell and thin apertural lip.

Pyrgulopsis pecosensis (Taylor, 1987), new combination

Fontelicella pecosensis Taylor, 1987:27, fig. 12.
"Fontelicella" pecosensis.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate- to narrowly conic, medium-sized, umbilicate. Penial filament short; lobe short, broad. Penial ornament a short Dg1, small Dg3 borne on lobule; curved, elongate, transverse terminal gland; and ventral gland.

DESCRIPTION.—Shell (Figure 23*a*) ovate- to narrowly conic; height, 2.0–2.9 mm; whorls, 4–5. Early protoconch weakly punctate, otherwise near smooth except for faint spiral lines. Teleoconch whorls moderately convex, sometimes weakly shouldered; sculpture of weak growth lines and occasionally weak spiral lines. Aperture ovate, angled above, usually adnate to body whorl. Inner lip complete, thickened; columellar lip sometimes slightly reflected. Outer lip thinner, prosocline. Umbilicus shallowly rimate or perforate. Periostracum tan.

Operculum (Figure 23*b,c*) ovate, amber, darker in nuclear region; nucleus slightly eccentric; dorsal surface strongly frilled. Attachment scar margin broadly thickened between nucleus and inner edge (extending slight distance along edge), otherwise very weak-smooth; callus weak.

Central radular tooth (Figure 38*e*) with moderately indented dorsal edge; lateral cusps, 6–7; central cusp rounded, considerably longer and broader than laterals. Basal cusps, 1, short, with slight dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles, snout moderate-dark brown. Tentacles sometimes with central unpigmented streak. Foot lightly pigmented except for darkened anterior and posterior edges. Opercular lobe with darkened edges. Neck pale. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 15–20, medium height and width. Osphradium positioned centrally to slightly posterior to middle of ctenidial axis. Kidney with prominent bulge (up to 40%) into pallial cavity; opening thickened. Stomach with medium-sized triangular caecum.

Testis, 1.5–2.0 whorls, overlapping stomach to edge of style sac. Prostate gland bean-like, strongly recurved, with large (25%) pallial section; pallial vas deferens with gentle proximal bend. Penis (Figure 49*f*) large; filament short, narrow; lobe short, broad. Dg1 short, extending along right edge slightly onto base of filament; Dg3 a small tubercle (sometimes absent) borne on pronounced distal lobule. Terminal gland elongate, transverse, curved, largely ventral. Ventral gland small, sub-terminal, borne on low swelling. Filament darkly pigmented.

Ovary, 1 whorl, overlapping posterior stomach chamber. Pallial albumen gland short, sometimes absent. Capsule gland shorter than albumen gland. Genital aperture a terminal broad pore without vestibule. Coiled oviduct of tight posterior oblique coil followed by (and overlapping) broad horizontal loop, positioned near middle of albumen gland. Oviduct and bursal duct join well posterior to pallial wall. Bursa copulatrix ovoid, elongate (up to 67%), broad (67%), with much of length (67%) posterior to albumen gland. Bursal duct medium length and width. Seminal receptacle finger-like, short, positioned alongside anteriormost bursa copulatrix and/or proximal bursal duct.

TYPE LOCALITY.—Blue Spring, center SW1/4 sec. 27, T 24S, R 26E, Eddy County, New Mexico.

DISTRIBUTION.—Pecos River drainage, southeastern New Mexico.

REMARKS.—This species appears more closely related to northern congeners (*P. hendersoni, P. idahoensis, P. robusta*) than to local species. It differs in its smaller size, superficial position of Dg1, anterior position of seminal receptacle, and location of seminal receptacle along ventral edge of albumen gland.

MATERIAL EXAMINED.—USNM 873131 (topotypes).

Pyrgulopsis perturbata Hershler, 1989

Pyrgulopsis perturbata Hershler, 1989:189, figs. 26e–g, 33–36.

DIAGNOSIS.—Shell ovate to low conical, medium to large-sized, narrowly umbilicate. Penial filament short, lobe medium length. Penial ornament a small Dg1, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 23*d*) ovate to low conical; height, 2.7–4.0 mm; whorls, 4.25–5.0. Early protoconch very weakly punctate, otherwise near smooth. Teleoconch whorls slightly convex, sometimes shouldered; sculpture of very faint growth lines. Aperture broadly adnate to very slightly separated from body whorl. Inner lip complete, usually thick; columellar lip well reflected. Outer lip thick, slightly prosocline. Umbilicus rimate. Periostracum tan.

Operculum (Figure 23*e,f*) ovate, moderately dark amber; nucleus slightly eccentric; dorsal surface slightly frilled. Attachment scar margin weakly thickened all around, stronger along inner edge; callus weak.

Central radular tooth (Figure 38*f*) with slightly indented dorsal edge; lateral cusps, 5; central cusp rounded, much longer and slightly broader than laterals; basal cusps, 1, elongate-triangular, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck weak-absent.

Cephalic tentacles pale to moderate brown-black. Snout light to dark gray. Foot light-moderate gray, with pigment darkest along anterior and posterior margins. Opercular lobe dark along margins, especially sides and outer edge. Neck pale to light gray. Pallial roof, visceral coil near pale to uniform black.

Ctenidial filaments, 27, tall and broad. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney with large (35%) pallial bulge; opening thickened (not white). Stomach

caecum prominent, broadly triangular.

Testis, 2 whorls, overlapping anterior stomach chamber to edge of style sac. Prostate gland with short pallial section; pallial vas deferens with weak proximal undulation. Penis (Figure 50*a*) large; filament short, narrow; lobe slightly longer than filament, broad, slightly oblique. Dg1 small, positioned near base of filament. Terminal gland usually transverse, borne along ventral surface. Ventral gland (rarely split into two) borne on sub-terminal swelling. Filament dark.

Ovary, 1 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Albumen gland as long as capsule gland. Genital aperture a broad terminal slit with short vestibule. Coiled oviduct a short horizontal twist followed by broad horizontal loop, often kinked near mid-length, positioned slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, short (32%–40%), narrow (33%), with 43%–80% of length posterior to gland. Bursal duct medium width, shallowly embedded in albumen gland, about as long as bursa copulatrix. Seminal receptacle pouch-like, narrow, folded, short, overlapping (or lateral to) proximal bursal duct.

TYPE LOCALITY.—Southern of two "Northwest Springs," Fish Slough, Mono County, California (T 5S, R 32E, SE1/4 sec. 13). Holotype, USNM 860407; paratypes, USNM 853546.

DISTRIBUTION.—Headsprings in Fish Slough, Owens River drainage.

MATERIAL EXAMINED.—USNM 857990 (topotypes); USNM 857991, northern of two "Northwest Springs" (data as above).

Pyrgulopsis pilsbryana (Baily and Baily, 1952)

Paludestrina longinqua.—Pilsbry, 1899:122 [in part].—Stearns, 1901:285 [in part].—Henderson and Daniels, 1917:58, 59.—Henderson, 1924:190; 1931:110.—Chamberlain and Jones, 1929:177 [in part].

Amnicola pilsbryi Baily and Baily, 1951:50, pl. 4: fig. 3 [not Walker, 1906].—Baker, 1964:175.

Pyrgulopsis pilsbryi.—Hershler and Thompson, 1987:30.

Amnicola pilsbryana Baily and Baily, 1952:144 [new name for above].—Taylor, 1965:599.

Fontelicella pilsbryana.—Gregg and Taylor, 1965:108.—Taylor, 1975:152.—Burch, 1982:26.—Turgeon et al., 1988:61.

DIAGNOSIS.—Shell conical, medium to large-sized, umbilicate. Penial filament medium length, lobe short. Penial ornament a small penial gland; small, weakly raised Dg3; and horizontal terminal gland.

DESCRIPTION.—Shell (Figure 23*g*) conical; height, 2.7–5.0 mm; whorls, 4–5. Protoconch near smooth except for a few adapical spiral lines on later portion. Teleoconch whorls highly convex, strongly shouldered; sculpture of variably expressed growth lines. Aperture narrowly adnate to body whorl, rarely separated. Inner lip complete, only very slightly thickened; columellar lip slightly reflected. Outer lip slightly prosocline. Umbilicus shallowly perforate. Periostracum brown.

Operculum (Figure 23*h,i*) ovate, amber, considerably darker in nuclear area; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened along inner edge (to nucleus), otherwise a faint trace; callus weak.

Central radular tooth (Figure 39*a*) with moderately indented dorsal edge; lateral cusps, 4; central cusp pointed, considerably broader, longer than laterals; basal cusps, 1, medium-sized, with weak-moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck weak.

Cephalic tentacles, snout, foot, neck light to dark brown-gray. Opercular lobe with dark internal pigment along sides. Neck sometimes with scattered dark internal granules. Pallial roof, visceral coil near uniform black. Entire animal sometimes black.

Ctenidial filaments, 23, medium height and width. Osphradium centrally positioned along ctenidial axis. Kidney opening slightly thickened. Stomach caecum prominent.

Testis, 1.5–2.0 whorls, overlapping stomach to posterior edge of style sac. Prostate gland with short pallial section; pallial vas deferens gently undulating proximally. Penis (Figure 50*b*) large; filament medium length, narrow; lobe short, tapered distally. Penial gland weak, covering only base of filament, sometimes extending slightly onto penis. Dg3 small, superficial or (less commonly) very weakly raised, near outer edge close to base of filament. Terminal gland horizontal (rarely split into two), borne distally, largely on ventral surface. Filament dark.

Ovary, 0.75–1.0 whorl, overlapping posterior stomach chamber. Pallial albumen gland short-long (15%–25%). Capsule gland as long as albumen gland. Genital aperture a subterminal pore without or with very short vestibule. Coiled oviduct a slight posterior oblique twist followed by broad horizontal loop slightly behind pallial wall. Oviduct and bursa duct join just behind pallial wall. Bursa copulatrix ovoid, medium length, broad (70%), with about 67% of length posterior to gland. Bursa duct narrow, shallowly embedded in albumen gland, about as long as bursa copulatrix. Seminal receptacle sac-like, narrow, short, overlapping proximal bursal duct.

TYPE LOCALITY.—Lifton, Ideal Beach, Bear Lake, Idaho. Holotype, ANSP 187691; paratypes, ANSP 368401.

DISTRIBUTION.—Bear Lake basin, southeastern Idaho-northeastern Utah.

REMARKS.—Distinguished from similar *P. trivialis* by weak ventral operculum attachment scar, absence of Dg2 and ventral gland, and anterior position of seminal receptacle.

MATERIAL EXAMINED.—USNM 858279, unnamed spring, about 0.6 km northwest of Lakota, Rich County, Utah (T 14N, R 5E, NE1/4 sec. 5).

Pyrgulopsis pisteri Hershler and Sada, 1987

Pyrgulopsis pisteri Hershler and Sada, 1987:804, figs. 29b,e, 33c, 34a–e, 35, 36.—USDI, 1991b:58822.

DIAGNOSIS.—Shell globose to broadly conical, small to medium-sized, umbilicate. Penial filament medium length, lobe very weak or absent. Penial ornament a large, superficial

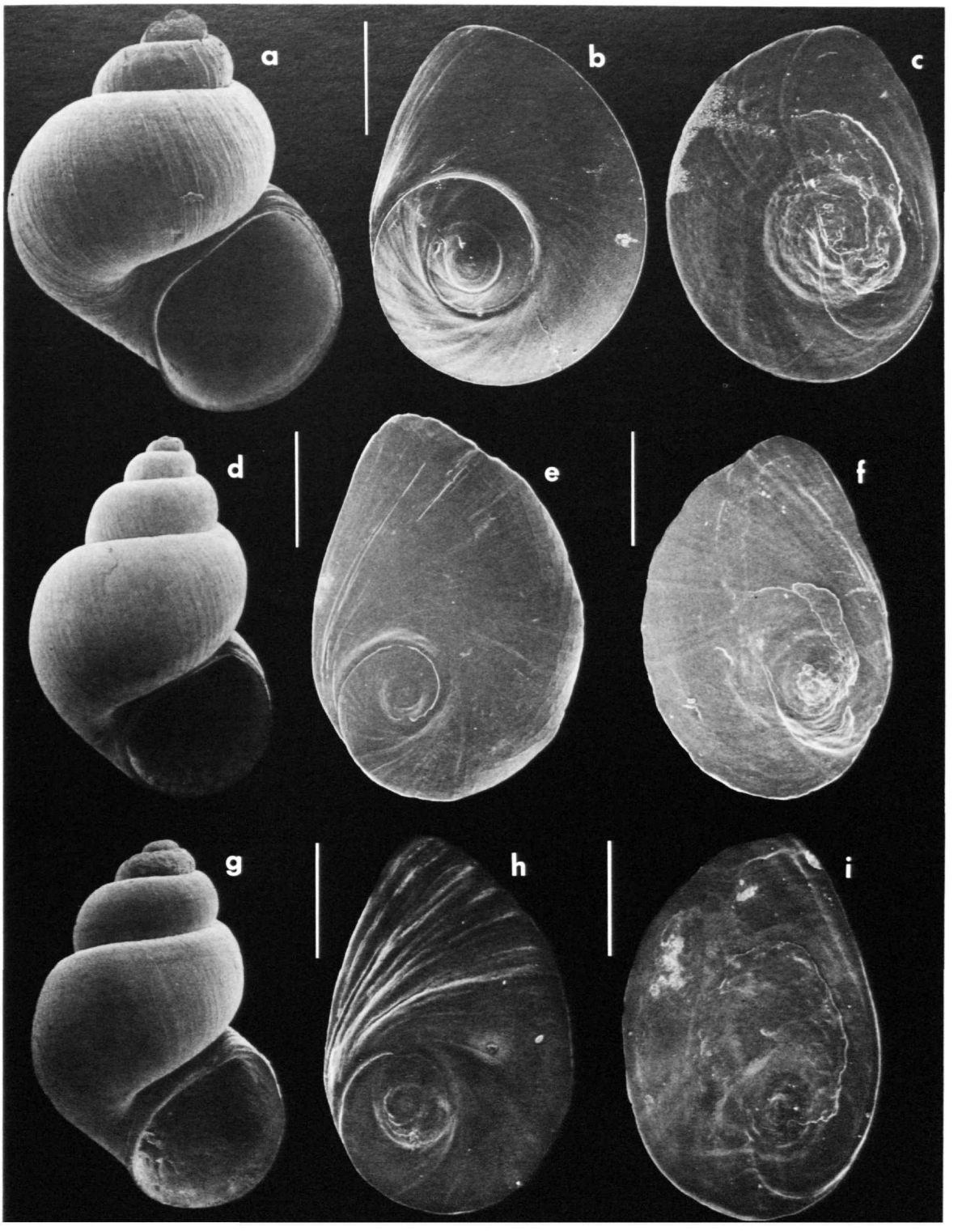


FIGURE 24.—Western *Pyrgulopsis*: *a–c*, *P. pisteri* (*a*, holotype, USNM 859197, 2.2 mm; *b*, *c*, opercula, USNM 850363, bar = 0.33 mm); *d–f*, *P. robusta*, USNM 874185 (*d*, shell, 5.5 mm; *e*,*f*, opercula, bars = 0.67 mm, 0.6 mm); *g–i*, *P. roswellensis*, USNM 873132 (*g*, shell, 2.1 mm; *h*, *i*, opercula, bars = 0.27 mm, 0.25 mm).

ventral gland.

DESCRIPTION.—Shell (Figure 24*a*) globose to broadly conical; height, 1.8–2.7 mm; whorls, 3.25–4.5. Early protoconch finely punctate, otherwise smooth except for weak spiral lines. Teleoconch whorls moderately convex, shouldered; sculpture of strong growth lines and occasionally numerous faint spiral striae. Aperture narrowly adnate to or slightly separated from body whorl. Inner lip complete, thickened; columellar lip slightly reflected. Outer lip prosocline, weakly sinuate. Umbilicus perforate. Periostracum light brown, very thin, often absent.

Operculum (Figure 24*b,c*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened all around, broadly so along inner edge near nucleus; callus moderately developed.

Central radular tooth (Figure 39*b*) with weakly indented dorsal edge; lateral cusps, 3–4; central cusp pointed, much longer and broader than laterals; basal cusps, 1, medium-sized, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles, neck pale to dark brown. Snout, foot pigment moderate to dark brown. Opercular lobe dark along inner edge. Pallial roof, visceral coil dark, uniform brown-black.

Ctenidial filaments, 21, very tall, medium width. Osphradium centered well posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum absent.

Testis, 1.5 whorls, overlapping anterior stomach chamber almost to edge of style sac. Prostate gland with short pallial section; pallial vas deferens with prominent proximal kink. Penis (Figure 50*c*) medium-sized; filament medium length, narrow, tapering; lobe absent or a slight bulge. Ventral gland large, circular, superficial, positioned close to left edge near mid-length. Filament dark.

Ovary, 1 whorl, overlapping posterior stomach chamber. Albumen gland without a pallial section. Capsule gland as long as albumen gland. Genital aperture a short terminal slit with very short vestibule. Coiled oviduct a horizontal loop slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix near globular, short (30%), medium width, with 25%–50% of length posterior to gland. Anterior bursa copulatrix sometimes embedded in albumen gland. Bursal duct very narrow, (deeply) embedded in albumen gland anteriorly, longer than bursa copulatrix. Seminal receptacle sac-like, narrow, often folded, short, positioned just anterior to or very slightly overlapping bursa copulatrix.

TYPE LOCALITY.—Marsh Spring, Ash Meadows, Nye County, Nevada (T 17S, R 50E, SE1/4 sec. 35). Holotype, USNM 859197; paratypes, USNM 859198, FSM 94958.

DISTRIBUTION.—Ash Meadows, Amargosa River drainage.

MATERIAL EXAMINED.—USNM 850363, 850364 (topotypes).

Pyrgulopsis robusta (Walker, 1908)

Pomatiopsis robusta Walker, 1908:97 [unlabeled figure]; 1918:148.—Henderson, 1918:41; 1924:192; 1932:133; 1933:1.—Baker, 1928:162.—Abbott 1948:66.

Amnicola robusta.—Pilsbry 1933:9, pl. 2: figs. 1, 7, 8.—Henderson, 1936a: 137, fig. 7.—Beetle, 1957:17; 1961:5.

Fontelicella (Natricola) robusta.—Gregg and Taylor, 1965:109.—Burch, 1982:26, figs. 230, 243.

Fontelicella robusta.—Taylor, 1975:167.—Beetle, 1989:639.—Turgeon et al., 1988:61.

Pyrgulopsis robusta.—Hershler and Thompson, 1987:30.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate- to narrowly-conic, large, umbilicate. Penial filament medium length; lobe medium length, broad. Penial ornament an elongate Dg1, short Dg2; small Dg3, sometimes absent, borne on lobule; elongate, transverse, slightly curved terminal gland; and ventral gland.

DESCRIPTION.—Shell (Figure 24*d*) ovate- to narrowly-conic; height, 5.5–6.3 mm; whorls, 5.0–5.5. Protoconch with small, very weakly punctate area near apex, otherwise smooth except for faint suggestion of spiral striae adapically. Teleoconch whorls moderately convex, shouldered; sculpture of weak growth lines. Aperture adnate to very slightly separated from body whorl. Inner lip complete, thickened. Outer lip slightly thinner, prosocline. Umbilicus narrowly rimate to perforate. Periostracum thick, brown.

Operculum (Figure 24*e,f*) ovate, amber, darker centrally; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin moderately thickened almost all around, sometimes broadly so along inner edge and between edge and nucleus; callus moderate-strongly developed.

Central radular tooth (Figure 39*c*) with weakly indented dorsal edge; lateral cusps, 5–6; central cusp rounded, much longer, slightly broader than laterals; basal cusps, 1, small, curved, with strong dorsal support. Basal process very broad; basal sockets deep. Lateral margins thickened; neck moderate.

Cephalic tentacles pale except for small internal pigment patch just distal to eyespots. Snout light to dark gray-brown. Foot pale-dark gray. Opercular lobe pale or with small patch of internal pigment along inner edge. Neck pale except for central patch of internal pigment. Pallial roof, visceral coil black.

Ctenidial filaments, 32, tall, very broad. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum large, broadly triangular.

Testis, 1.75 whorls, overlapping stomach to edge of style sac. Prostate gland with large (40%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 50*d*) large; base broadly rectangular; filament medium length, narrow, tapering; lobe about as long as filament, stout. Dg1 elongate, extending from base of filament (slightly overlapped) along right edge, posterior portion curving inward, slightly raised; Dg2 short, horizontal or tilted toward Dg3, sometimes broken into two

units; Dg3 small (sometimes absent), borne on pronounced proximal lobule. Dorsal penis also sometimes ornamented with 1–3 small glandular dots centrally and/or along near right side. Terminal gland elongate, transverse, slightly curved, borne along distal edge (mostly on ventral surface). Ventral gland borne on swelling near base of filament (gland sometimes absent), sometimes with adjacent glandular dot. Filament dark.

Femalia genitalia are shown in Figure 5*f*. Ovary, 1 whorl, overlapping posterior stomach chamber. Pallial albumen gland short or absent. Capsule gland as long as albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct of two overlapping horizontal loops positioned slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, posterior end often blunt, long (67%), broad (58%), with 33%–67% of length posterior to albumen gland. Bursal duct relatively narrow, short. Seminal receptacle pouch-like, broad, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Jackson Lake, Wyoming. Holotype presumably in UMMZ collection (could not be found).

DISTRIBUTION.—Jackson Lake and Polecat Creek (tributary), northwest Wyoming, Snake River drainage.

REMARKS.—This snail is similar to other large-sized species from southeast Oregon (*P. hendersoni*) and Snake River (*P. idahoensis*). It differs in its weaker ventral operculum callus, pointed central cusp on central radular tooth, presence of anterior capsule gland vestibule, and broad bursa copulatrix.

MATERIAL EXAMINED.—USNM 874185, Polecat Creek, Teton County, Wyoming (T 48N, R 115W, NE1/4 sec. 20).

Pyrgulopsis roswellensis (Taylor, 1987), new combination

Fontelicella roswellensis Taylor, 1987:14, fig. 6.
"Fontelicella" roswellensis.—USDI, 1991b:58819.

DIAGNOSIS.—Shell ovate-conic, medium to large-sized, weakly umbilicate. Penial filament medium length, lobe short. Penial ornament an elongate, sometimes proximally bifurcate penial gland; small Dg2, sometimes absent; small Dg3, sometimes absent, borne on low swelling; curved, transverse terminal gland; and ventral gland.

DESCRIPTION.—Shell (Figure 24*g*) ovate-conic; height, 2.4–3.8 mm; whorls, 4–5. Protoconch finely punctate. Teleoconch whorls slightly-moderately convex, often strongly shouldered; sculpture of weak-moderate growth lines. Aperture adnate to slightly separated from body whorl. Inner lip complete, thickened; columellar lip reflected. Outer lip slightly prosocline. Umbilicus very narrowly rimate to shallowly perforate. Periostracum light tan.

Operculum (Figure 24*h,i*) ovate, amber, sometimes with internal calcareous smears; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin thickened all around, broadly so along inner edge and between edge and nucleus; callus well developed.

Central radular tooth (Figure 39*d*) with moderately indented dorsal edge; lateral cusps, 5–6; central cusp pointed, considerably longer, slightly broader than laterals; basal cusps, 1, narrowly elongate, with strong dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles light-moderate brown. Snout moderate-dark brown. Foot dark along anterior and posterior edges, variably pigmented along sides. Opercular lobe margins dark, especially anterior edge; central region variably pigmented. Neck pale to light brown. Pallial roof, visceral coil dark brown-black.

Ctenidial filaments, 18, tall, narrow. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum small.

Testis, 1.25 whorls, completely overlapping posterior stomach chamber. Prostate gland with large (31%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 50*e*) large; base narrowly rectangular; filament medium length, strongly tapered; lobe short, slightly narrower than base. Penial gland covering most of filament, sometimes bifurcate proximally. Dg2 small, horizontal, sometimes absent. Dg3 small, borne on low swelling near base of lobe (gland, swelling sometimes absent). Terminal gland transverse, curved, borne along distal edge, mostly on ventral surface. Ventral gland borne on swelling near base of filament; glandular dot sometimes present proximal to above. Filament pale to darkly pigmented.

Ovary, 0.75 whorl, overlapping posterior stomach chamber. Albumen gland with large (28%) pallial section. Capsule gland slightly shorter than albumen gland. Genital aperture a terminal slit without vestibule. Coiled oviduct a slight horizontal twist followed by broad horizontal loop (kinked at mid-point) slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid-pyriform, posterior end rounded, long (60%), as broad as albumen gland, with 70%–83% of length posterior to albumen gland. Bursal duct short, narrow. Seminal receptacle sac-like, stubby, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Seepage 1250 ft E, 2100 ft S, sec. 21, T10S, R25E, Chaves County, New Mexico. Holotype, LACM 2213; paratypes, UTEP 10057.

DISTRIBUTION.—Pecos River drainage, central New Mexico.

REMARKS.—Amongst species of *Pyrgulopsis*, only this snail and *P. metcalfi* and *P. davisi* have a proximally bifurcate penial gland. *Pyrgulopsis roswellensis* is distinguished from these two species by its weak development of dorsal glands and small bursa copulatrix.

MATERIAL EXAMINED.—USNM 873132, unnamed spring, Roswell Country Club, Chaves County, New Mexico (T 10S, R 24E, SE1/4 sec. 22).

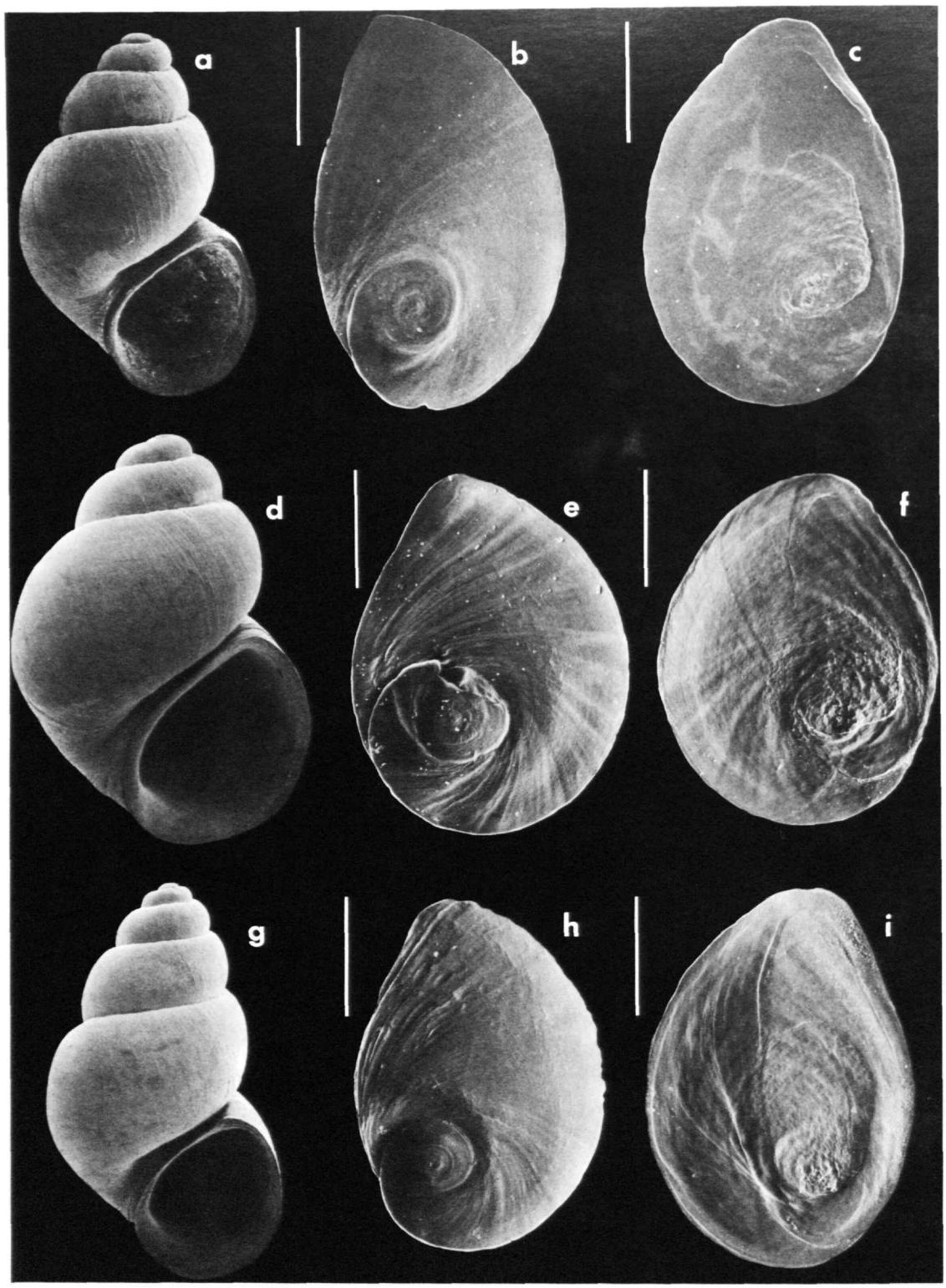


FIGURE 25.—Western *Pyrgulopsis: a–c, P. simplex*, USNM 847236 (*a*, shell, 2.3 mm; *b,c*, opercula, bars = 0.23 mm, 0.27 mm); *d–f, P. sola*, USNM 850290 (*d*, shell, 1.7 mm; *e,f*, opercula, bars = 0.22 mm, 0.25 mm); *g–i, P. stearnsiana*, USNM 873366 (*g*, shell, 2.9 mm; *h,i*, opercula, bars = 0.39 mm, 0.34 mm).

Pyrgulopsis simplex Hershler, 1988

Pyrgulopsis simplex Hershler in Hershler and Landye, 1988:32, figs. 21g–j, 26b, 27, 28.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate-conic, medium-sized, umbilicate. Penial filament medium length, lobe short. Penial ornament a variably shaped terminal gland.

DESCRIPTION.—Shell (Figure 25*a*) ovate-conic; height, 2.0–2.5 mm; whorls, 3.5–4.25. Early protoconch finely punctate, later portion near smooth except for weak adapical spiral striae. Teleoconch whorls slightly convex, shouldered; sculpture of weak growth lines. Aperture usually separated from body whorl, sometimes narrowly adnate. Inner lip complete, thickened; columellar lip reflected. Outer lip slightly thinner, weakly prosocline. Umbilicus near absent to broadly rimate. Periostracum light brown.

Operculum (Figure 25*b,c*) ovate, light amber; nucleus highly eccentric; dorsal surface smooth. Attachment scar margin slightly thickened along portion of inner edge; callus moderately developed.

Central radular tooth (Figure 39*e*) with moderately indented dorsal edge; tooth face near-square; lateral cusps, 4–5; central cusp pointed, narrow, slightly longer and broader than laterals; basal cusps, 1, medium-sized, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck moderate.

Head-foot pale except for internal black pigment patch on sides of neck and (sometimes) black internal streak along inner edge of opercular lobe. Pallial roof black; visceral coil black.

Ctenidial filaments, 18, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum very small.

Testis, 1.5 whorls, overlapping stomach to edge of style sac. Prostate gland small, ellipsoidal, with short pallial section; pallial vas deferens simple. Penis (Figure 50*f*) medium-sized; base elongate-rectangular; filament medium length, tapering; lobe short, slightly narrower than base. Terminal gland medium-sized, variably shaped, borne along distal edge of lobe (ventral surface). Filament dark.

Ovary, 0.5 whorl, overlapping posterior stomach chamber. Pallial albumen gland short (24%). Capsule gland as long as albumen gland. Genital aperture a broad subterminal pore with short vestibule. Coiled oviduct a horizontal loop. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid, short (33%), medium width, with 45%–60% of length posterior to gland. Bursal duct medium width, shallowly embedded in albumen gland, about as long as bursa copulatrix. Seminal receptacle pouch-like, slender, short, overlapping anteriormost bursa copulatrix or proximal bursal duct.

TYPE LOCALITY.—Spring near Strawberry, Gila County, Arizona (T 12N, R 7E, SW1/4 sec. 22). Holotype, USNM 859049; paratypes, USNM 859050.

DISTRIBUTION.—Springs along Fossil Creek, lower Verde River drainage.

MATERIAL EXAMINED.—USNM 847236 (topotypes).

Pyrgulopsis sola Hershler, 1988

Pyrgulopsis solus Hershler in Hershler and Landye, 1988:30, figs. 21d–f, 24, 25, 26a.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate-conic, small, weakly umbilicate. Penial filament medium length, lobe short, often bifurcate distally. Penial ornament a transverse, often fragmented terminal gland.

DESCRIPTION.—Shell (Figure 25*d*) ovate-conic; height, 1.4–2.0 mm; whorls, 3.5–4.0. Early protoconch weakly punctate, later portion near-smooth. Teleoconch whorls moderately convex, often slightly shouldered; sculpture of moderate growth lines. Aperture usually slightly separated from body whorl, sometimes narrowly adnate. Inner lip complete, thickened; columellar lip strongly reflected. Outer lip thick, slightly prosocline. Umbilicus narrowly rimate or weakly perforate. Periostracum light amber.

Operculum (Figure 25*e,f*) broadly ovate, amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin thickened all around, broadly so along inner edge; callus moderate.

Central radular tooth (Figure 39*f*) with weak-moderately indented dorsal edge; tooth face square; lateral cusps, 6; central cusp pointed, narrow, slightly longer and wider than laterals; basal cusps, 1, small to medium-sized, with strong dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck weak.

Cephalic tentacles pale or with scattered light brown patches on proximal half. Snout pale to moderate brown. Foot pale. Opercular lobe darkly streaked along inner edge. Neck with light-dark internal gray-black pigment. Pallial roof, visceral coil moderate to (more commonly) dark brown-black.

Ctenidial filaments, 15, medium height and width. Osphradium centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum medium-sized.

Testis, 1.5 whorls, overlapping stomach to edge of style sac. Prostate gland with large (32%) pallial section; pallial vas deferens simple. Penis (Figure 50*a*) very small; filament medium length, narrow; lobe short, broad, often distally bifurcate. Terminal gland large, transverse, borne along distal edge of lobe (both surfaces), usually fragmented into two units. Filament dark.

Ovary, 0.5–0.75 whorl, very slightly overlapping posterior stomach chamber. Pallial albumen gland short (23%). Capsule gland as long as albumen gland. Genital aperture a subterminal slit with very short vestibule. Coiled oviduct a weak horizontal kink followed by broad, horizontal loop slightly behind pallial wall. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix sub-globular, short (30%), narrow (37%), with 33%–50% of length posterior to gland. Bursal duct medium width, about as long as bursa copulatrix, shallowly embedded in albumen gland proximally. Seminal receptacle

pouch-like, narrow, medium length, positioned just anterior to or slightly overlapping bursa copulatrix.

TYPE LOCALITY.—Brown Spring, Yavapai County, Arizona (T 12N, R 9E, SE1/4 sec. 23). Holotype, USNM 859045; paratypes, USNM 859046.

DISTRIBUTION.—Endemic to type locality, Verde River drainage.

MATERIAL EXAMINED.—USNM 850290 (topotypes).

Pyrgulopsis stearnsiana (Pilsbry, 1899)

Paludestrina stearnsiana Pilsbry, 1899:122.—Walker, 1918:139.—Baker, 1964:176 [in part].
Fontelicella stearnsiana.—Gregg and Taylor, 1965:108.—Taylor, 1975:180; 1981:152.—Burch, 1982:26.—Turgeon et al., 1988:61.
Pyrgulopsis stearnsiana.—Hershler and Thompson, 1987:30.

DIAGNOSIS.—Shell ovate-conic, medium-sized, weakly umbilicate. Penial filament elongate, lobe very short. Penial ornament a circular terminal gland.

DESCRIPTION.—Shell (Figure 25*g*) ovate-conic; height, 2.5–3.1 mm; whorls, 4.5–5.0. Early protoconch weakly punctate, otherwise near smooth. Teleoconch whorls moderately convex, slightly shouldered; sculpture of weak growth lines. Aperture narrowly adnate to slightly separated from the body whorl. Inner lip complete, thin; columellar lip sometimes slightly reflected. Outer lip near orthocline. Umbilicus rimate to weakly perforate. Periostracum light brown.

Operculum (Figure 25*h,i*) ovate, amber, darker centrally; nucleus highly eccentric; dorsal surface weakly frilled. Attachment scar margin thickened all around, broadly so along most of inner edge (sometimes all around); callus weak.

Central radular tooth (Figure 40*a*) with moderately indented dorsal edge; lateral cusps, 5–6; central cusp pointed, tongue-like, slightly broader and longer than laterals; basal cusps, 1, large, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins slightly thickened; neck weak-absent.

Cephalic tentacles, snout pale to moderate gray-black. Foot pale to light gray. Opercular lobe dark along margins, especially sides. Neck pale-light. Pallial roof, visceral coil black.

Ctenidial filaments, 19, tall, broad. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum large.

Testis, 2 whorls, overlapping stomach to edge of style sac. Prostate gland with large (25%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 51*b*) medium-sized; filament almost as long as base, tapering; lobe very short to near-absent, narrow. Terminal gland small, circular, borne along distal edge of lobe (ventral surface). Filament dark.

Ovary, 0.5–0.75 whorl, overlapping entirety of posterior stomach chamber. Pallial albumen gland large (25%–30%). Capsule gland as long as albumen gland. Genital aperture a broad, subterminal slit with short vestibule. Coiled oviduct a posterior oblique coil overlapping broader, horizontal loop slightly behind pallial wall. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix ovoid, medium length and width, with 65%–75% of length posterior to gland. Bursa duct narrow, shallowly embedded in albumen gland distally, medium length. Seminal receptacle pouch-like, long (60%), lateral to proximal bursal duct or slightly overlapping anterior bursa copulatrix.

TYPE LOCALITY.—Near Oakland (California). Lectotype (Baker, 1964:176), ANSP 27961; paralectotypes, ANSP 396667.

DISTRIBUTION.—Central, coastal California, from Sonoma County to Monterey County (Taylor, 1981). Sierra Nevada populations mentioned by Taylor require confirmation.

MATERIAL EXAMINED.—USNM 873366, USNM 874181, Palo Seco creek, terminal pool, Alameda County, California.

Pyrgulopsis thermalis (Taylor, 1987), new combination

Fontelicella thermalis Taylor, 1987:28, fig. 13.
"Fontelicella" thermalis.—USDI, 1991b:58819.

DIAGNOSIS.—Shell globose to broadly conical, small, umbilicate. Penial filament medium length, lobe short. Penial ornament an elongate penial gland, curved Dg1, Dg2; elongate, transverse, curved terminal gland; and ventral gland. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 26*a*) globose to broadly conical; height, 1.5–2.0 mm; whorls, 3.0–3.5. Early protoconch very weakly punctate, later portion smooth. Teleoconch whorls moderately convex, strongly shouldered; sculpture of moderate growth lines. Aperture large, adnate to body whorl. Inner lip complete, highly thickened (forming broad callus). Outer lip thick, strongly prosocline. Umbilicus near absent to perforate. Periostracum tan, thin.

Operculum (Figure 26*b,c*) ovate, amber, darkened centrally; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin broadly thickened along inner edge (sometimes to nucleus); outer edge slightly thickened or near smooth; callus well developed, elongate.

Central radular tooth (Figure 40*b*) with moderately indented dorsal edge; tooth face near square; lateral cusps, 4–5; central cusp pointed, extremely elongate, considerably longer than laterals; basal cusps, 1, small, short, with strong dorsal support. Basal process broad; basal sockets deep. Lateral margins slightly thickened; neck moderate.

Cephalic tentacles, snout light-dark brown. Foot usually light, sometimes dark. Opercular lobe dark along anterior edge, sometimes moderately pigmented along entire margin. Neck light-moderate, with central unpigmented strip. Pallial roof, visceral coil usually dark (near uniformly) brown-black; mantle pigment rarely light.

Ctenidial filaments, 15, short, medium width. Osphradium centered slightly posterior to middle of ctenidium. Kidney opening unthickened. Stomach caecum small, narrow.

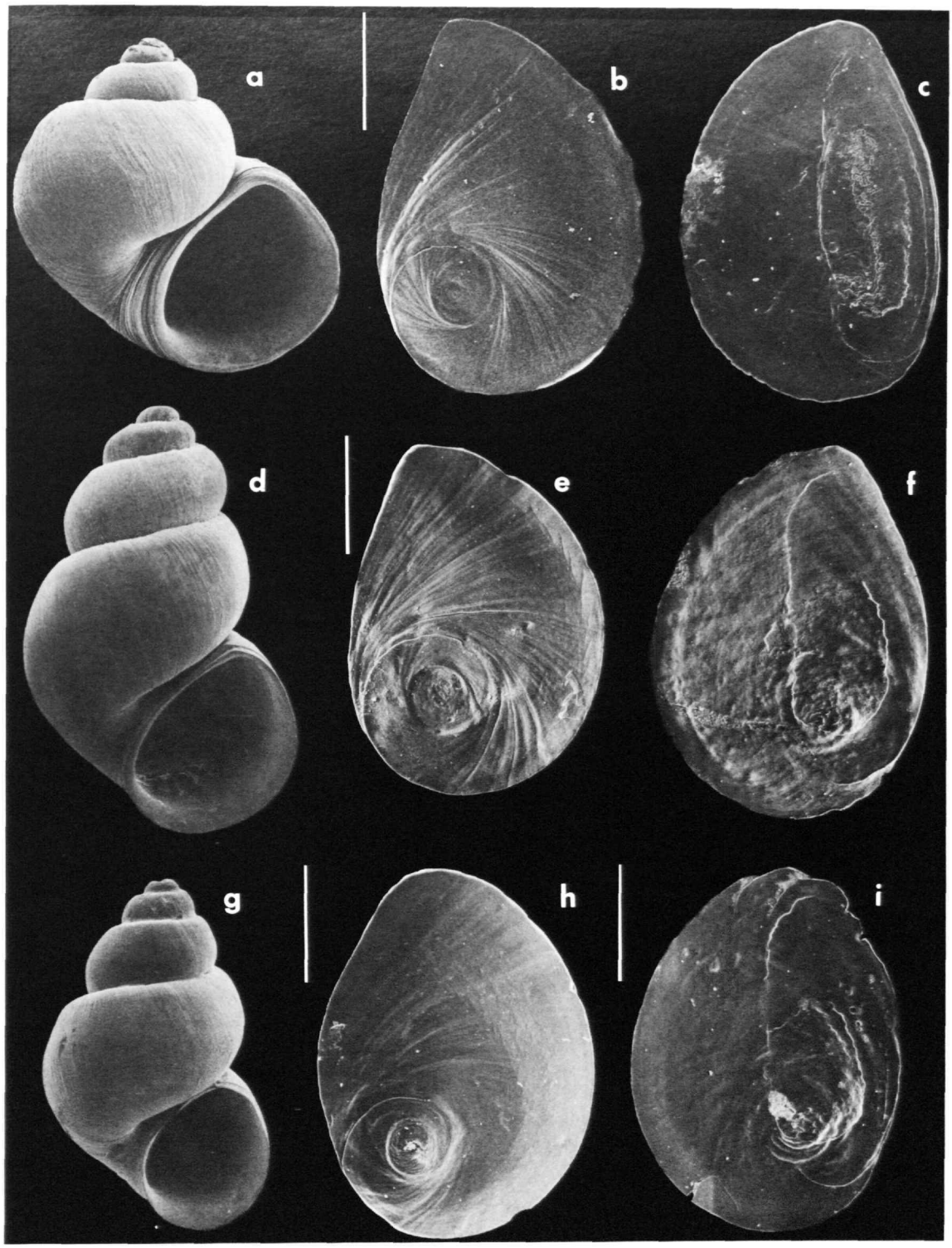


FIGURE 26.—Western *Pyrgulopsis*: *a–c*, *P. thermalis*, USNM 873250 (*a*, shell, 1.9 mm; *b,c*, opercula, bar = 0.3 mm); *d–f*, *P. thompsoni*, USNM 847238 (*d*, shell, 2.4 mm; *e, f*, opercula, bar = 0.29 mm); *g–i*, *P. trivialis*, USNM 847234 (*g*, shell, 3.0 mm; *h, i*, opercula, bars = 0.38 mm, 0.35 mm).

Testis, 0.75 whorl, slightly overlapping posterior stomach chamber. Prostate gland pea shaped, with short pallial section; pallial vas deferens simple. Penis (Figure 51*c*) medium-sized; filament medium length, stout; lobe short, narrowing distally. Penial gland covering most of filament, fused posteriorly with Dg1. Dg1 curving across penis near mid-length, fused with Dg2. Dorsal region enclosed by above unit covered with 3–4 transverse glandular strips (sometimes merging to various extents). Terminal gland elongate, transverse, curving (strongly) across distal edge of lobe, largely borne on ventral surface. Ventral gland small, borne on sub-terminal swelling. Filament weak-moderately pigmented.

Ovary, 0.75 whorls, slightly overlapping posterior stomach chamber. Pallial albumen gland very short or absent. Capsule gland as long as albumen gland. Genital aperture a terminal slit without vestibule. Coiled oviduct a near-circular loop just behind pallial wall. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix pyriform, posterior end rounded, long (64%), broad (70%), with most of length (80%) posterior to gland. Bursa duct narrow, medium length. Seminal receptacle sac-like, narrow, short, positioned alongside bursa duct and/or partly overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland. Seminal receptacle duct elongate.

TYPE LOCALITY.—Hot spring on east side of Gila River, NE1/4 SW1/4 sec. 17 T13S, R 13W, unsurveyed, Grant County, New Mexico. Holotype, LACM 2224; paratypes, UTEP 10058, ANSP 376026, FSM 160941, USNM 854086.

DISTRIBUTION.—Upper Gila River drainage, southwest New Mexico.

MATERIAL EXAMINED.—USNM 873250, Hot Spring, *ca.* 2.5 km below HWY 15 crossing of Gila River, Grant County, New Mexico (T 13S, R 13W, SW1/4 sec. 17).

Pyrgulopsis thompsoni Hershler, 1988

Paludestrina stearnsiana.—Pilsbry and Ferriss, 1910:516.

Fontelicella species.—Bequaert and Miller, 1973:214.—Williams et al., 1985:19.

Pyrgulopsis thompsoni Hershler in Hershler and Landye, 1988:41, figs. 26f, 36–38.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized, umbilicate. Penial filament medium length, lobe very short. Penial ornament a small, variably shaped terminal gland.

DESCRIPTION.—Shell (Figure 26*d*) ovate-conic; height, 1.7–3.2 mm; whorls, 3.25–5.0. Protoconch near smooth, with little or no suggestion of punctate sculpture; later portion with faint abapical spiral lines. Teleoconch whorls moderately convex, slightly shouldered; sculpture of moderate-strong growth lines. Aperture broadly adnate to slightly separated from body whorl. Inner lip complete, thin or slightly thickened; columellar lip often well reflected. Outer lip orthocline or slightly prosocline. Umbilicus narrowly to broadly rimate. Periostracum tan-light brown.

Operculum (Figure 26*e,f*) ovate, light amber (darker centrally); nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin slightly thickened all around; callus weak.

Central radular tooth (Figure 40*c*) with moderately indented dorsal edge; lateral cusps, 4–6; central cusp pointed or weakly rounded, slightly broader, considerably longer than laterals; basal cusps, 1, medium-sized, with weak to moderately strong dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles pale or with very small gray patch distal to eyespots. Snout pale to moderate brown. Foot pale to light gray. Opercular lobe often with dark internal black streaks on sides and inner margin. Neck pale or with scattered gray patches. Head-foot sometimes entirely pale. Pallial roof, visceral coil moderate-dark brown-black.

Ctenidial filaments, 15, medium length and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum prominent.

Testis, 1.75–2.0 whorls, overlapping stomach to edge of style sac. Prostate gland without a pallial section; pallial vas deferens gently undulating proximally. Penis (Figure 51*d*) medium-sized; base near-square; filament medium length, narrow; lobe very short. Terminal gland small, circular-horizontal, borne along distal edge of lobe (usually ventral surface). Filament dark.

Ovary, 0.5 whorl, slightly overlapping posterior stomach chamber. Pallial albumen gland medium long (20%–25%). Capsule gland as long as albumen gland. Genital aperture a subterminal slit with very short vestibule. Coiled oviduct a weak horizontal kink followed by broad horizontal loop positioned slightly behind pallial wall. Oviduct and bursal duct join just behind wall. Bursa copulatrix sub-globular, medium length, broad (60%–65%), with 50%–65% of length posterior to gland. Bursal duct medium width, slightly longer than bursa copulatrix. Seminal receptacle sac-like, narrow, folded, short, slightly overlapping anterior bursa copulatrix.

TYPE LOCALITY.—Peterson Ranch Springs, Santa Cruz County, Arizona (T 23S, R 19E, SE1/4 sec. 3). Holotype, USNM 859057; paratypes, USNM 859058.

DISTRIBUTION.—Upper Santa Cruz River drainage (tributary to Gila River), southeast Arizona and north-central Sonora (Mexico).

REMARKS.—Amongst the group of species having penis ornamented solely by a terminal gland, *P. thompsoni* shares with *P. stearnsiana* a highly reduced penial lobe, but differs in its simple oviduct coil and broad bursa copulatrix.

MATERIAL EXAMINED.—USNM 847238 (topotypes).

Pyrgulopsis trivialis (Taylor, 1987)

Fontelicella trivialis Taylor, 1987:30, fig. 14.

"Fontelicella" trivialis.—USDI, 1991b:58819.

Pyrgulopsis confluentis Hershler in Hershler and Landye, 1988:32, figs. 3d–g, 26c, 29, 30.

DIAGNOSIS.—Shell ovate- to narrowly-conic, small to large, weakly umbilicate. Penial filament short, lobe medium length. Penial ornament a short penial gland, short Dg2, short Dg3 borne on low swelling, transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 26*g*) ovate- to narrowly-conic; height, 1.5–4.5 mm; whorls, 3.5–5.0. Early protoconch very weakly punctate, later portion smooth or with faint spiral lines. Teleoconch whorls slight-moderately convex, rarely shouldered; sculpture of weak growth lines. Aperture usually adnate to (rarely slightly separated from) body whorl. Inner lip complete, thin; columellar lip often reflected. Outer lip slightly prosocline. Umbilicus narrowly rimate (near absent) to weakly perforate. Periostracum tan.

Operculum (Figure 26*h,i*) ovate, amber; nucleus highly eccentric; dorsal surface smooth. Attachment scar margin moderately thickened all around; callus moderate.

Central radular tooth (Figure 40*d*) with moderate-highly indented dorsal edge; lateral cusps, 5–6; central cusp pointed or rounded, considerably broader and longer than laterals; basal cusps, 1, medium-sized, with strong dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck pronounced.

Cephalic tentacles, snout, foot pale or near pale to dark brown. Opercular lobe pale or moderate-dark brown-black along sides; inner edge sometimes with black internal streak. Neck pale to moderate. Pallial roof, visceral coil, near-uniform black.

Ctenidial filaments, 21, medium height, narrow. Osphradium centered well posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum large.

Testis, 1.5 whorls, overlapping stomach almost to edge of style sac. Prostate gland with large (25%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 51*e*) large; filament short, broad; lobe slightly longer than filament, tapered. Penial gland short, restricted to base of filament. Dg2 short; Dg3 short, usually borne on weak swelling. Terminal gland small, largely transverse, near straight, borne along distal edge (largely ventral surface) of lobe. Ventral gland borne on sub-terminal swelling; occasionally accompanied by smaller, stalked gland proximal to above. Filament pale.

Ovary, 0.75–1.0 whorl, overlapping posterior stomach chamber. Pallial albumen gland large (28%–33%). Albumen gland longer than capsule gland. Genital aperture a subterminal slit; vestibule absent or very short. Coiled oviduct a slight horizontal kink followed by broad horizontal loop slightly behind pallial wall. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix ovoid, short to medium length (38%–48%), medium width, with about 55% of length posterior to gland. Bursal duct medium width, shallowly embedded in albumen gland, medium length. Seminal receptacle pouch-like, folded, long (60%), positioned lateral to or overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—*Pyrgulopsis trivialis:* Spring-fed pond, 1,000 ft N of SW corner sec. 5, T5N, R29E, Apache County, Arizona. Holotype, LACM 2225; paratypes, UTEP 10059, ANSP 376022, FSM 160941, USNM 854080. *Pyrgulopsis confluentis:* Spring on north side of Blanket Creek at Three Forks, Apache County, Arizona (T 5N, R 29E, SE1/4 sec. 6). Holotype, USNM 859053; paratypes, USNM 859054.

DISTRIBUTION.—Upper Black River drainage (tributary to Gila River), southeast Arizona.

MATERIAL EXAMINED.—USNM 847234 (topotypes, *confluentis*).

Pyrgulopsis wongi Hershler, 1989

Pyrgulopsis wongi Hershler, 1989:196, figs. 41–47.—Hershler and Pratt, 1990:286, fig. 7.

DIAGNOSIS.—Shell globose to low-conical, small to medium-sized, umbilicate. Penial filament and lobe medium length. Penial ornament an elongate penial gland, curved Dg1, Dg2, Dg3 borne on moderate swelling; elongate, transverse, curved terminal gland; and two ventral glands. Dorsal glands sometimes fused.

DESCRIPTION.—Shell (Figure 27*a*) globose to low-conical; height, 1.2–3.0 mm; whorls, 3.25–4.5. Protoconch very weakly punctate. Teleoconch whorls moderately convex, shouldered; sculpture of weak growth lines. Aperture narrowly adnate or slightly separated from body whorl. Inner lip complete, usually thin. Outer lip orthocline or slightly prosocline. Umbilicus narrowly rimate to perforate. Periostracum tan.

Operculum (Figure 27*b,c*) broadly ovate, amber, with dark central region; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin moderately thickened all around; callus moderate.

Central radular tooth (Figure 40*e*) with moderately indented dorsal edge; lateral cusps, 4–7; central cusp pointed, usually considerably broader and longer than laterals; basal cusps, 1, medium-sized, with moderate dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck weak-absent.

Cephalic tentacles, foot pale to moderate gray-black. Snout, neck pale to dark gray-black. Opercular lobe pale to moderate gray-black along sides and inner edge, occasionally black all around (with central region light). Pallial roof, visceral coil light-dark gray-black, sometimes uniformly dark.

Ctenidial filaments, 16, medium height and width. Osphradium centered well posterior to middle of ctenidial axis. Kidney opening white. Stomach caecum broad, crescent-shaped.

Testis, 1 whorl, slightly overlapping posterior stomach chamber. Prostate gland with short pallial section; pallial vas deferens with proximal kink. Penis (Figure 51*f*) very large, broad; filament medium length, tapered; lobe medium length, with little or no taper distally. Penial gland covering most of

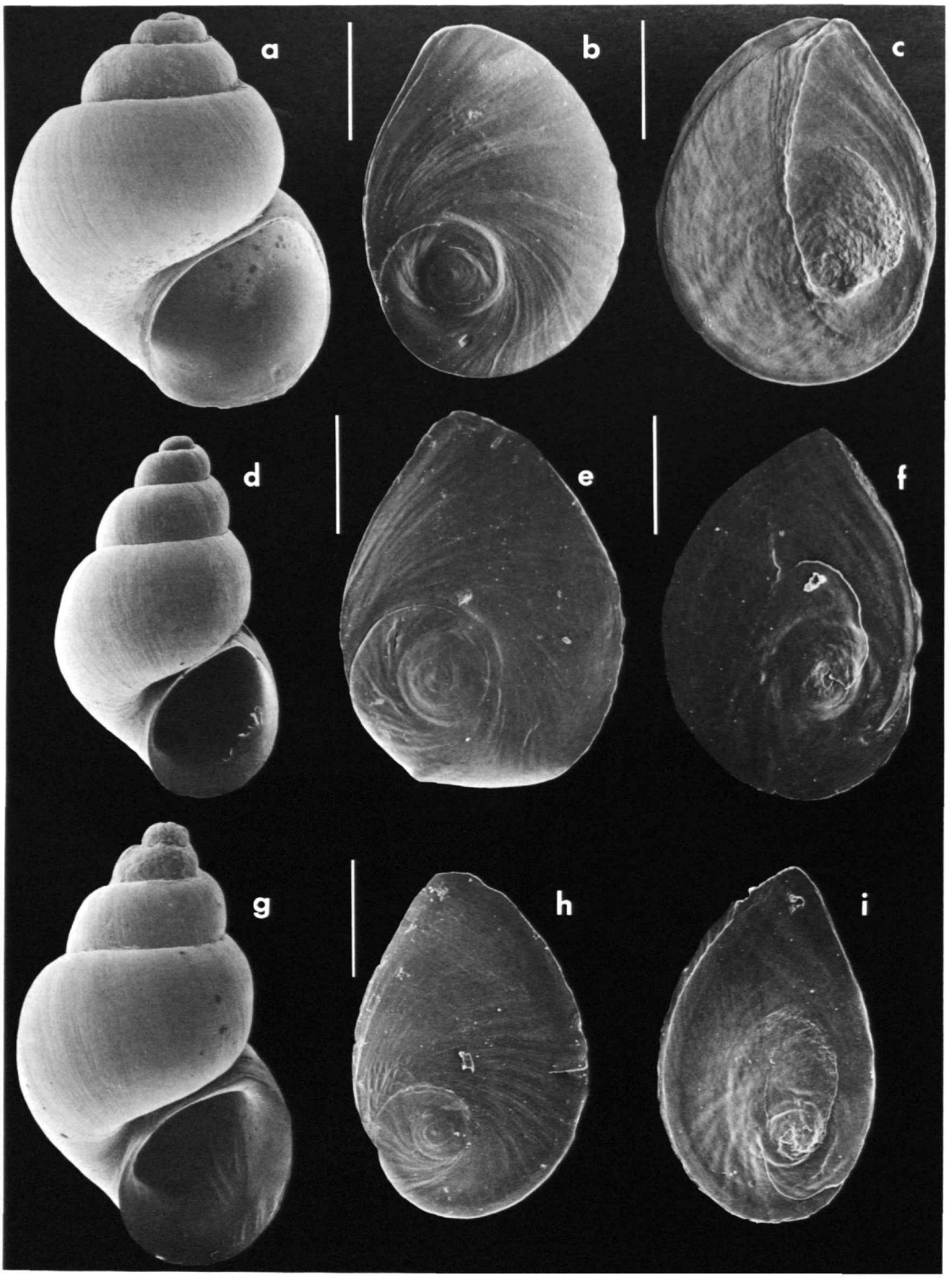


FIGURE 27.—*Pyrgulopsis: a–c, P. wongi* (*a*, holotype, USNM 860403, 2.0 mm; *b, c*, opercula, USNM 857941, bars = 0.33 mm, 0.3 mm); *d–f, P. agarhectus* (*d*, shell, FSM uncat., 2.1 mm; *e, f*, opercula, FSM 189468, bars = 0.25 mm, 0.3 mm); *g–i, P. arga* (*g*, shell, FSM 22287, 3.2 mm; *h, i*, opercula, FSM uncat., bar = 0.43 mm).

filament, extending slightly onto right edge of penis. Dg1 elongate, curving from right edge near base of lobe transversely across penis, generally raised, usually fused with Dg2; Dg2, when separate, horizontal, short to medium length; Dg3 narrowly elongate, borne on moderate swelling. Dorsal penis also with 2–5 small glands in central region (variable in size and placement, sometimes reduced in number through apparent fusion) between Dg1-Dg2 and base of lobe. Terminal gland elongate, transverse, curved, covering distal edge of lobe (mostly ventral surface). Ventral gland stalked, sub-terminal, positioned just proximal to lobe; accompained by smaller, stalked gland (sometimes greatly reduced) just proximal to above (sometimes with third smaller gland on either side of above). Filament dark.

Ovary, 0.75–1.0 whorl, slightly overlapping posterior stomach chamber. Albumen gland without a pallial section. Capsule gland as long as albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a broad, open, horizontal loop a moderate distance behind pallial wall. Oviduct and bursal duct join well behind pallial wall. Bursa copulatrix pyriform, posterior end pointed, as long or longer than and almost as wide as (92%) albumen gland, with about 67% of length posterior to gland. Bursal duct narrow proximally, broadening at junction with oviduct, short. Seminal receptacle pouch-like, short, overlapping anterior bursa copulatrix, extending to posterior edge of albumen gland.

TYPE LOCALITY.—Unnamed western spring tributary to Pine Creek, Birchim Canyon, Owens Valley, Inyo County, California (T 6S, R 31E, SE1/4 sec. 9).

DISTRIBUTION.—Pluvial Owens River drainage, and several endorheic basins to the east (Deep Springs, Fish Lake, Huntoon Valleys), California-Nevada.

MATERIAL EXAMINED.—USNM 857941 (paratypes).

Eastern American Species

Pyrgulopsis agarhecta (Thompson, 1970)

Marstonia agarhecta Thompson, 1970:243, figs. 1a–f, 11.—Thompson, 1977:130, figs. 3b, 23, 24, 25h.—Burch, 1982:27, figs. 214, 232.—Turgeon et al., 1988:61.

Pyrgulopsis agarhecta.—Hershler and Thompson, 1987:29.—USDI, 1991b:58821.

DIAGNOSIS.—Shell conical, medium-sized, inner lip usually incomplete, umbilicate. Penial filament medium length, lobe short. Penial ornament a variably shaped terminal gland.

DESCRIPTION.—Shell (Figure 27*d*) conical; height, 2.3–2.7 mm; whorls, 4.5. Early protoconch strongly punctate adapically. Teleoconch whorls strongly convex, weakly shouldered; sculpture of faint growth lines and very weak spiral striae. Aperture ovate, medium-sized, slightly angled above, adnate to body whorl. Parietal lip usually incomplete or a weak glaze; columellar lip thin, slightly reflected. Outer lip prosocline. Umbilicus open. Periostracum light brown.

Operculum (Figure 27*e,f*) broadly ovate, very thin, light amber (almost pale), slightly indented along outer edge; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin slightly thickened along inner edge; callus very weak.

Central radular tooth (Figure 41*a*) with slightly indented dorsal edge; lateral cusps, 3–5; central cusp weakly rounded, broader and longer than laterals; basal cusps, 1 (second, weak outer cusp sometimes present), elongate, with weak dorsal support. Basal process rounded, weakly excavated. Lateral margins slightly thickened; neck near absent.

Head-foot unpigmented. Pallial roof with two black streaks along edges of ctenidium. Streaks darkened and usually connected anteriorly; streak along osphradial margin short. Dorsal edge of glandular oviduct lined with small black granules. Testis black.

Ctenidial filaments, 22, tall, narrow. Osphradium elongate (33%), centered posterior to middle of ctenidial axis. Kidney opening slightly thickened. Stomach caecum broadly triangular, large.

Testis, 1.5 whorls, overlapping posterior stomach. Coils of seminal vesicle extremely thickened, conspicuously overlapping stomach. Prostate gland ovoid, with short pallial section; pallial vas deferens simple. Penis (Figure 52*a*) medium-sized, extending only slightly beyond mantle edge; base short; filament medium length, gently tapering; lobe short, broad. Terminal gland large, variably shaped, borne on ventral surface of lobe distally. Penis unpigmented.

Ovary, 1 whorl, slightly overlapping posterior stomach. Pallial albumen gland large (30%). Capsule gland slightly longer than albumen gland. Genital aperture sub-terminal, short, with vestibule. Coiled oviduct of two broadly overlapping horizontal loops just behind pallial wall. Oviduct and bursal duct join anterior to loop in posterior pallial cavity. Bursa copulatrix pouch-like, short (28%), narrow (25%), extending almost to posterior edge of albumen gland; anterior bursa partly embedded in gland. Bursal duct scarcely narrower than bursa copulatrix, embedded in albumen gland, more than twice as long as bursa copulatrix. Seminal receptacle stubby, short, positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—Bluff Creek, 10.4 miles south-southeast of Hawkinsville, Pulaski County, Georgia. Holotype, FSM 20528; paratypes, FSM 20569.

DISTRIBUTION.—Known only from the type locality, Ocmulgee River drainage (Atlantic Coastal; Thompson, 1977, fig. 20).

REMARKS.—This snail differs from similar *P. castor* and *P. halcyon* by its more elongate shell and absence of a ventral penial gland.

MATERIAL EXAMINED.—FSM 189468, FSM 193381 (topotypes).

Pyrgulopsis arga (Thompson, 1977), new combination

Marstonia arga Thompson, 1977:119, figs. 1a,b, 4f, 6–8, 25b.—Burch, 1982: 27, figs. 215, 233.—Turgeon et al., 1988:61.

DIAGNOSIS.—Shell ovate- to narrowly-conic, medium to large-sized, weakly umbilicate. Penial filament medium length; lobe short, oblique. Penial ornament a transverse terminal gland.

DESCRIPTION.—Shell (Figure 27*g*) ovate to narrowly conic; height, 3.2–3.9 mm; whorls, 5; generally thickened and often whitened. Early protoconch strongly punctate adapically, otherwise near smooth. Teleoconch whorls weakly convex, slightly shouldered; sculpture of weak growth lines and occasional faint spiral striae. Aperture broadly ovate, moderately large, narrowly adnate to or slightly separated from body whorl. Inner lip complete, thickened; columellar lip sometimes slightly reflected. Outer lip usually thickened, often with broad internal ridge, sinuate (advanced abapically). Umbilicus weakly rimate or absent. Periostracum light brown.

Operculum (Figure 27*h,i*) ovate, light amber, slightly indented along outer edge; nucleus highly eccentric. Dorsal surface smooth. Attachment scar margin moderately thickened between nucleus and inner edge; callus moderate.

Central radular tooth (Figure 41*b*) with moderately indented dorsal edge; lateral cusps, 4; central cusp pointed, considerably longer and slightly broader than laterals; basal cusps, 1 (second, rudimentary outer cusp sometimes present), short, broad, with weak dorsal support. Basal process tongue-shaped; basal sockets deep. Lateral margins thickened; neck weak-absent.

Snout, neck unpigmented or light brown. Cephalic tentacles, foot, opercular lobe unpigmented. Pallial roof with prominent narrow brown streaks along margins of ctenidium (often connected anteriorly) and sometimes along dorsal edge of glandular oviduct (occasionally as broad bands covering entire dorsal surface of structure). Dorsal testis often dark brown, visceral coil otherwise unpigmented.

Ctenidial filaments, 28, tall, narrow. Osphradium centered posterior to middle of ctenidial axis. Kidney with slight bulge into pallial cavity; opening white. Caecum of stomach large, broadly triangular.

Testis, 1.25–1.5 whorls, overlapping stomach to posterior edge of style sac. Prostate gland thickened, with large (40%) pallial section; vas deferens opening from near anterior end of prostate gland, pallial section with several tight loops. Penis (Figure 52*b*) large, extending well beyond mantle edge; filament medium length, thickened, with pointed tip; lobe short, broad, oblique. Terminal gland transverse, borne along distal edge of lobe. Filament sometimes darkly pigmented internally.

Ovary, 1 whorl, overlapping posterior stomach. Pallial albumen gland large (33%). Capsule gland as long as albumen gland. Genital aperture a short, terminal slit with vestibule. Coiled oviduct a proximal twist followed by narrow vertical loop just behind pallial wall. Oviduct and bursal duct join anterior to loop in posterior pallial cavity. Bursa copulatrix ovoid, long (60%), about half as broad as albumen gland, with about 50% of length posterior to gland. Bursal duct broad posteriorly, narrowing anteriorly, largely embedded in albumen gland, slightly shorter than bursa copulatrix. Seminal receptacle pouch-like, short, positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—Guntersville Reservoir, at mouth of Mint Creek, 9.8 mi. (15.8 km) southwest of Scottsboro, Jackson County, Alabama. Holotype, FSM 22286; paratypes, FSM 22287.

DISTRIBUTION.—Tennessee River drainage, northeast Alabama and southeast Tennessee (Thompson, 1977, fig. 8).

REMARKS.—This snail is distinguished from other eastern forms by its highly reduced penial lobe and medium length bursal duct.

MATERIAL EXAMINED.—FSM uncat. (paratypes).

Pyrgulopsis castor (Thompson, 1977)

Marstonia castor Thompson, 1977:130, figs. 3c, 4h, 21, 22, 25e.—Burch, 1982:27, figs. 216, 234.—Turgeon et al., 1988:61.

Pyrgulopsis castor.—Hershler and Thompson, 1987:29.—USDI, 1991b:58821.

DIAGNOSIS.—Shell ovate-conic, small to medium-sized, umbilicate. Penial filament medium length, lobe short. Penial ornament a horizontal terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 28*a*) ovate-conic; height, 1.9–2.7 mm; whorls, 4.0–4.5. Early protoconch (Figure 1*e*) strongly punctate adapically, later portion smooth. Teleoconch whorls moderately convex, shouldered; sculpture of faint growth lines. Aperture ovate, slightly angled above, narrowly adnate or slightly separated from body whorl. Parietal lip usually incomplete; in a few large specimens lip complete, moderately thick; columellar lip slightly reflected. Outer lip prosocline, often with thickened internal callus. Umbilicus narrowly perforate. Periostracum light brown.

Operculum (Figure 28*b,c*) ovate, very thin, light amber, slightly indented along outer edge; nucleus slightly eccentric. Dorsal surface weakly frilled. Attachment scar margin smooth except for slight thickening along inner edge; callus near-absent.

Central radular tooth (Figure 41*c*) with moderately indented dorsal edge; lateral cusps, 4; central cusp pointed, slightly longer and broader than laterals; basal cusps, 1 (sometimes accompanied by small or rudimentary outer cusp), long, with weak dorsal support. Basal process of medium width and excavated. Lateral margins thickened; neck weak-absent.

Cephalic tentacles, foot, neck unpigmented. Snout pale or light brown. Opercular lobe with dark internal pigment along anterior edge. Pallial roof with prominent dark brown pigment streaks along margins of ctenidium; dorsal edge of glandular gonoducts with weaker streaks. Gonads light to dark brown.

Ctenidial filaments, 20, tall, medium width. Osphradium large (45%), extending almost to posterior end of ctenidium. Kidney with prominent (50%) bulge into pallial cavity; opening white. Caecum of stomach prominent, triangular.

Testis, 1 whorl, overlapping posterior stomach. Prostate

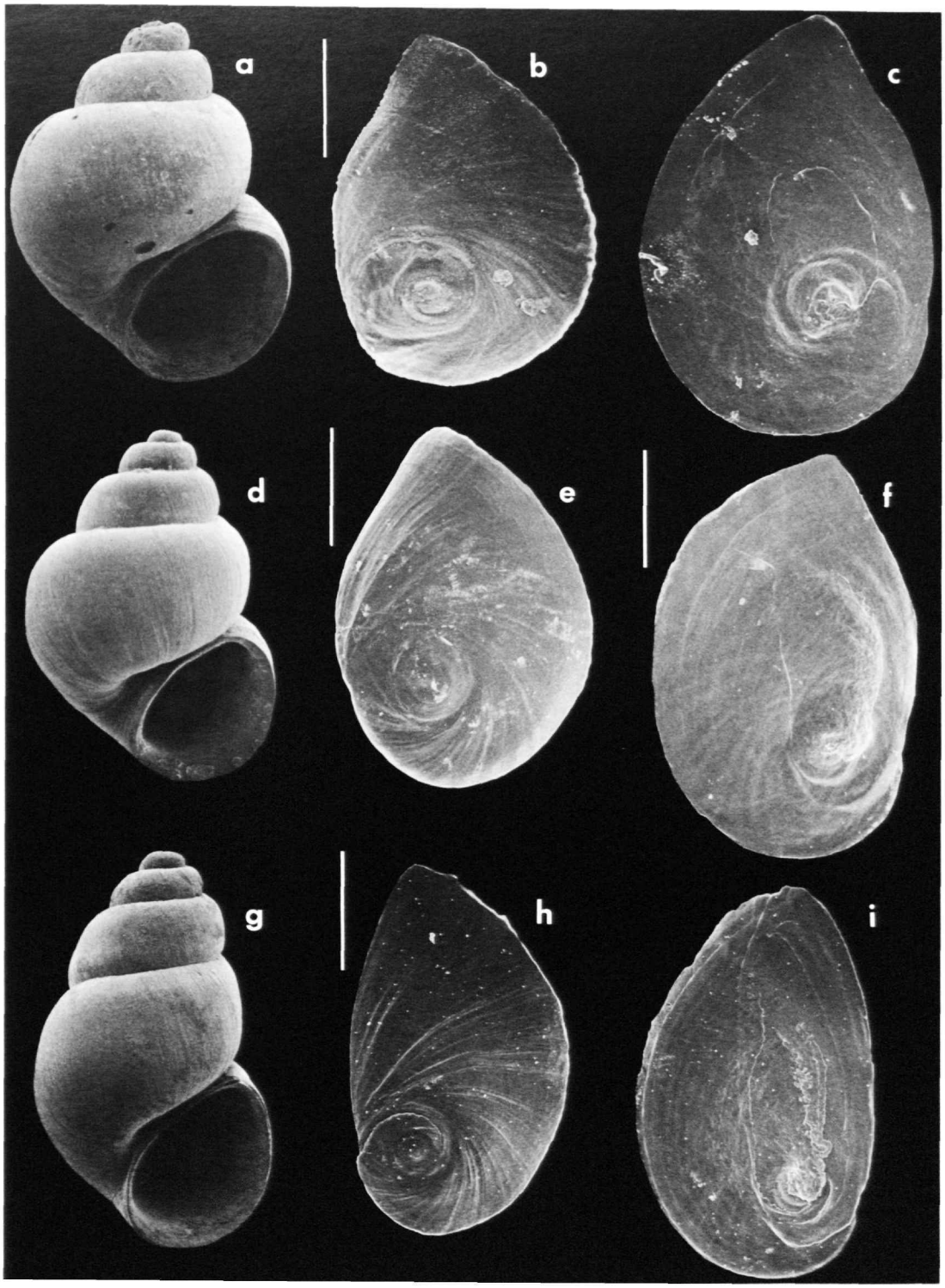


FIGURE 28.—Eastern *Pyrgulopsis*: *a–c*, *P. castor* (*a*, shell, Uf 222178, 2.0 mm; *b*, *c*, opercula, FSM 189470, bar = 0.25 mm); *d–f*, *P. halcyon* (*d*, shell, FSM 22311, 2.2 mm; *e*, *f*, opercula, FSM 189465; bars = 0.25 mm, 0.3 mm); *g–i*, *P. letsoni* (*g*, shell, FSM 189460, 2.8 mm; *h*, *i*, opercula, FSM 91726, bar = 0.43 mm).

gland stunted, ellipsoidal, slightly thickened, with large (33%) pallial section; pallial vas deferens gently undulating. Penis (Figure 52*c*) small, slender, scarcely extending beyond mantle edge; filament medium length, gently tapering; lobe short, finger-like. Terminal gland horizontal, borne along ventral surface of lobe. Ventral gland small, positioned near mid-line, usually borne on short stalk. Penis unpigmented.

Ovary, 1.25 whorls, overlapping posterior stomach. Pallial albumen gland large (30%). Capsule gland as long as albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct a tall, narrow, vertical loop just behind pallial wall. Oviduct and bursal duct join well anterior to pallial wall. Bursa copulatrix ovoid, short (25%), narrow (30%), positioned on posterior albumen gland but not extending to tip of gland. Bursal duct medium width, deeply embedded in albumen gland along most of length, about twice as long as bursa copulatrix. Seminal receptacle pouch-like, short, positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—Cedar Creek, 3.4 mi (5.5 km) south-southwest of Coney, Crisp County, Georgia. Holotype, FSM 22176; paratypes, FSM 22176.

DISTRIBUTION.—Known only from the type locality, Flint River drainage (Gulf Coastal; Thompson, 1977, fig. 20).

REMARKS.—This snail differs from closely similar *P. halcyon* by its elongate osphradium, large caecal chamber of stomach, and horizontal penial lobe.

MATERIAL EXAMINED.—FSM 189470 (topotypes).

Pyrgulopsis halcyon (Thompson, 1977)

Marstonia halcyon Thompson, 1977:128, figs. 3d, 4i, 17–19.—Burch, 1982: 27, figs. 217, 249.—Turgeon et al., 1988:61.

Pyrgulopsis halcyon.—Hershler and Thompson, 1987:29.

DIAGNOSIS.—Shell broadly ovate, medium-sized, umbilicate. Penial filament medium length; lobe medium length, oblique. Penial ornament a transverse terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 28*d*) broadly ovate; height, 2.0–2.5 mm; whorls, 4. Early protoconch (Figure 1*b*) strongly punctate adapically. Teleoconch whorls highly convex, strongly shouldered; sculpture of moderate growth lines and occasional weak spiral striae. Aperture ovate, angled above, narrowly adnate or slightly separated from body whorl. Parietal lip usually incomplete or a thin glaze; lip complete in largest specimens, slightly thickened; columellar lip slightly reflected. Outer lip prosocline. Umbilicus broadly perforate. Periostracum light gray.

Operculum (Figure 28*e,f*) ovate, light amber, slightly indented along outer edge; nucleus slightly eccentric; dorsal surface smooth. Attachment scar margin smooth except for faint trace along outer edge; outlines of early whorls bulging slightly above ventral surface; callus very small, weak.

Central radular tooth (Figure 41*d*) with weakly indented dorsal edge; lateral cusps, 3–4; central cusp pointed, broader and longer than laterals; basal cusps, 1 (sometimes accompanied by weak outer cusp), medium-sized, with slight dorsal support. Lateral margins scarcely thickened; neck weak-moderate.

Head-foot pale except for occasional dark pigment along margins of opercular lobe. Pallial roof with prominent brown-black streaks along margins of ctenidium; weaker streak lining dorsal edge of glandular gonoducts. Visceral coil with dark band along gonads.

Ctenidial filaments, 22, tall, medium width. Osphradium elongate (40%), vermiform, centered posterior to middle of ctenidial axis. Kidney with prominent bulge (50%) into pallial cavity; opening slightly thickened. Stomach caecum small.

Testis, 1 whorl, slightly overlapping posterior stomach. Prostate gland elongate, thin-walled, with large pallial section (30%); pallial vas deferens without proximal kink. Penis (Figure 52*d*) medium-sized; filament medium length, tapering distally; lobe slightly shorter than filament, oblique, club-shaped. Terminal gland usually elongate, transverse, borne on distal lobe (ventral surface). Ventral gland small, with short stalk, positioned near mid-length. Penis unpigmented.

Ovary, 0.5 whorl, slightly overlapping posterior stomach. Pallial albumen gland large (33%). Capsule gland as long as albumen gland. Genital aperture near terminal, short, slit-like, without vestibule. Coiled oviduct a narrow, vertical loop just behind pallial wall. Oviduct and bursal duct join well anterior to oviduct coil and pallial wall. Bursa copulatrix ovoid, short (20%), narrow (20%–25%), extending to posterior edge of albumen gland, sometimes partly or entirely embedded in gland. Bursal duct broad, largely embedded in albumen gland, more than five times as long as bursa copulatrix. Seminal receptacle sac-like, large (83%), positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—Buckhead Creek, 0.6 mi. (0.97 km) west of Millen, Jenkins County, Georgia. Holotype, FSM 22312; paratypes, FSM 22313.

DISTRIBUTION.—Lower portion of Ogeechee River drainage, Georgia (Atlantic coastal; Thompson, 1977, fig. 20).

MATERIAL EXAMINED.—FSM 144698, Ogeechee River, 2.7 km southwest of Guyton, Effingham County, Georgia; FSM 189465, FSM 189466 (topotypes).

Pyrgulopsis letsoni (Walker, 1901)

Amnicola letsoni Walker, 1901:113.—Letson, 1901:241, fig. 165.—Sterki, 1914:271.

Pyrgulopsis letsoni.—Walker, 1918:139.—Baker, 1928:140, pl. VII: figs. 28, 29.—Berry, 1943:41, fig. 6; pl. I: fig. 13; pl. II: fig. 7; pl. IV: fig. 1; pl. VI: fig. 4; pl. VII: fig. 2.—Robertson and Blakeslee, 1948:85, pl. X: fig. 14.—Taylor, 1965:599.—LaRocque, 1968:399, pl. 10: fig. 13; pl. 11: fig. 7.—Burch, 1982:27, fig. 261.—Hershler and Thompson, 1987:29.—Turgeon et al., 1988:62.

DIAGNOSIS.—Shell ovate to narrowly conic, medium to large-sized, umbilicate. Penial filament medium length; lobe

medium length, oblique. Penial ornament a transverse terminal gland.

DESCRIPTION.—Shell (Figure 28*g*) ovate to narrowly conic; height, 2.5–4.0 mm; whorls, 4.5–5.5. Early protoconch strongly punctate, sculpture weaker on remaining portion. Teleoconch whorls slightly to moderately convex, sometime weakly shouldered; sculpture of weak growth lines. Aperture small, ovate, adnate or slightly separated from body whorl. Inner lip complete (rarely a thin glaze across parietal wall), thin to moderately thick; columellar lip sometimes slightly reflected. Outer lip thin to moderately thick, orthocline. Umbilicus rimate-perforate. Periostracum light brown.

Operculum (Figure 28*h,i*) narrowly ovate, amber; nucleus highly eccentric; dorsal surface frilled. Attachment scar margin thickened all around, often broadly so (especially between along inner edge to nucleus); callus moderate, elongate.

Central radular tooth (Figure 41*e*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp pointed, considerably broader and longer than laterals; basal cusps, 1 (often accompanied by weak outer cusp), short, with moderate dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck very weak.

Snout pale to dark brown. Foot, neck pale. Tentacles pale or gray, with small dark internal pigment patch distal to eyespots. Opercular lobe with dark internal pigment patch along anterior edge. Pallial roof, visceral coil light to dark brown.

Ctenidial filaments, 22, medium height and width. Osphradium centered slightly posterior to middle of ctenidial axis. Kidney with large (50%) pallial bulge; opening weakly differentiated. Stomach with prominent triangular caecum

Testis, 2 whorls, overlapping stomach to edge of style sac. Prostate gland with large (30%) pallial section; pallial vas deferens with proximal loop. Penis (Figure 52*e*) large; base expanded proximally; filament medium length, gently tapered; lobe about as long as filament, broad, strongly oblique. Terminal gland small, narrow, transverse, borne along distal edge of lobe. Filament darkly pigmented internally.

Ovary, 1 whorl, slightly overlapping posterior stomach. Pallial albumen gland with large (29%) pallial section. Capsule gland as long as albumen gland. Genital aperture a sub-terminal slit; vestibule weakly developed. Coiled oviduct a tall, narrow, vertical loop (strongly kinked near mid-length) slightly behind pallial wall. Oviduct and bursal duct join well anterior to oviduct coil and pallial wall. Bursa copulatrix pouch-like, short (25%), narrow (20%), extending almost to posterior edge of albumen gland. Bursal duct broad, deeply embedded in albumen gland, more than three times length of bursa copulatrix. Seminal receptacle pouch-like, fat, long (60%), positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—Post-glacial deposit, Goat Island, Niagara River, New York. Holotype, UMMZ 117363.

DISTRIBUTION.—Michigan, Ohio, Ontario (Canada), Great Lakes drainage.

REMARKS.—This snail is distinguished from similar *P. scalariformis* by its smooth teleoconch, large caecal chamber of stomach, longer penial lobe; narrowly vertical oviduct coil; and narrow, sac-like bursa copulatrix positioned entirely lateral to albumen gland.

MATERIAL EXAMINED.—FSM 91727, creek west of Crescent Lake, Oakland County, Michigan.

Pyrgulopsis lustrica (Pilsbry, 1890)

Amnicola lustrica Pilsbry, 1890:53.—Baker, 1964:174.

Amnicola lacustris Pilsbry, 1891a:iii [of Index; nomen nudum, probably misspelling of above].

Amnicola (Marstonia) lustrica.—Baker, 1926:195.—Berry, 1943:29, fig. 3; pl. 1: figs. 4–6; pl. 3: fig. 3; pl. 5: fig. 6.—Robertson and Blakeslee, 1948:84, pl. X: fig. 11.

Lyogyrus (Marstonia) lustrica.—Thiele, 1928:378.

Marstonia lustrica.—Thompson, 1977:124, figs. 2, 4d, 5, 16.—Turgeon et al., 1988:61.

Pyrgulopsis lustrica.—Hershler and Thompson, 1987:29, fig. 5.

Amnicola lustrica gelida Baker, 1921:22.

Marstonia gelida.—Clarke, 1973:247, pl. 21: figs. 7, 8.—Nielsen et al., 1987:1480.

Amnicola lustrica decepta Baker, 1928:108, fig. 45 [in part].

Marstonia decepta.—Clarke, 1973:244, pl. 21: fig. 6.

Amnicola lustrica perlustrica Baker, 1928:109, pl. VI: figs. 15, 45 [in part].

Amnicola oneida Pilsbry, 1917:46.—Baker, 1964:175.—Richardson et al., 1991:64.

DIAGNOSIS.—Shell ovate- to narrowly-conic, medium to large-sized, umbilicate. Penial filament short, stubby; lobe short, oblique. Penial ornament an elongate, usually transverse terminal gland.

DESCRIPTION.—Shell (Figure 29*a*) ovate- to narrowly-conic; height, 3–5 mm; whorls, 4.5–6.0. Early protoconch strongly punctate. Teleoconch whorls moderate to highly convex; sculpture of weak growth lines. Aperture ovate, small, adnate or slightly separated from body whorl. Inner lip complete, sometimes slightly thickened; columellar lip sometimes slightly reflected. Outer lip usually thin, orthocline to slightly prosocline. Umbilicus open. Periostracum olive-gray.

Operculum (Figure 29*b,c*) ovate, amber, slightly indented along outer edge; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin slightly thickened along outer edge and between nucleus and inner edge; callus weak.

Central radular tooth (Figure 41*f*) with weakly indented dorsal edge; lateral cusps, 3–5; central cusp rounded, slightly broader and considerably longer than laterals; basal cusps, 1 (sometimes with weak suggestion of outer cusp), medium-sized, curved, with moderate dorsal support. Basal process broad; basal sockets deep. Lateral margins thickened; neck weak-absent.

Head-foot entirely pale or with light brown tentacles, light-dark snout, light-moderate brown foot (especially anterior and posterior edges). Pallial roof uniform brown-black or pale except for strong black bands along edges of ctenidium and (sometimes) along dorsal edge of glandular gonoduct (Figure

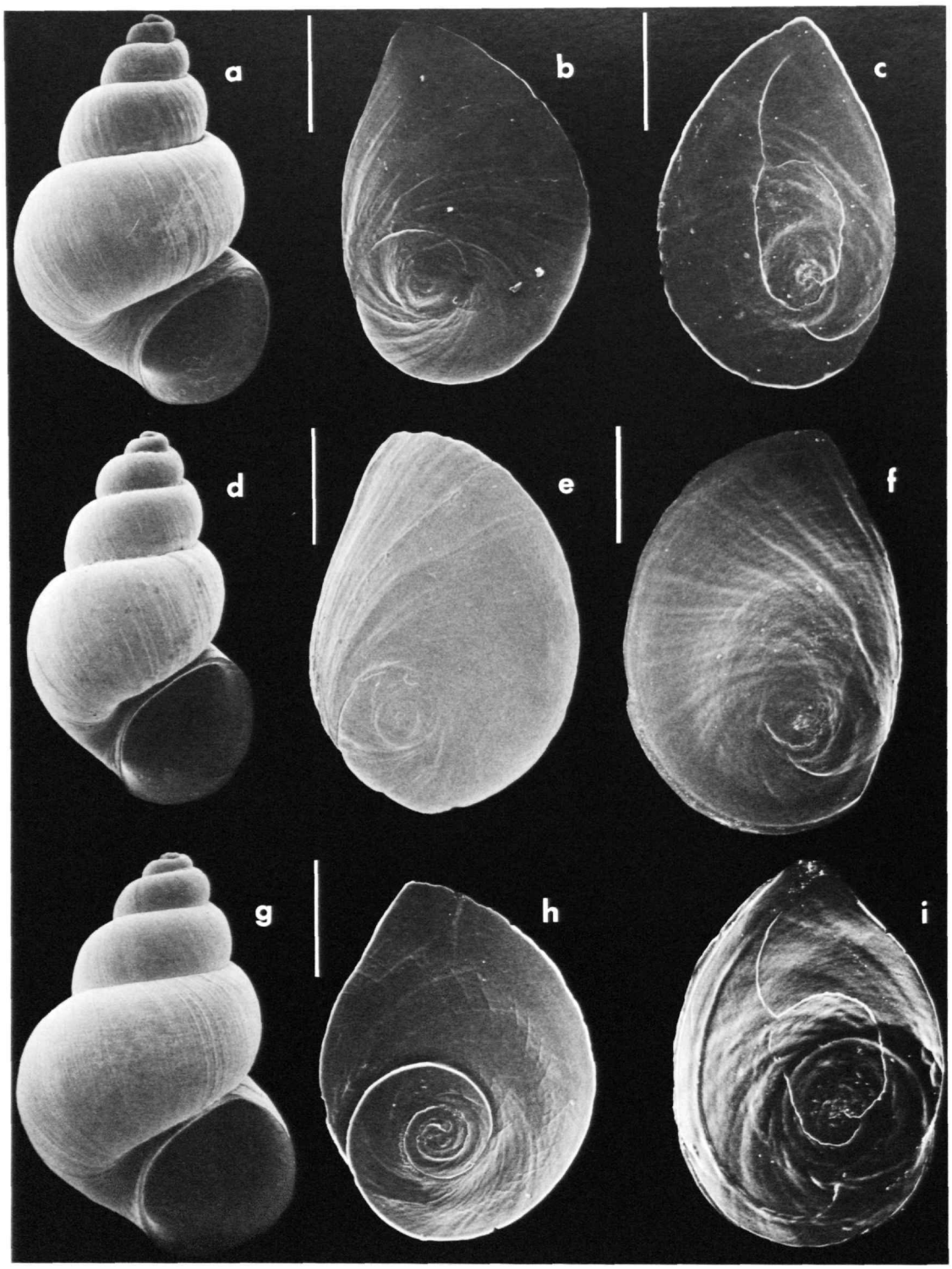


FIGURE 29.—Eastern *Pyrgulopsis*: *a–c*, *P. lustrica* (*a*, shell, USNM 622764, 3.3 mm; *b*, *c*, opercula, FSM 22227, bars = 0.43 mm, 0.38 mm); *d–f*, *P. ogmorphaphe* (*d*, shell, FSM 22180, 3.8 mm; *e*, *f*, opercula, FSM 146697, bars = 0.52 mm, 0.43 mm); *g–i*, *P. olivacea* (*g*, shell, ANSP 65466, 3.4 mm; *h*,*i*, opercula, USNM 528038, bar = 0.38 mm).

2*e*). Visceral coil light to dark.

Ctenidial filaments, 25, medium height and width. Osphradium centered from middle to within posterior half of ctenidial axis. Kidney with moderate-large bulge into pallial cavity. Hypobranchial gland well-developed, often with thickened amber portion near kidney. Stomach with small to medium-sized caecum.

Testis, 1.5–2.0 whorls, overlapping stomach to edge of style sac. Prostate gland broad, with small-large pallial section (15%–25%); pallial vas deferens with proximal loop. Penis (Figure 52*f*) medium-sized; filament short, stubby, without taper; lobe shorter than filament, oblique. Terminal gland elongate, often transverse, borne along distal edge (both surfaces). Filament light to darkly pigmented internally.

Female genitalia are shown in Figure 5*c*. Ovary, 0.5–1.0 whorl, overlapping posterior stomach chamber. Pallial albumen gland large (35%). Capsule gland longer than albumen gland, thickened. Genital aperture a sub-terminal slit with vestibule. Coiled oviduct a slight anterior bend followed by tall, narrow, vertical loop just behind pallial wall. Oviduct and bursal duct join well anterior to oviduct coil in front of pallial wall. Bursa copulatrix ovoid, medium length, broad (65%), with about half of length posterior to albumen gland. Bursal duct medium width, deeply embedded in albumen gland, about twice as long as bursa copulatrix. Seminal receptacle pouch-like, short, with very short duct, positioned lateral to proximal bursal duct along ventral edge of albumen gland.

TYPE LOCALITY.—*Pyrgulopsis lustrica:* "New York to Illinois and Minnesota" (Pilsbry, 1890). The type is labeled Little Lakes (Wayne County), New York. Holotype, ANSP 284061; paratypes, ANSP 396955. *Pyrgulopsis oneida:* Lower South Bay, Oneida Lake, New York. Lectotype (Baker, 1964:175), ANSP 283876; paralectotypes, ANSP 317030, ANSP 396989. *Pyrgulopsis gelida:* Pleistocene, near Morris, Grundy County, Illinois. Holotype, UIMNH P926 (possibly lost); paratypes, UIMNH P927. *Pyrgulopsis decepta:* Silver Lake, Waukesha County, Wisconsin. Holotype, UIMNH Z22501; paratypes, UIMNH Z22502. *Pyrgulopsis perlustrica:* Michigan shore east of Sturgeon Bay, Door County, Wisconsin. Holotype, UIMNH Z18365a (presumably lost; Franzen, 1956:22); paratypes, UIMNH Z18365a.

DISTRIBUTION.—Great Lakes region, upper Mississippi River drainage and (rarely) Atlantic Coastal drainage, northeastern United States and southeastern Canada (Thompson, 1977, fig. 15).

REMARKS.—This snail is distinguished from other eastern American forms by combination of simple, ovate-conic shell; small caecal chamber of stomach, and strongly oblique penial lobe.

MATERIAL EXAMINED.—FSM 22227, Midland, Clarke County, Ohio.

Pyrgulopsis ogmorphaphe (Thompson, 1977)

Marstonia ogmorphaphe Thompson, 1977:120, figs. 4e, 9–11.—Burch, 1982:27, figs. 220, 252.—Turgeon et al., 1988:61.
Pyrgulopsis ogmorphaphe.—Hershler and Thompson, 1987:30.
Pyrgulopsis ogmoraphe [sic].—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate to narrowly conic, large, umbilicate. Penial filament short, stubby; penial lobe very short. Penial ornament a transverse terminal gland.

DESCRIPTION.—Shell (Figure 29*d*) ovate to narrowly conic; height, 4.0–5.1 mm; whorls, 5–6. Early protoconch moderately punctate adapically. Teleoconch whorls highly convex; sculpture of moderate growth lines. Aperture adnate to body whorl. Inner lip complete in larger specimens, thin; columellar lip slightly reflected. Outer lip slightly prosocline. Umbilicus narrowly perforate. Periostracum light brown. Operculum (Figure 29*e,f*) ovate, light amber, sometimes slightly indented along outer edge; nucleus highly eccentric; dorsal surface weakly frilled. Attachment scar margin very weakly thickened along inner edge (to nucleus); callus weak-absent.

Central radular tooth (Figure 42*a*) with moderately indented dorsal edge; lateral cusps, 2–3; central cusp rounded, considerably broader and longer than laterals; basal cusps, 1 (sometimes with weak suggestion of outer cusp), elongate, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck weak-absent.

Cephalic tentacles, snout dark brown; dorsal tentacles with central unpigmented streak. Foot pigment light-moderate along anterior and posterior edges. Opercular lobe dark along sides and anterior edge. Neck usually pale. Pallial roof, visceral coil moderate to dark brown-black; mantle sometimes with two black streaks along sides of ctenidium.

Ctenidial filaments, 25, tall, broad. Osphradium centered posterior to middle of ctenidial axis. Kidney opening undifferentiated. Stomach caecum very large (66% of width of posterior stomach), broadly triangular.

Testis, 1.75 whorls, overlapping anterior stomach chamber to edge of style sac. Prostate gland bean-like, strongly reflexed, with large (39%) pallial section; pallial vas deferens with proximal kink. Penis (Figure 52*g*) large; filament short, stubby; lobe near-absent, consisting of a broad, hemispherical swelling. Terminal gland small, narrow, transverse, borne along distal edge (mostly on ventral surface). Filament dark.

Ovary, 0.5 whorl, positioned behind stomach. Albumen gland with large (48%) pallial section. Capsule gland slightly longer than albumen gland. Genital aperture a terminal slit with vestibule. Coiled oviduct of 2 slightly overlapping horizontal loops just behind pallial wall. Oviduct and bursal duct join well anterior to pallial wall. Bursa copulatrix ovoid, medium length, broad (66%), with almost entire length (87%) posterior to gland. Bursal duct broad proximally, ventral edge embedded in albumen gland, about 1.5 times length of bursa copulatrix. Seminal receptacle sac-like, short, lateral to anteriormost bursa copulatrix or proximal bursal duct, positioned near ventral edge of albumen gland.

TYPE LOCALITY.—Owen Springs, Sequatchie, Marion County, Tennessee. Holotype, FSM 22179; paratypes, FSM 22180.

DISTRIBUTION.—Endemic to type locality, Tennessee River drainage (Thompson, 1977, fig. 8).

REMARKS.—Among Eastern American species, this snail shares with several species a weak penial lobe. It differs from other members of this fauna by the broad central cusp of central radular tooth, posterior-oblique shape of oviduct coil, broad bursa copulatrix, and largely posterior position of bursa copulatrix.

MATERIAL EXAMINED.—FSM 146697 (topotypes).

Pyrgulopsis olivacea (Pilsbry, 1895)

Amnicola olivacea Pilsbry in Sargent, 1894a:121 [nomen nudum].—Sargent, 1894b:95.

Amnicola olivacea Pilsbry, 1895a:115.—Walker, 1918:135.—Baker, 1964:174.

Marstonia olivacea.—Stein, 1976:26.—Thompson, 1977:122, fig. 1d.—Burch, 1982:27, fig. 247.—Turgeon et al., 1988:61.

Pyrgulopsis olivacea.—Hershler and Thompson, 1987:30.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate-conic, large, variably umbilicate. Penial filament, lobe very short. Penial ornament a terminal gland.

DESCRIPTION.—Shell (Figure 29*g*) ovate-conic; height, 3.9–4.5 mm; whorls, 5.0–5.4. Protoconch moderately punctate over most of length; later portion lined with several strong spiral lines. Teleoconch whorls highly convex, shouldered; sculpture of weak growth lines and fine spiral striations. Aperture ovate, adnate to body whorl. Inner lip usually complete, thin. Outer lip prosocline. Umbilicus narrowly to broadly perforate. Periostracum brown.

Operculum (Figure 29*h,i*) thin, amber, outer edge strongly indented; nucleus slightly eccentric; dorsal surface strongly frilled. Attachment scar margin slightly thickened along most of length, early whorl outlines bulging slightly above ventral surface; callus very weak.

Central radular tooth (Figure 42*b*) with moderately indented dorsal edge; lateral cusps, 3–4; central cusp rounded, slightly longer and broader than laterals; basal cusps, 1 (with faint suggestion of second, outer cusp), short, narrowly triangular, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened; neck absent.

Animal black.

Penis medium-sized; filament very short, stockly; lobe about as long as filament, broadly triangular. Terminal gland borne along distal edge of lobe (ventral side). Filament dark; black granules also scattered on distal penis.

TYPE LOCALITY.—Huntsville, Alabama. Lectotype (Baker, 1964:174), ANSP 65466; paralectotypes, ANSP 396952.

DISTRIBUTION.—Known only from type locality, Tennessee River drainage (Thompson, 1977, fig. 15), where it is now extinct (Thompson, 1977).

REMARKS.—This snail resembles widely disjunct *P. lustrica* in shape of shell and penis, but differs in having strong spiral lines on the teleoconch.

Extralimital collections referred to by Goodrich (1939, 1944) probably were misidentified (fide Thompson, 1977).

Pyrgulopsis ozarkensis Hinkley, 1915

Pyrgulopsis ozarkensis Hinkley, 1915:588, pl. 78: fig. 2.—Walker, 1918: 140.—Burch, 1982:28.—Hershler and Thompson, 1987:30.—Turgeon et al., 1988:62.—USDI, 1991b:58822.

Marstonia ozarkensis.—Gordon, 1986:76.

DIAGNOSIS.—Shell narrowly conic, medium-sized, variably umbilicate. Animal unknown.

DESCRIPTION.—Shell (Figure 30*a*) narrowly conic; height, 2.5–3.0 mm; whorls, 5. Protoconch blunt, strongly punctate near apex, usually slightly eroded. Teleoconch whorls weakly convex, body whorl often with angulation or weak keel below periphery; sculpture of weak growth lines and sometimes faint spiral lines. Aperture ovate, broadly adnate to or slightly separated from body whorl. Inner lip complete, moderately thick; columellar lip slightly reflected. Outer lip moderately thick, orthocline. Umbilicus absent to rimate. Periostracum olive-tan.

TYPE LOCALITY.—North Fork of White River, 2 or 3 miles (3.2–4.8 km) above Norfolk, Arkansas. Holotype, USNM 271765; paratypes, USNM 860581, ANSP 115102.

DISTRIBUTION.—Known only from the type locality, Mississippi River drainage. A limited survey of this region in 1991–1992 did not yield this species.

REMARKS.—This species is similar to *P. scalariformis*, but has a wider shell without basal carina.

Pyrgulopsis pachyta (Thompson, 1977)

Marstonia sp.—Stein, 1976:26.

Marstonia pachyta Thompson, 1977:121, figs. 3a, 12, 13.—Burch, 1982:27, figs. 221, 253.—Turgeon et al., 1988:61.

Pyrgulopsis pachyta.—Hershler and Thompson, 1987:30.—USDI, 1991b:58822.

DIAGNOSIS.—Shell ovate-conic, medium to large-sized, weakly umbilicate. Penial ornament a dorsal gland borne along left distal edge; near-circular terminal gland, and ventral gland.

DESCRIPTION.—Shell (Figure 30*b*) ovate-conic; height, 3.3–4.0 mm; whorls, 5. Earliest protoconch strongly punctate adapically (Figure 1*f*). Teleoconch whorls weakly convex, slightly shouldered; sculpture of strong growth lines and faint spiral striae. Aperture usually broadly adnate to body whorl. Inner lip complete, thickened, especially adapically. Outer lip thick, slightly prosocline. Umbilicus imperforate to narrowly rimate. Periostracum light brown.

Operculum (Figure 30*c,d*) ovate, light amber; nucleus highly eccentric; dorsal surface slightly frilled. Attachment scar margin slightly thickened between nucleus and inner edge, weak-smooth elsewhere; callus moderate.

Central radular tooth (Figure 42*c*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp weakly pointed, tongue-like, broader and longer than laterals; basal cusps, 1,

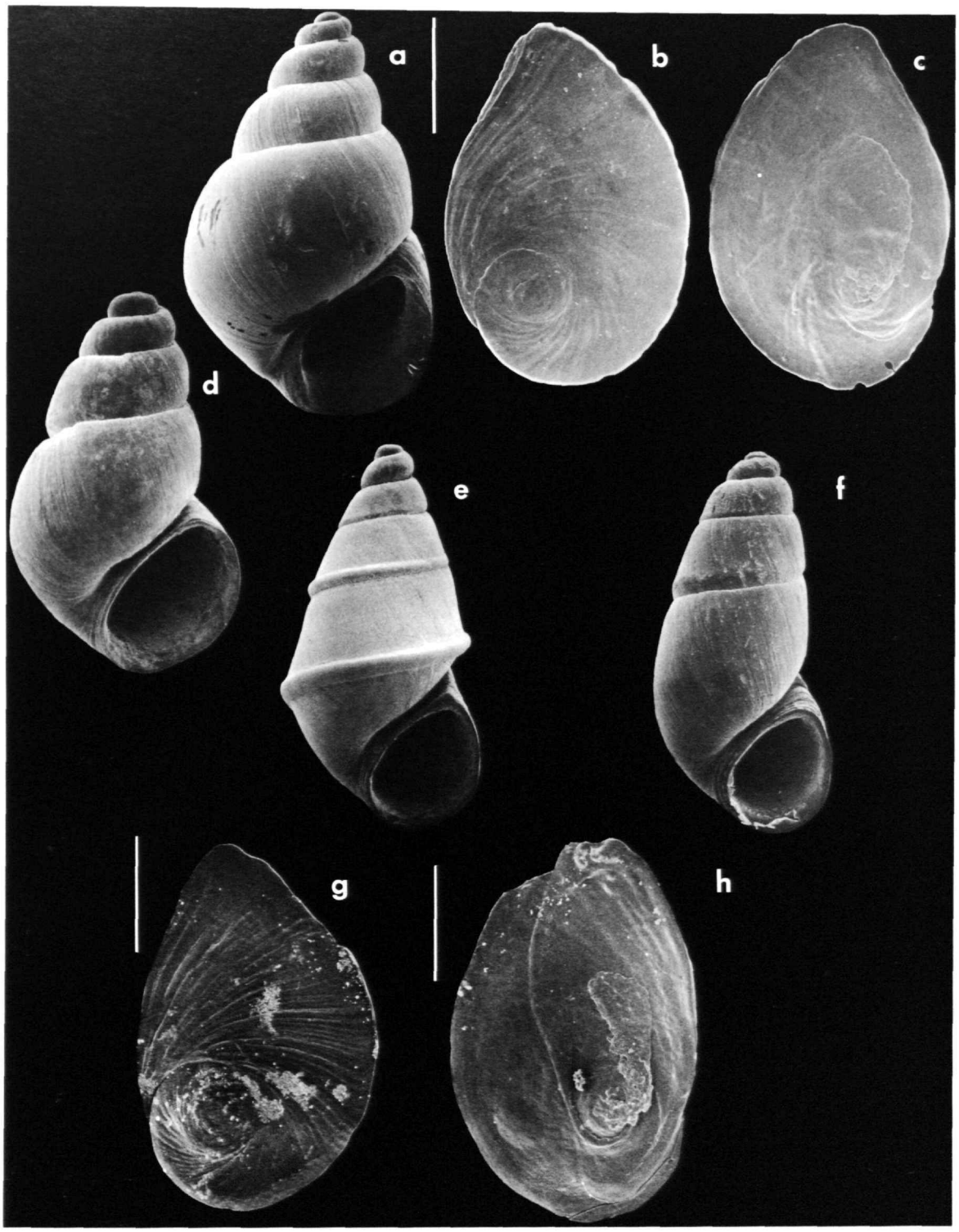


FIGURE 30.—Eastern *Pyrgulopsis*: *a*, *P. ozarkensis* (shell, ANSP 115102, 2.3 mm); *b–d*, *P. pachyta* (*b*, shell, FSM 22228, 3.5 mm; *c*, *d*, opercula, FSM 189462, bar = 0.38 mm); *e–h*, *P. scalariformis* (*e*, shell, USNM 526623, 3.3 mm; *f*, shell, ANSP 96607, 3.0 mm; *g*, *h*, opercula, FSM 91726, bars = 0.3 mm, 0.27 mm).

medium-sized, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened; neck weak-absent.

Cephalic tentacles dark brown distally, with central unpigmented streak. Snout light-dark. Foot dark along anterior edge. Opercular lobe sometimes dark along sides. Neck pale. Pallial roof, visceral coil light-dark.

Ctenidial filaments, 33, tall, broad. Osphradium extending almost to posterior end of ctenidial axis. Kidney opening slightly thickened. Stomach caecum prominent, broadly triangular.

Testis, 1.5 whorls, overlapping anterior stomach chamber almost to edge of style sac. Prostate gland with large (33%) pallial section; pallial vas deferens with gentle proximal undulation. Penis (Figure 53*a*) medium-sized; filament short, stubby; lobe very short, narrow. Terminal gland small, near-circular, borne along distal edge of lobe (ventral surface). Second, similar gland borne along edge of small accessory lobe along left distal corner of penis (rarely absent). Ventral gland positioned near base close to right edge (sometimes with short stalk). Filament dark.

Ovary, 0.5–0.75 whorls, abutting or very slightly overlapping posterior stomach chamber. Pallial albumen gland large (30%). Capsule gland as long as albumen gland. Genital aperture a subterminal slit with short vestibule. Coiled oviduct a tall, narrow, slightly oblique (posterior) loop just behind pallial wall. Oviduct and bursal duct join well anterior to pallial wall. Bursa copulatrix ovoid, medium length and width, with about half of length posterior to gland. Bursal duct medium width, deeply embedded in albumen gland distally, about one and a half times length of bursa copulatrix. Seminal receptacle pouch-like, short, positioned lateral to proximal bursal duct near ventral edge of albumen gland.

TYPE LOCALITY.—Limestone Creek, 0.7 mi. (1.1 km) east of Mooresville, Limestone County, Alabama. Holotype, FSM 22179; paratypes, FSM 22180.

DISTRIBUTION.—Limestone and Piney Creeks, Tennessee River drainage, northern Alabama (Thompson, 1977, fig. 8).

REMARKS.—This snail is distinguished from other eastern American forms by its very thick inner lip of shell, numerous ctenidial filaments, presence of dorsal gland on penis, and posterior location of ventral gland.

MATERIAL EXAMINED.—FSM 189462 (topotypes).

Pyrgulopsis scalariformis (Wolf, 1869)

Pyrgula scalariformis Wolf, 1869:198, pl. 17: fig. 3.—Baker, 1964:176.

Pyrgulopsis scalariformis.—Call and Pilsbry, 1886:14, pl. II: fig. 13.—Walker, 1918:140.—Baker, 1928:138, pl. VII: figs. 24–27.—Burch, 1982: 28, fig. 273.—Hershler and Thompson, 1987:30, fig. 31.—Turgeon et al., 1988:62.

Pyrgula scalariformis mississippiensis Pilsbry, 1886:75.

Pyrgulopsis mississippiensis.—Call and Pilsbry, 1886:13, pl. II: figs. 14–16.—Pilsbry, 1891c:330.—Hinkley, 1906:43.—Walker, 1906:116, pl. 5: fig. 15.—Baker, 1964:174.—Johnson, 1975:142.

Pyrgulopsis wabashensis Hinkley, 1908a:117; 1908b:56.—Goodrich and Schalie, 1944:300.—Baker, 1964:177.—Hershler and Thompson, 1987:30.

DIAGNOSIS.—Shell pupiform to narrowly conic, basally carinate, medium to large-sized, narrowly umbilicate. Penial filament medium length, lobe short. Penial ornament a transverse terminal gland.

DESCRIPTION.—Shell (Figure 30*e,f*) pupiform-narrowly conic; height, 3.5–4.7 mm; whorls, 5.5–6.0. Early protoconch strongly punctate, later portion with weaker sculpture; protoconch often eroded. Earliest teleoconch with rounded whorls; later whorls near flat; broad peripheral keel (varying from weak to well developed) appearing at middle or end of third whorl and extending to aperture. Aperture ovate, broadly adnate to very slightly separated from body whorl. Inner lip complete, usually thickened; columellar lip slightly reflected. Outer lip similarly thickened, prosocline. Umbilicus near absent to narrowly rimate. Periostracum light brown.

Operculum (Figure 30*g,h*) ovate, light amber; nucleus slightly-highly eccentric; dorsal surface frilled. Attachment scar margin often thickened all around, sometimes broadly so along inner edge (to nucleus); callus small, but well developed.

Central radular tooth (Figure 42*d*) with moderately indented dorsal edge; lateral cusps, 4–5; central cusp rounded-pointed, slightly broader and longer than laterals; basal cusps, 1–3 (innermost largest), short, broadly triangular, with weak dorsal support. Basal process narrow, weakly excavated. Lateral margins thickened; neck weak-absent.

Animal completely unpigmented except for black eyespots.

Ctenidial filaments, 22, medium height, narrow. Osphradium large (31%), centered slightly posterior to middle of ctenidial axis. Kidney opening slightly thickened and whitened. Stomach caecum broad, short.

Testis, 1.5 whorls, overlapping stomach to edge of style sac. Prostate gland with large (43%) pallial section; pallial vas deferens with prominent kink considerably distal to edge of prostate gland. Penis (Figure 53*b*) large; base elongate-rectangular, narrowing distally; filament medium length and width, tapered distally; lobe short, broad. Terminal gland elongate, transverse, borne along distal edge of lobe. Filament unpigmented.

Ovary, 0.5 whorl, abutting posterior edge of stomach. Pallial albumen gland very large (75%). Capsule gland slightly shorter than albumen gland. Genital aperture an elongate, subterminal slit without vestibule. Coiled oviduct of two overlapping, near horizontal loops just behind pallial wall (extending to near posterior edge of albumen gland). Oviduct and bursal duct join well anterior to oviduct coil just anterior to pallial wall. Bursa copulatrix ovoid, short (24%), broad (64%), with 33% of length posterior to gland. Bursal duct broad, very slightly embedded in albumen gland, about twice as long as bursa copulatrix. Seminal receptacle stubby, short, positioned lateral to anterior bursa copulatrix and along ventral edge of albumen gland.

TYPE LOCALITY.—*Pyrgulopsis scalariformis:* Tazewell shore of the Illinois River, Illinois. Lectotype (Baker, 1964:176), ANSP 27822; paralectotypes, ANSP 375740. *Pyrgulopsis mississippiensis:* near mouth of Rock River, a few miles below Davenport, Iowa. Lectotype (Baker, 1964:174),

ANSP 61606; paralectotypes, ANSP 375747. *Pyrgulopsis wabashensis:* Wabash River, at The Chains in Posey County, Indiana. Lectotype (Baker, 1964:177), ANSP 27824; paralectotypes, ANSP 96607, ANSP 396953.

DISTRIBUTION.—Ohio, Mississippi, Tennessee River drainages, eastern United States (very incompletely known).

REMARKS.—Wolf (1869) described *Pyrgula scalariformis* from empty shell collected along the Illinois River. Pilsbry (1886) introduced *Pyrgula scalariformis mississippiensis* in a short note based on empty shell collected along the Mississippi River (Illinois side). Later in the same year, Call and Pilsbry fully described *Pyrgulopsis mississippiensis,* with the above listed as a synonym followed by the comment (1886:13), "No description." Clench and Turner (1962:99) and others have treated the earlier name as a nomen nudum, however, Pilsbry (1886) did provide a description of this taxon ("...smaller, stouter than typical fossil *scalariformis,* and more compactly coiled–never exhibiting the peripheral carina on upper whorls. The shorter forms remind one of the common rhomboidal variety of *Anculosa dissimilis* Say."), thus rendering the name valid under ICZN Article 12. Fortunately the authorship of *mississippiensis* is not a critical issue given its status as junior subjective synonym of *scalariformis* Wolf, 1869 (see below).

Shimek (1892) argued that the differences between *scalariformis* and *mississippiensis* reported by Call and Pilsbry (1886; stronger carina of shells of the former, and different aperture and sutures) are not consistent when a large series of specimens is examined. The author concurs, and suggests that a single species, with variable carina development, is involved. Hinkley's (1908) description of *wabashensis* emphasized the absence of a carinate body whorl; in fact many of the paratypes and other material from the type locality are carinate and very closely resemble some *scalariformis.* Although Wabash River shells are usually small and occasionally quite narrow, I see no reason to consider them a separate species from the above. A completely satisfactory treatment of this problem is precluded by paucity of anatomical material for these animals. Two of the three taxa (*scalariformis, mississippiensis*) were described from empty shell and all three apparently are extinct at their respective type localities. Living material later was obtained from the rather distant locality (Tennessee River drainage) of Shoal Creek, Alabama (Hinkley, 1906; Walker, 1906; operculum and radula figured by Baker [1928]); as well as Meramec River, Missouri (FSM collections). Unfortunately no alcohol-preserved material is available for the Shoal Creek population, which may no longer be extant (Fred G. Thompson, pers. comm., 5/1992), and only a few such specimens are available from the Meramec River, thus providing a meager sample for the snail.

MATERIAL EXAMINED.—FSM 91725, Meramec River, 2.9 km north-northwest of Steeleville, Crawford County, Missouri; FSM 91726, ibid., 12.0 km southeast of Leesburg.

Cladistic Analysis

The "m*" option produced a single tree of consistency index of 0.26 and retention index of 0.61. Branch and bound ("bb*") search based on this tree yielded more than 1559 trees of equal length. The "nelsen" option then was used to obtain a strict consensus tree for these solutions, which is shown in Figure 53. Lists of character-state transformations supporting clades of interest are in Table 2.

The consensus tree provides support for monophyly of *Pyrgulopsis* (referred to as Clade 1 in Table 2) in that our genus is differentiated from the outgroup by 15 character-state transformations, including six non-homoplasious synapomorphies: densely pitted protoconch (character 3-1), broad operculum attachment scar (8-1), narrow basal process on central radular tooth (16-1), well developed lateral angles of central tooth (17-1), simple anterior vas deferens (25-1), and horizontally oriented bursa copulatrix (55-1).

Within *Pyrgulopsis,* four large clades are reasonably supported and may merit recognition as species groups. The nine eastern American species (Clade 2), comprising all species allocated to *Marstonia* by Thompson (1977) plus *P. scalariformis,* are defined by 10 character-state transformations, including non-homoplasious synapomorphies of coarse protoconch microsculpture (3-2) and anterior junction between oviduct and bursal duct (49-1). Homoplasious characters supporting this clade include a banded pattern of mantle pigmentation (18-1; reversed in one eastern species), narrowly vertical oviduct coil (50-1; reversed or transformed in two eastern species), elongate bursal duct (58-1; paralleled in a western species), and bursal duct deeply embedded in albumen gland (59-2; reversed in one eastern species). Other characters uniquely, but not universally, found in this clade are an incomplete inner shell lip (2-1), indented outer edge of operculum (7-1), strongly oblique penial lobe (29-1), and narrow, sac-like bursa copulatrix (53-3). Members of this clade have ovate-conic shells and relatively simple penes usually ornamented by a terminal gland and, in some cases, a ventral gland.

The other three clades are comprised of subsets of the western American fauna. Six species from southern Nevada

TABLE 2.—List of character-state transformations at ancestral nodes (defining clades of interest) on the consensus tree (Figure 53).

Clade 1: 2-1, 4-1, 7-1, 8-1, 13-1, 14-1, 15-1, 16-1, 18-1, 19-1, 24-1, 47-1, 54-1, 55-1, 61-1
Clade 2: 2-2, 8-0, 17-1, 20-2, 31-0, 48-1, 49-1, 57-1, 58-2, 62-0
Clade 3: 29-3, 31-3, 49-0
Clade 4: 9-1, 35-1, 36-1, 37-2, 40-1
Clade 5: 9-1, 32-1, 33-1, 34-1, 47-0

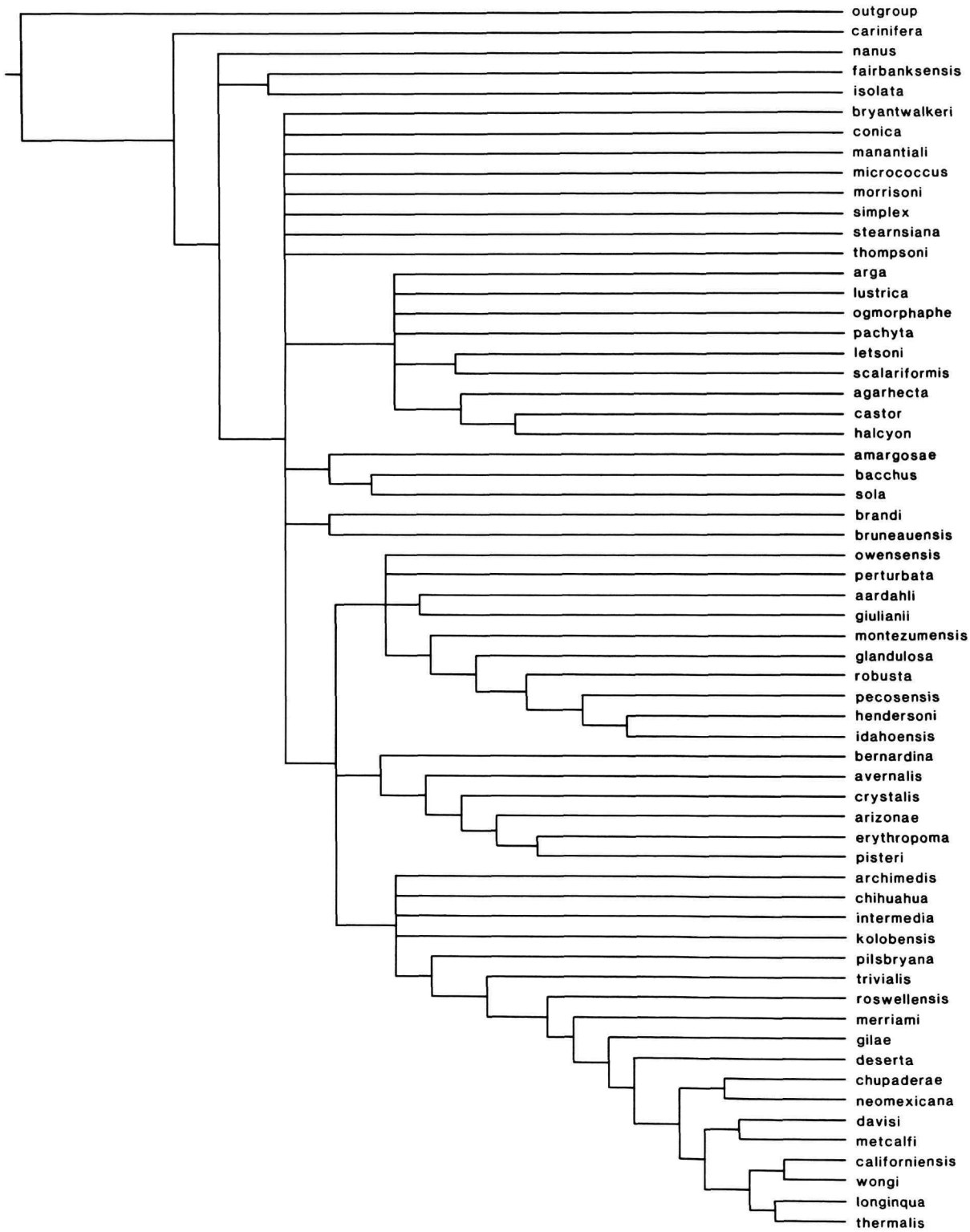


FIGURE 31.—Strict consensus cladogram for *Pyrgulopsis* species (ci = 0.24, ri = 0.57).

and southeastern Arizona form a clade (Clade 3) defined by three transformations, including unique synapomorphies involving loss of penial lobe (30-3) and terminal gland (32-3). Other unique synapomorphies defining sub-clades within this group are an enlarged ventral gland (43-2) and superficial position of ventral gland (44-1). Members of this clade usually have globose shells, and their penes are ornamented by a ventral gland, sometimes accompanied by a large dorsal gland.

A second western clade (Clade 4) is comprised of 10 species from eastern California, northern Arizona, and Snake River environs of Wyoming, Idaho, and Oregon; and includes all members of the subgenus *Natricola* sensu Gregg and Taylor (1965). This group is defined by five synapomorphies, of which only one, presence of a dot-like Dg1 penial gland, is unique; this character is transformed in advanced members of this clade. Other defining characters are homplasious, and include a strong ventral callus on the operculum (10-1), and three features relating to Dg1 (37-1, 38-2, 40-1). There is extensive parallelism in penial and female genitalic character transformations between this clade and that discussed below. Members of this group often are large, have ovate-conic shells, and have penes ornamented by terminal gland, Dg1, and sometimes Dg2 and/or Dg3.

A third western clade (Clade 5), comprised of 18 species from various drainages, closely approximating the "*F[ontelicella]. californiensis* series" of Taylor (1987), is defined by five character-state transformations. Three of these (33-1, 34-1, 35-1) are associated with the unique occurrence of a penial gland (Pg) in this clade. The other two, involving a strong ventral callus on operculum (10-1) and loss of anterior capsule gland vestibule (48-0), are homoplasious. Within this group, sub-clades are defined by the following unique or near-unique character-state transformations: proximally bifurcate penial gland (35-2, one parallel within this clade), Dg1 a short strip (36-2), multiple minor dorsal glands (42-2, paralleled by two species), posterior position of ovary (46-1, parallel by one species within this clade), multiple ventral glands (43-2), and elongate bursa copulatrix (52-1, two parallels and one reversal). Members of this group have globose to elongate-conic shells and penes ornamented by a terminal and penial gland, often accompanied by one or more dorsal glands.

The 17 Western American species having a relatively simple penis (ornamented solely by terminal gland) do not comprise a monophyletic group and, in general, are poorly resolved on the cladogram. Four globose-shelled species from southern Nevada (*carinifera, nanus, fairbanksensis, isolata)* are basally placed on the cladogram, but are not a well-defined group; and an assemblage of eight species scattered throughout the West, approximating the "*F[ontelicella]. stearnsiana* series" of Taylor, 1987), forms an unsupported polytomy. On the other hand, two small groups of species are more strongly supported. One pair from Gila River drainage of Arizona (*bacchus, sola*) is defined by a small penis (26-1, unique synapomorphy), bifurcate penial lobe (paralleled in one species), and simple terminal gland on penis (32-0, a homoplasious reversal). A second group, comprised of three highly disjunct species from internal drainage of northern Mexico (*brandi*), Amargosa River drainage (*amargosae*) and lower Snake River drainage (*bruneauensis*); is defined by three character-state transformations: weak ventral operculum attachment scar (9-0, homoplasious), penial filament (28-1, paralleled in one species), and bursal duct positioned lateral to albumen gland (59-0, homoplasious).

Appendix 1

Recent Species Incorrectly Described As or Allocated to *Pyrgulopsis* or Its Junior Synonyms

(Unless otherwise stated, all Central American species of Ancey were allocated to *Pyrgophorus* by Hershler and Thompson, 1992.)

Pyrgulopsis conoidea Ancey, 1888:196. Nicaragua.

Pyrgulopsis coronatus Ancey, 1888:197. Vera-Cruz, Mexico.

Amnicola (Marstonia) greenensis Baker, 1928:113. Holocene, off Sherwood Forest Hotel, Green Lake, Green Lake County, Wisconsin. Generic status of this extinct species is uncertain.

Pyrgulopsis hydrobioides Ancey, 1888:201. Lago de Coatepeque, El Salvador.

Pyrgulopsis newcombiana Ancey, 1888:196. Nicaragua.

Pyrgulopsis nicaraguanus Ancey, 1888:194. Nicaragua.

Pyrgulopsis nicaraguanus costulifera Ancey, 1888:195. Nicaragua.

Pyrgulopsis nicaraguanus duplicata Ancey, 1888:195. Nicaragua.

Pyrgulopsis nicaraguensis Ancey, 1888:194. Nicaragua.

Pyrgulopsis patzcuarensis Pilsbry, 1891b:9. Lake Patzcuaro, West Mexico. Allocated to *Tryonia* by Taylor (1966).

Amnicola pilsbryi Walker, 1906:116. Rockford, Illinois. Allocated to *Marstonia* by Walker (1926). Transferred to *Lyogyrus* by Thompson (1968).

Pyrgulopsis producta Ancey, 1888:197. Nicaragua.

Amnicola sheldoni Pilsbry, 1890:52. Lake Michigan, at Racine, Wisconsin. Allocated to *Pyrgulopsis* by Walker (1918:140). Is the type species of *Hoyia* F.C. Baker, 1926 (monotypic).

Pyrgulopsis spinosus Call and Pilsbry, 1886. Comal Creek, New Braunfels, Texas. Transferred to *Pyrgophorus* by Martens (1899).

Pyrgulopsis spinosa brevispira Ancey, 1888:193. Comal Creek at New Braunfels, Texas.

Amnicola walkeri Pilsbry, 1898:43. Lake Michigan at High Island Harbor, Beaver Islands [Michigan]. Allocated to *Marstonia* by Baker (1926). Transferred to *Lyogyrus* by Thompson (1968).

Amnicola (Marstonia) walkeri foxensis Baker, 1928:116. Fox River, 1 mile (1.6 km) north of Portage, Columbia County, Wisconsin. Generic status uncertain; probably a *Lyogyrus* as above.

Amnicola winkleyi Pilsbry, 1912:1. Saco, Maine. Allocated to *Marstonia* by Baker (1926). Placed in synonymy with *Marstonia lustrica* by Thompson (1977). Transferred to *Cincinnatia* by Davis and Mazurkiewicz (1985).

Pyrgulopsis wrighti Ancey, 1888:199. Lago de Coatepeque, El Salvador.

Pyrgulopsis wrighti minima Ancey, 1888:201. Lago de Coatepeque, El Salvador.

Pyrgulopsis wrighti obesa Ancey, 1888:201. Lago de Coatepeque, El Salvador.

Pyrgulopsis wrighti oblonga Ancey, 1888:200. Lago de Coatepeque, El Salvador.

Pyrgulopsis wrighti plicosa Ancey, 1888:199. Lago de Coatepeque, El Salvador.

Pyrgulopsis wrighti transitans Ancey, 1888:200. Lago de Coatepeque, El Salvador.

Appendix 2

Fossil Species Described As or Allocated to *Pyrgulopsis* or Its Junior Synonyms.

Lithasia antiqua Gabb, 1866:13. Tertiary (Pliocene-Pleistocene; Taylor 1966), on Snake River, Idaho Territory, on the road from Fort Boisé to the Owyhee mining country. Allocated to *Pyrgulopsis* by Hannibal (1912b:189). Transferred to *Lithoglyphus (= Fluminicola)* by Taylor (1966a; as synonym of *L. occidentalis* (Hall, 1845)).

Pyrgulopsis blakeana Taylor, 1950:30. Subfossil, shore of Salton Sea by Fish Springs, Imperial County, California. Allocated to *Tryonia* by Taylor (1975).

Marstonia bucciniformis Youlou, 1978:42. Early Tertiary, Bohai Coastal Plain, China.

Pyrgulopsis cahuillarum Taylor, 1950:31. Subfossil, fifty yards northeast of the so-called Fish Traps, 7.9 miles (12.6 km) west of Mecca, Riverside County, California. Allocated to *Tryonia* by Taylor (1975).

Pyrgulopsis carinata Yen, 1944:103. Pliocene, Idaho Formation, Hammett, Elmore County, Idaho.

Amnicola crybetes Leonard, 1952:38. Pleistocene, Blanco Formation, 15 miles (24 km) east of Liberal, Seward County, Kansas. Allocated to *Marstonia* by Taylor (1960b).

Nematurella euzona Hanna, 1923:33. Miocene, Sonoma County, California. Allocated to *Savaginius* by Taylor (1975).

Pyrgulopsis imminens Taylor, 1950:28. Subfossil, shore of Salton Sea by Fish Springs, Imperial County, California.

Marstonia inflata Wang in Yu and Wang, 1977:21. Late Cretaceous/Cenozoic, China.

Amnicola (Marstonia) leightoni Baker, 1920:125. Pleistocene, near Rush Lake, Logan County, Ohio. Described as subspecies of *Amnicola winkleyi;* elevated to full species status by Baker (1928).

Fontelicella (Natricola) melina Taylor in Taylor and Smith, 1981:350. Pliocene, Honey Lake, Lassen County, California.

Amnicola micra Yen, 1946:488. Late Tertiary, 9 miles (14.4 km) northwest of Montpelier, Bear Lake County, Idaho. Allocated to *Fontelicella* by Gregg and Taylor (1965).

Paludestrina nanna Chamberlain and Berry, 1933:28. Pliocene, Collinston, Utah. Allocated to *Savaginius* by Taylor (1966).

Fluminicola percarinata Pilsbry, 1934:16. Late Pliocene-Early Pleistocene, Lost Hills Oil Field, California. Allocated to *Savaginius* by Taylor (1966).

Fluminicola perditicollis Pilsbry, 1934:16. Late Pliocene-Early Pleistocene, Lost Hills Oil Field, California. Allocated to *Savaginius* by Taylor (1966).

Fluminicola pilula Pilsbry, 1934:15. Late Pliocene-Early Pleistocene, Lost Hills Oil Field, California. Allocated to *Savaginius* by Taylor (1966).

Pyrgulopsis polynematicus Pilsbry, 1934:15. Pliocene, Buttonwillow Gas Field, California.

Amnicola (Marstonia) precursor Baker, 1928:116. Pleistocene, Green Lake, Green Lake County, Wisconsin.

Amnicola puteana Pilsbry, 1935b:559. Pliocene, Buttonwillow Gas Field, California. Allocated to *Savaginius* by Taylor (1966).

Pyrgulopsis? satilla Dall, 1913:236. Pliocene, near Alexandria, Louisiana.

Fluminicola siegfusi Pilsbry, 1934:16. Late Pleistocene-Early Pliocene, Lost Hills Oil Field, California. Allocated to *Savaginius* by Taylor (1966).

Fluminicola spiralis Pilsbry, 1934:16. Late Pliocene-Early Pleistocene, McKittrick Front Oil Field, California. Allocated to *Savaginius* by Taylor (1966).

Marstonia stenothyroides Youlou, 1978:42. Early Tertiary, Bohai Coastal Plain, China.

Pyrgulopsis tectoformis Youlou, 1978:37. Early Tertiary, Bohai Coastal Plain, China.

Pyrgulopsis tropidogyra Pilsbry, 1935b:555. Late Pliocene-Early Pleistocene, Santa Clara Lake beds, west side of Santa Clara Valley near Los Gatos, California.

Hydrobia truckeensis Yen, 1950:186. Pliocene, Truckee Formation, Nevada. Allocated to *Fontelicella* by Gregg and Taylor (1965).

Pyrgulopsis vincta Pilsbry, 1934:15. Pliocene, [basal] Tulare Formation, Kettleman Hills, California. *Pyrgulopsis williamsi* Hannibal, 1912b:189. Pliocene, Kettleman Lake beds, California.

Amnicola yatesiana Cooper, 1894:171. Late Pliocene-early Pleistocene, Santa Clara Lake beds, San Jose Mission, California. Allocated to *Pyrgulopsis* by Hannibal (1912b).

Fluminicola yatesiana utahensis Yen, 1947:273. Pliocene, Salt Lake Formation, near Logan, Utah. Allocated to *Savaginius* by Taylor (1966).

Marstonia xinminensis Youlou, 1978:43. Type locality, Early Tertiary, Bohai Coastal Plain, China.

Appendix 3

Data Matrix of 64 Characters for 60 Species of *Pyrgulopsis* and a Single Outgroup.

Nymphophilus minckleyi
00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 0000

Pyrgulopsis agarchecta
11211 11100 10010 11111 20001 00000 00000 00000 00000 01110 00231 20120 0100

Pyrgulopsis arga
10211 11110 10011 11111 20001 00012 00000 00000 00000 01111 10001 10010 0100

Pyrgulopsis castor
11211 11100 10010 11110 20001 00000 00000 00000 00112 01111 10231 20120 0100

Pyrgulopsis halcyon
11211 11100 10010 11111 00001 00010 00000 00000 00112 01011 10231 20120 0100

Pyrgulopsis letsoni
10211 10111 10011 11011 20001 00010 00000 00000 00000 01011 00231 20120 0100

Pyrgulopsis lustrica
10211 11100 10001 11111 00001 00010 00000 00000 00000 01111 00001 10120 0100

Pyrgulopsis ogmorphaphe
11211 10100 10101 11111 20001 00000 00000 00000 00000 11112 00101 00110 0100

Pyrgulopsis pachyta
10211 10100 10011 11001 20001 00000 00000 00000 00112 11111 00001 10120 0100

Pyrgulopsis scalariformis
10201 10111 10011 11211 00001 00010 00000 00000 00000 11010 00001 10120 0100

Pyrgulopsis aardahli
10111 10111 10011 11011 00001 00002 02000 11200 10112 01102 00001 10010 0110

Pyrgulopsis amargosae
10111 10100 10011 11011 00001 00100 02000 00000 00000 01002 00201 10000 0110

Pyrgulopsis archimedis
10101 10111 10011 11001 20001 00000 00111 00000 00112 01002 00001 00010 0110

Pyrgulopsis arizonae
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Pyrgulopsis avernalis
00111 10110 10011 11011 00001 000?3 ?3000 00000 00122 00100 00001 10010 0100

Pyrgulopsis bacchus
10111 10110 10011 11011 00001 10000 10000 00000 00000 01002 00001 10010 0100

Pyrgulopsis bernardina
10111 10110 11011 11011 00001 010?3 ?3000 00000 01112 01100 10021 10110 0110

Pyrgulopsis brandi
00?11 10110 10011 11011 00011 00100 02000 00000 00000 00102 20001 1001? 1010

Pyrgulopsis bruneauensis
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Pyrgulopsis bryantwalkeri
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Pyrgulopsis californiensis
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Pyrgulopsis carinifera
00101 00110 00011 11011 00111 00000 10000 00000 00000 00100 00201 20001 0100

Pyrgulopsis chihuahua
00111 10111 10011 11011 00011 00000 00121 00000 00112 00000 00001 10000 0110

Pyrgulopsis chupaderae
10111 10110 11011 11011 01001 00000 01121 22211 20112 01000 11111 01210 0001

Pyrgulopsis conica
10111 10110 10011 11011 00001 00000 02000 00000 00000 01102 00201 10000 0100

Pyrgulopsis crystalis
00111 10110 00011 11011 10101 010?3 ?3000 00000 00121 01000 00001 20010 0110

Pyrgulopsis davisi
10111 10111 10011 11011 00001 00000 01122 22211 20112 11100 10101 00001 0110

Pyrgulopsis deserta
10111 10110 11011 11011 00001 00000 02121 00000 00112 01100 11111 01000 0011

Pyrgulopsis erythropoma
00111 00111 11011 11011 00001 010?3 ?3000 00000 00121 00002 00021 10000 0110

Pyrgulopsis fairbanksensis
00111 00100 00111 11011 10011 00000 02000 00000 00000 00100 10101 10011 0110

Pyrgulopsis gilae
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Pyrgulopsis giulianii
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Pyrgulopsis glandulosa
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Pyrgulopsis hendersoni
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Pyrgulopsis idahoensis
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Pyrgulopsis intermedia
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Pyrgulopsis isolata
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Pyrgulopsis kolobensis
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Pyrgulopsis longinqua
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Pyrgulopsis manantiali
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Pyrgulopsis merriami
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Pyrgulopsis metcalfi
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Pyrgulopsis micrococcus
10111 10100 10011 11011 00001 00000 02000 00000 00000 00102 00001 10000 0110

Pyrgulopsis montezumensis
10111 10111 10011 11011 00001 00002 00000 31110 20112 01102 00001 10010 0110

Pyrgulopsis morrisoni
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Pyrgulopsis nana
00111 00111 01011 11011 00001 00001 00000 00000 00000 01100 10001 10010 0110

Pyrgulopsis neomexicana
10?11 10110 11011 11011 01001 00000 01121 21211 20212 11102 11111 00201 0011

Pyrgulopsis owensensis
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Pyrgulopsis pecosensis
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Pyrgulopsis perturbata
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Pyrgulopsis pilsbryana
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Pyrgulopsis pisteri
00111 00111 10011 11011 00001 000?3 ?3000 00000 00121 00102 00021 10010 0110

Pyrgulopsis robusta
10111 10111 10011 11001 20001 00000 01000 32111 20112 00102 00001 10000 0011

Pyrgulopsis roswellensis
10111 10111 10011 11011 00001 00000 01122 00011 20112 01002 00101 00001 0011

Pyrgulopsis simplex
10111 10100 10011 11011 00001 00000 02000 00000 00000 01100 10001 10010 0110

Pyrgulopsis sola
10111 10110 10011 11011 00001 10000 10000 00000 00000 01102 00201 10010 0110

Pyrgulopsis stearnsiana
10111 10110 10011 11011 00001 00002 02000 00000 00000 01102 00001 10010 0110

Pyrgulopsis thermalis
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Pyrgulopsis thompsoni
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Pyrgulopsis trivialis
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Pyrgulopsis wongi
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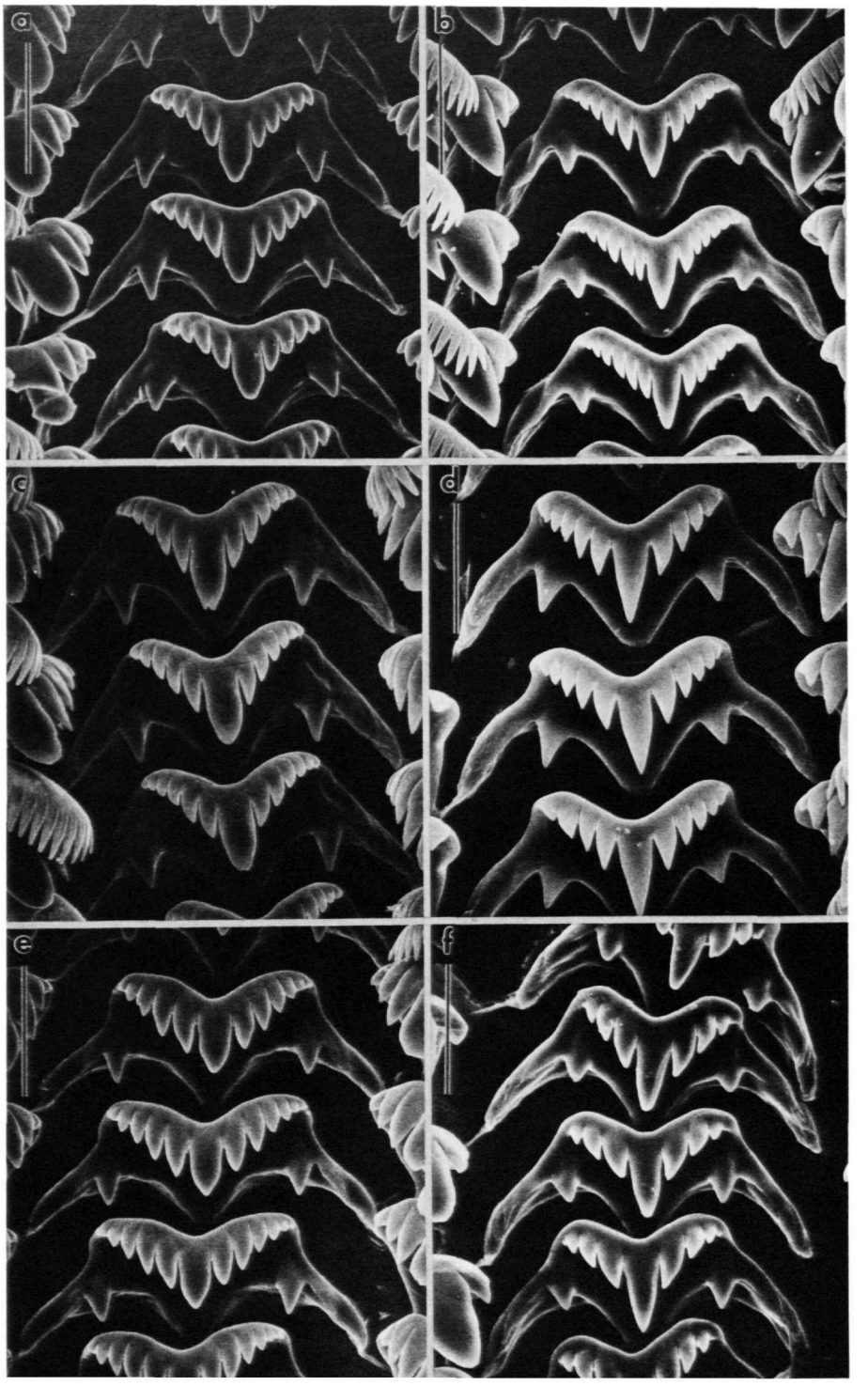

FIGURE 32.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. aardahli*, USNM 857951 (bar = 20 μm); *b*, *P. amargosae*, USNM 857972 (bar = 13.6 μm); *c*, *P. archimedis*, USNM 874190 (scale as in *b*); *d*, *P. arizonae*, USNM 847226 (bar = 8.6 μm); *e*, *P. avernalis*, USNM 874003 (bar = 17.6 μm); *f*, *P. bacchus*, USNM 847203 (bar = 15.0 μm).

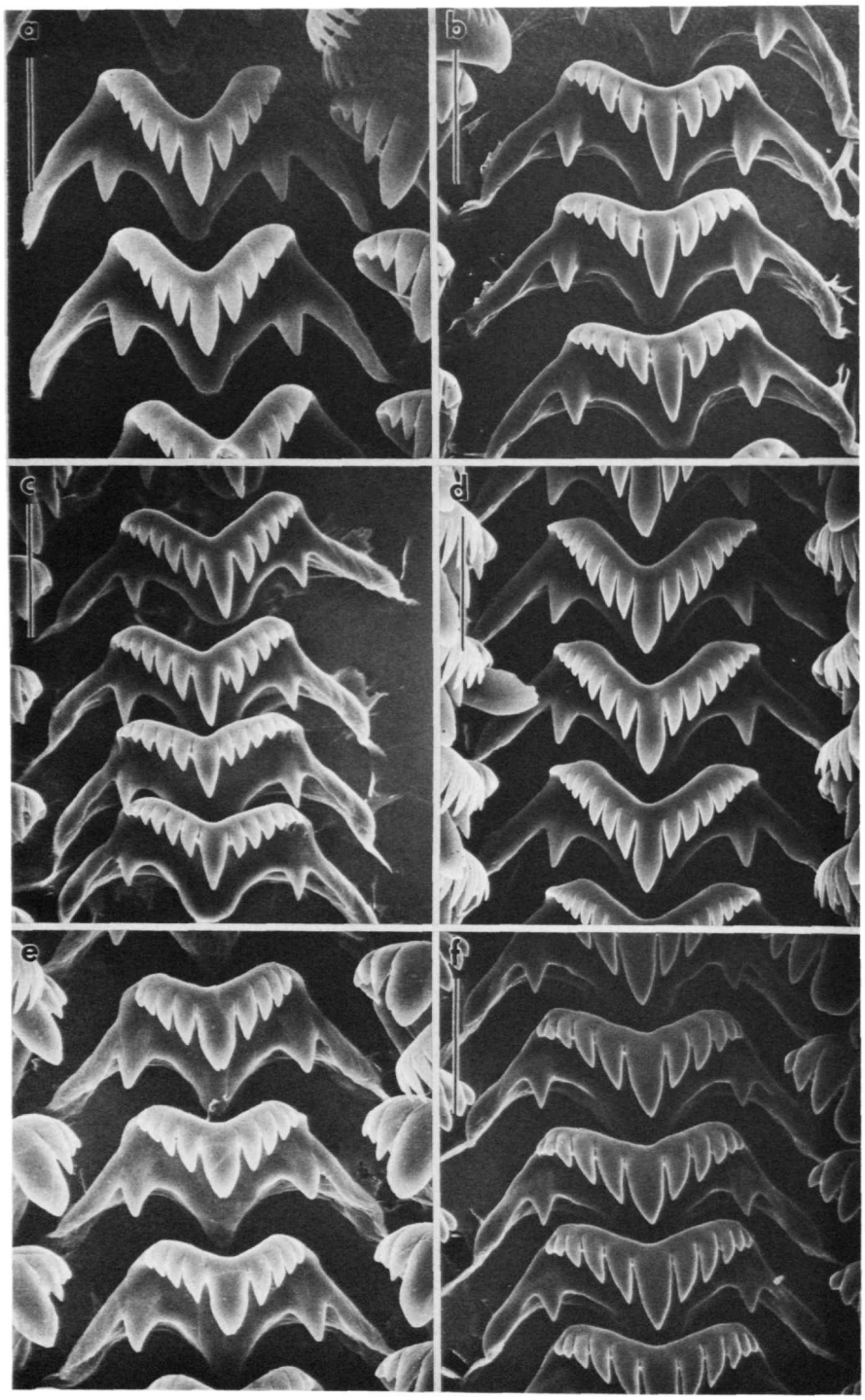

FIGURE 33.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. bernardina*, USNM 847218 (bar = 6.7 μm); *b*, *P. brandi*, USNM 600499 (bar = 13.6 μm); *c*, *P. bruneauensis*, USNM 860508 (bar = 15.0 μm); *d*, *P. bryantwalkeri*, USNM 858278 (bar = 10.0 μm); *e*, *P. californiensis*, SBMNH uncat. (scale as in *b*); *f*, *P. carinifera*, USNM 874001 (bar = 23.1 μm).

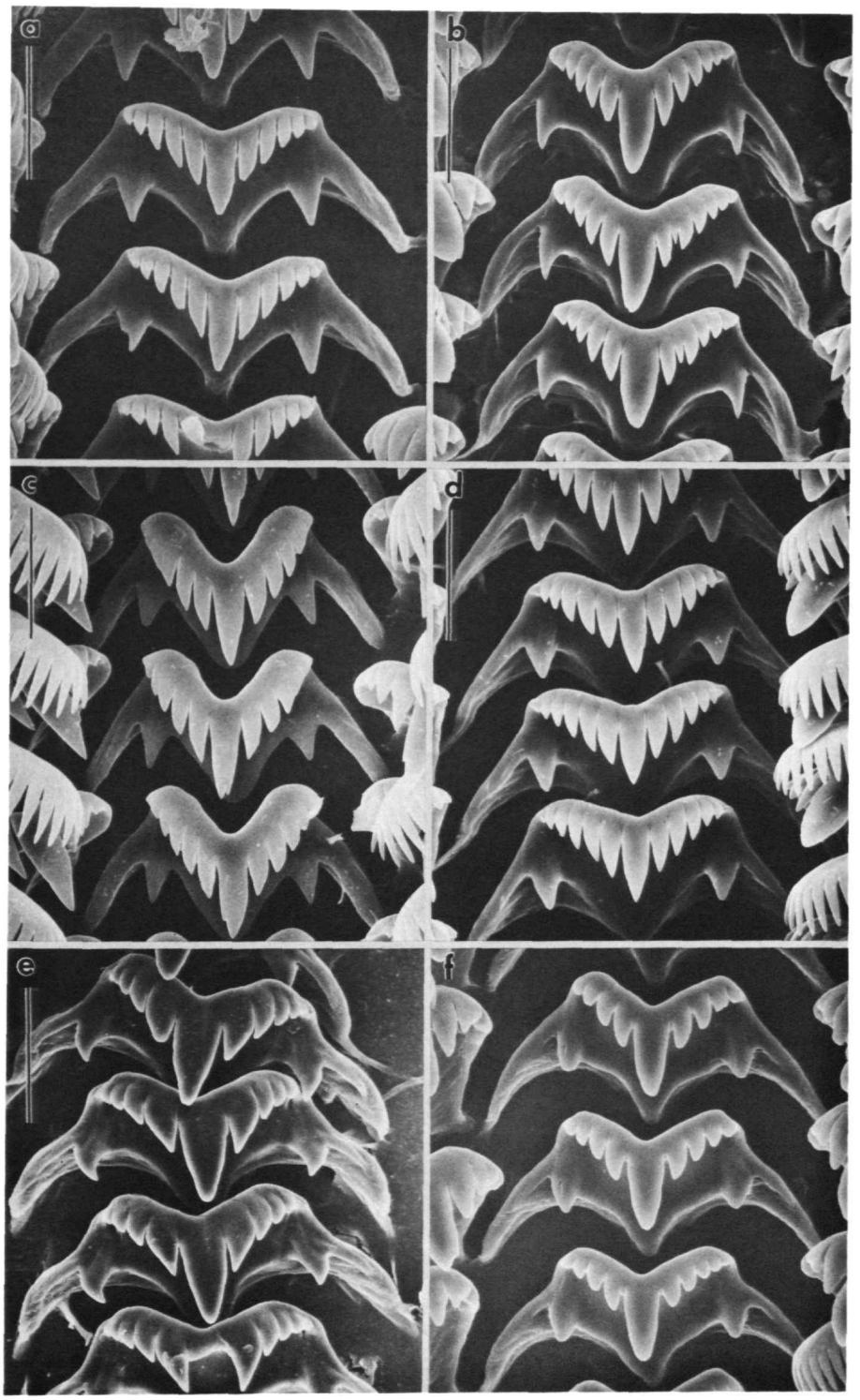

FIGURE 34.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. cedrosensis*, ANSP 141408 (bar = 8.6 µm); *b*, *P. chihuahua*, USNM 873296 (bar = 13.6 µm); *c*, *P. chupaderae*, USNM 873426 (bar = 7.5 µm); *d*, *P. conica*, USNM 847237 (bar = 8.6 µm); *e*, *P. crystalis*, USNM 850370 (bar = 17.6 µm); *f*, *P. davisi*, USNM 873427 (scale as in *b*).

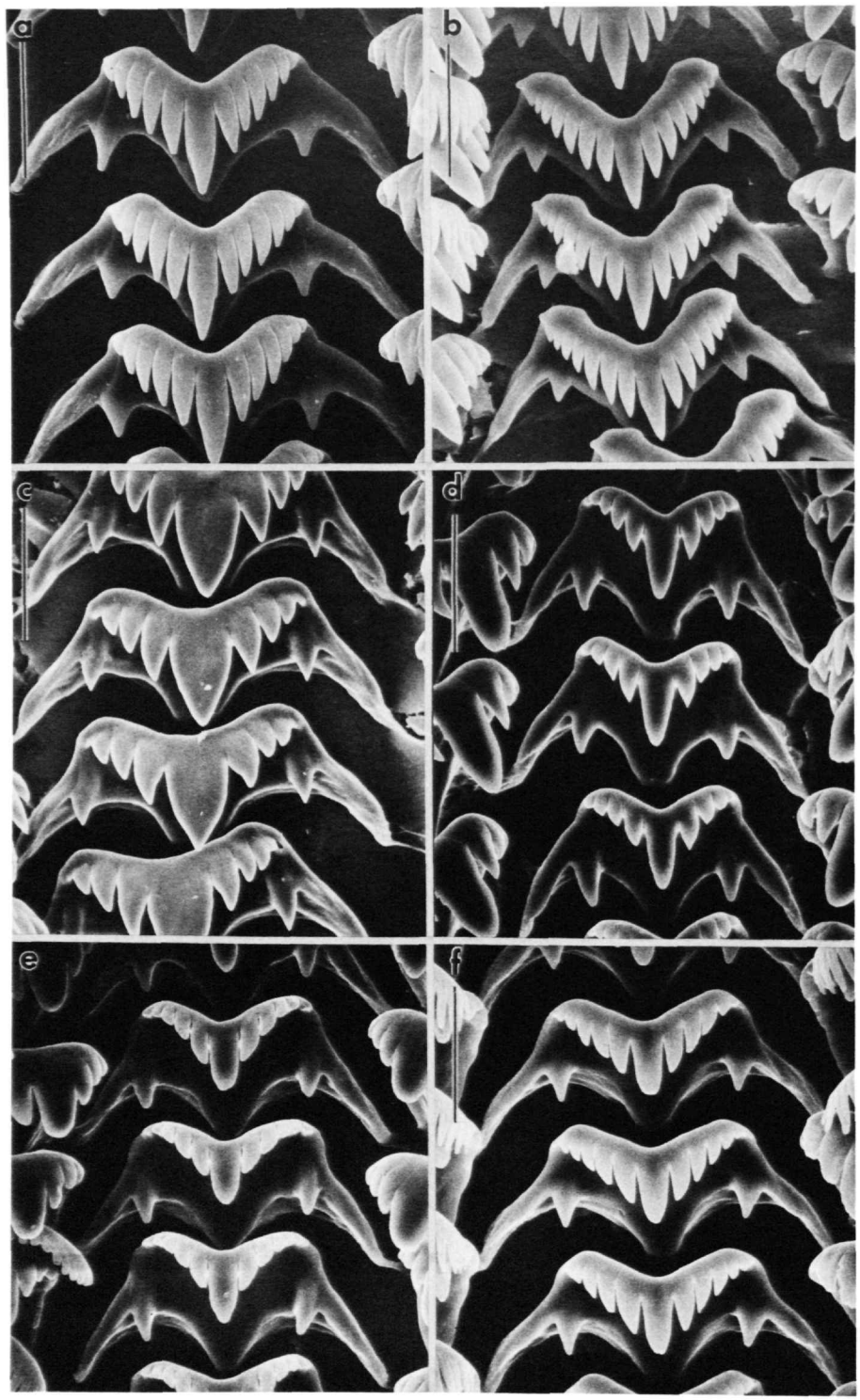

FIGURE 35.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. deserta*, USNM 847202 (bar = 8.6 μm); *b*, *P. erythropoma*, USNM 857864 (bar = 12.0 μm); *c*, *P. fairbanksensis*, USNM 850368 (bar = 20.0 μm); *d*, *P. gilae*, USNM 873211 (bar = 13.6 μm); *e*, *P. giulianii*, USNM 857974 (scale as in *d*); *f*, *P. glandulosa*, USNM 847205 (bar = 10.0 μm).

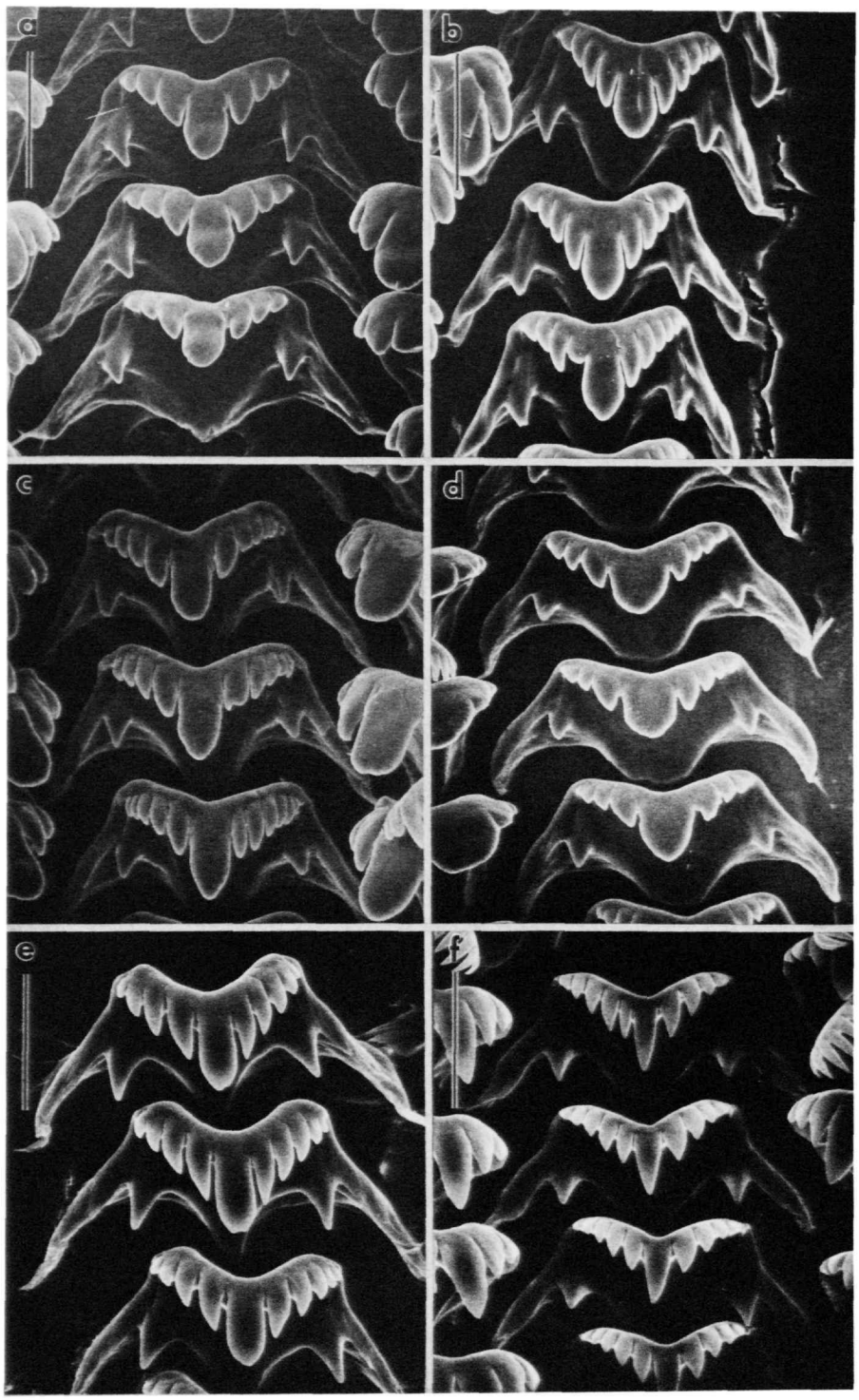

FIGURE 36.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. hendersoni*, USNM 874386 (bar = 27 µm); *b*, *P. idahoensis*, USNM 874698 (bar = 20.0 µm); *c*, *P. intermedia*, USNM 874195 (scale as in *b*); *d*, *P. isolata*, USNM 850366 (scale as in *b*); *e*, *P. kolobensis*, USNM 847249 (bar = 13.6 µm); *f*, *P. longinqua*, USNM 874059 (bar = 10.0 µm).

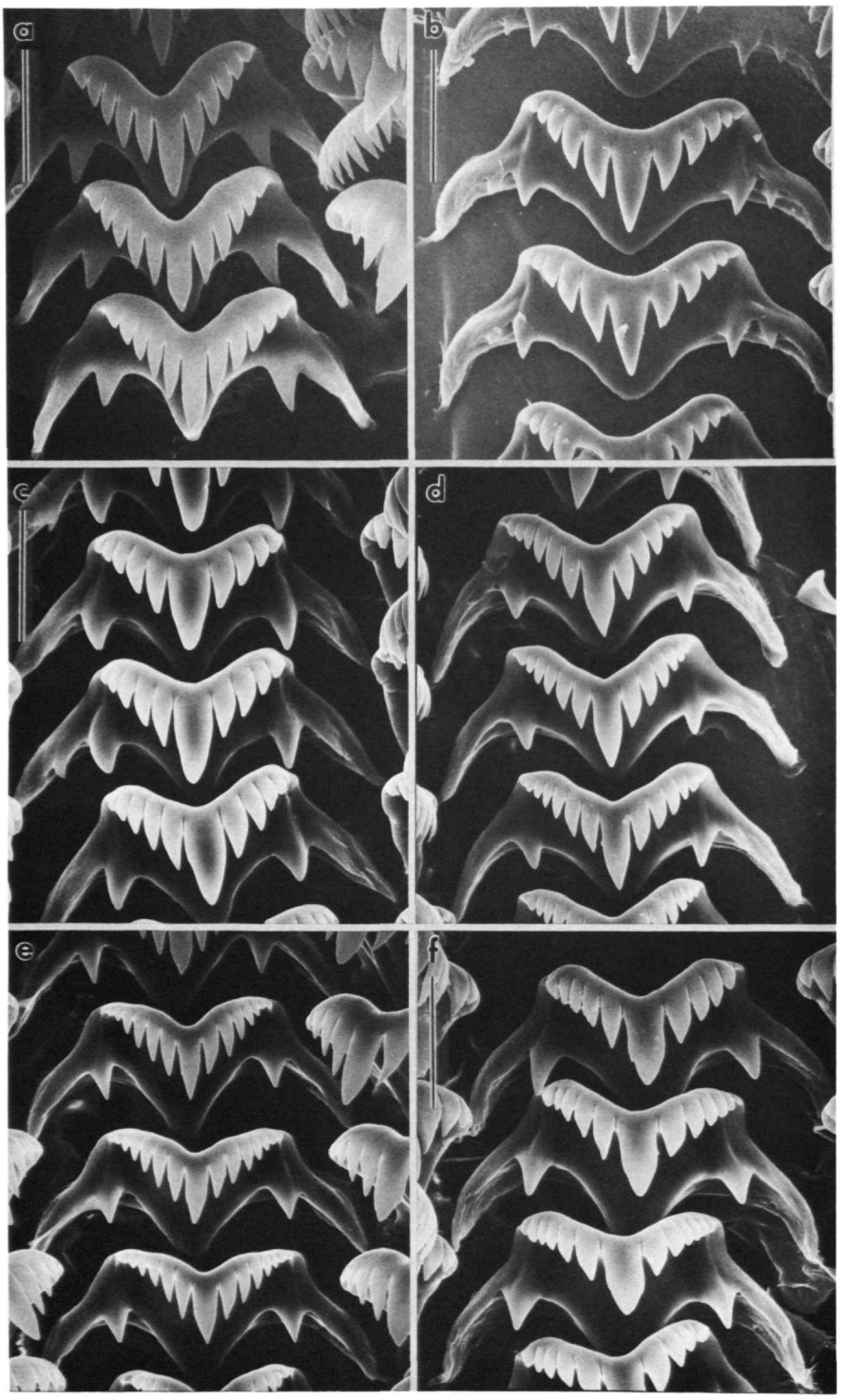

FIGURE 37.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. manantiali*, ANSP A98881 (bar = 5.5 µm); *b*, *P. merriami*, USNM 873395 (bar = 15.0 µm); *c*, *P. metcalfi*, USNM 873301 (bar = 10.0 µm); *d*, *P. micrococcus*, USNM 847246 (scale as in *c*); *e*, *P. montezumensis*, USNM 847233 (scale as in *c*); *f*, *P. morrisoni*, USNM 847231 (bar = 8.6 µm).

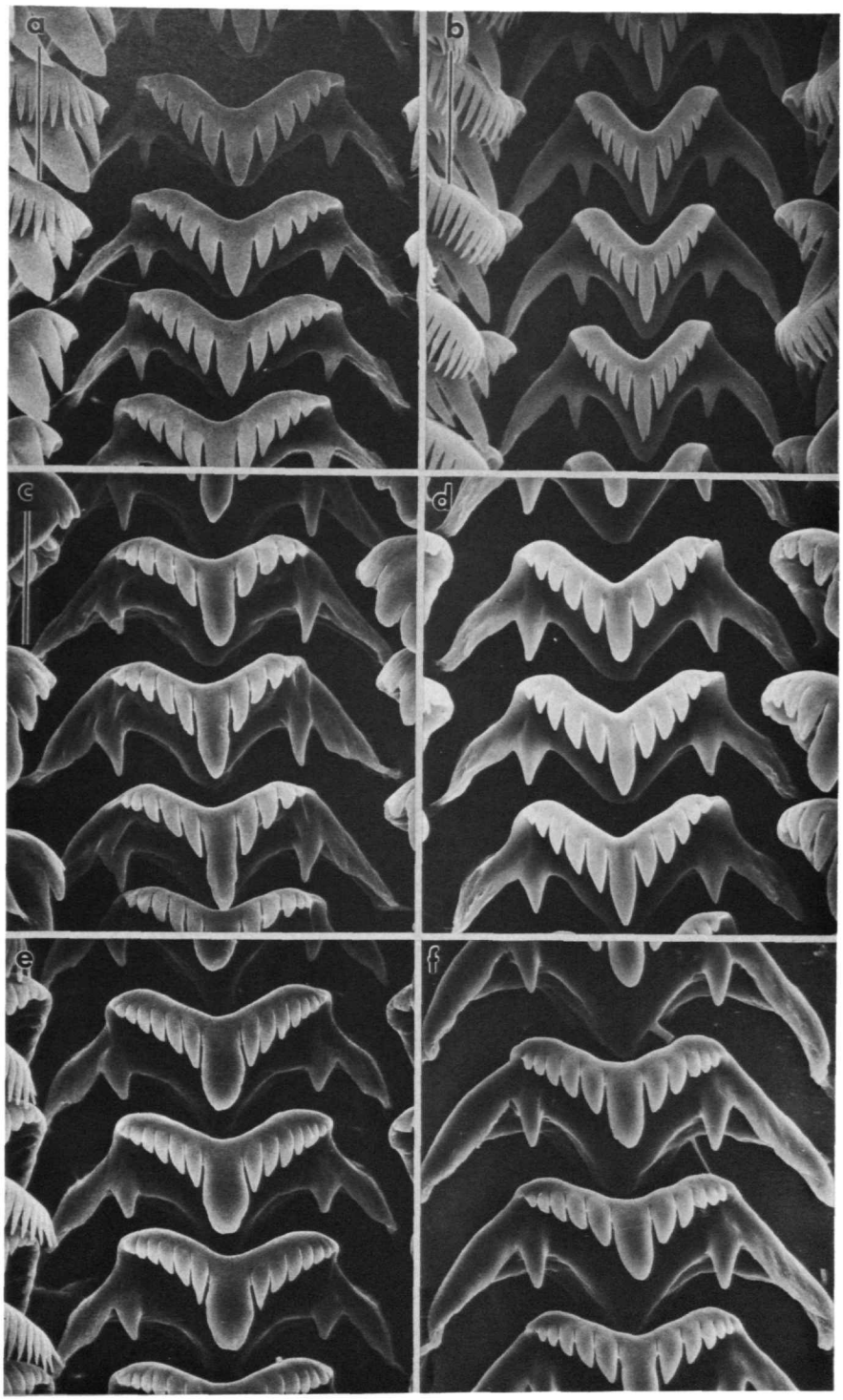

FIGURE 38.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. nanus*, USNM 850354 (bar = 15.0 µm); *b*, *P. neomexicana*, USNM 873227 (bar = 8.6 µm); *c*, *P. nevadensis*, USNM 63992 (bar = 13.6 µm); *d*, *P. owensensis*, USNM 857955 (scale as in *b*); *e*, *P. pecosensis*, USNM 873131 (scale as in *c*); *f*, *P. perturbata*, USNM 857990 (scale as in *c*).

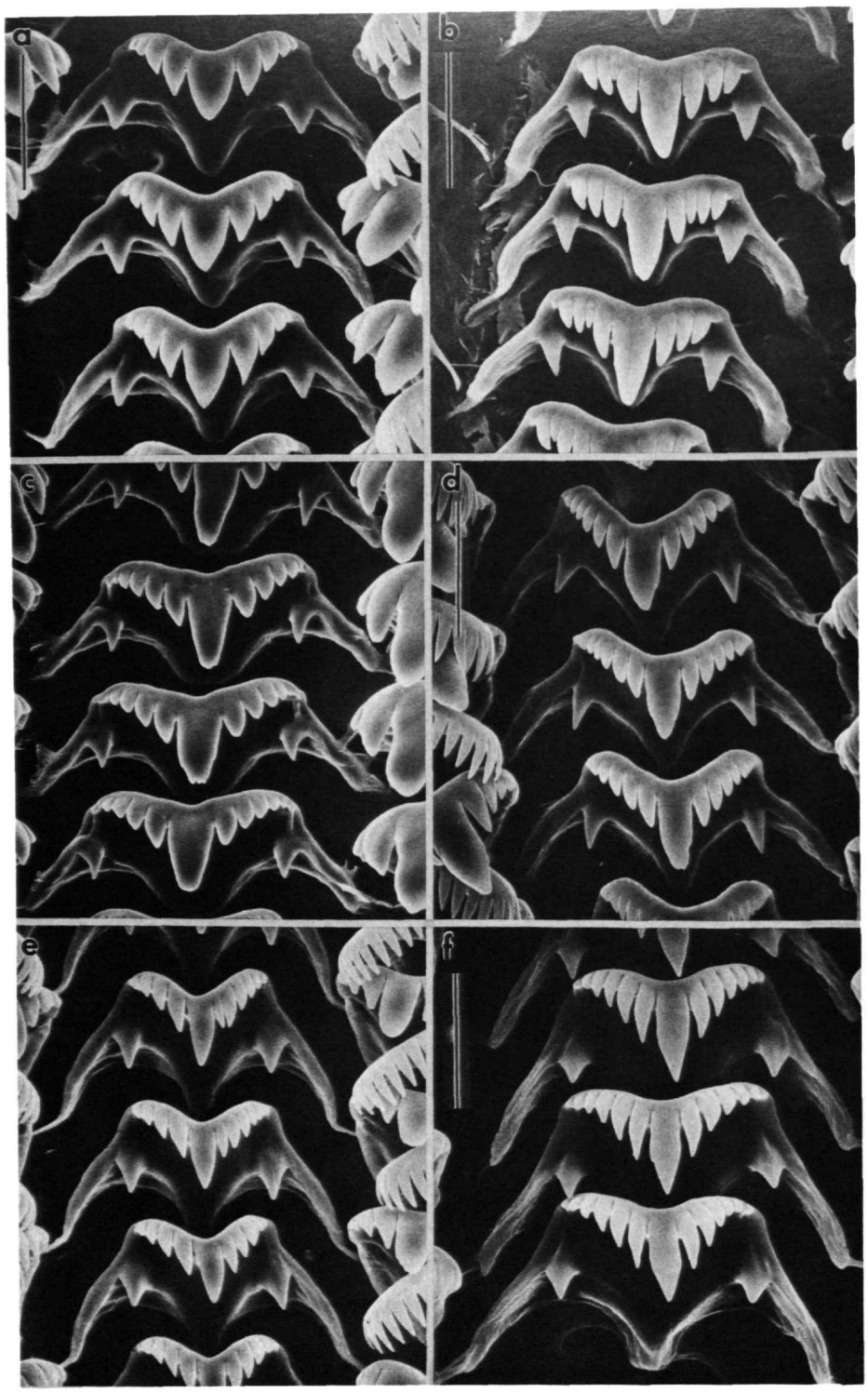

FIGURE 39.—Central radular teeth of western *Pyrgulopsis*: *a*, *P. pilsbryana*, USNM 858279 (bar = 13.6 µm); *b*, *P. pisteri*, USNM 850364 (bar = 20.0 µm); *c*, *P. robusta*, USNM 874185 (scale as in *b*); *d*, *P. roswellensis*, USNM 873132 (bar = 12.0 µm); *e*, *P. simplex*, USNM 847236 (scale as in *d*); *f*, *P. sola*, USNM 850290 (bar = 7.5 µm).

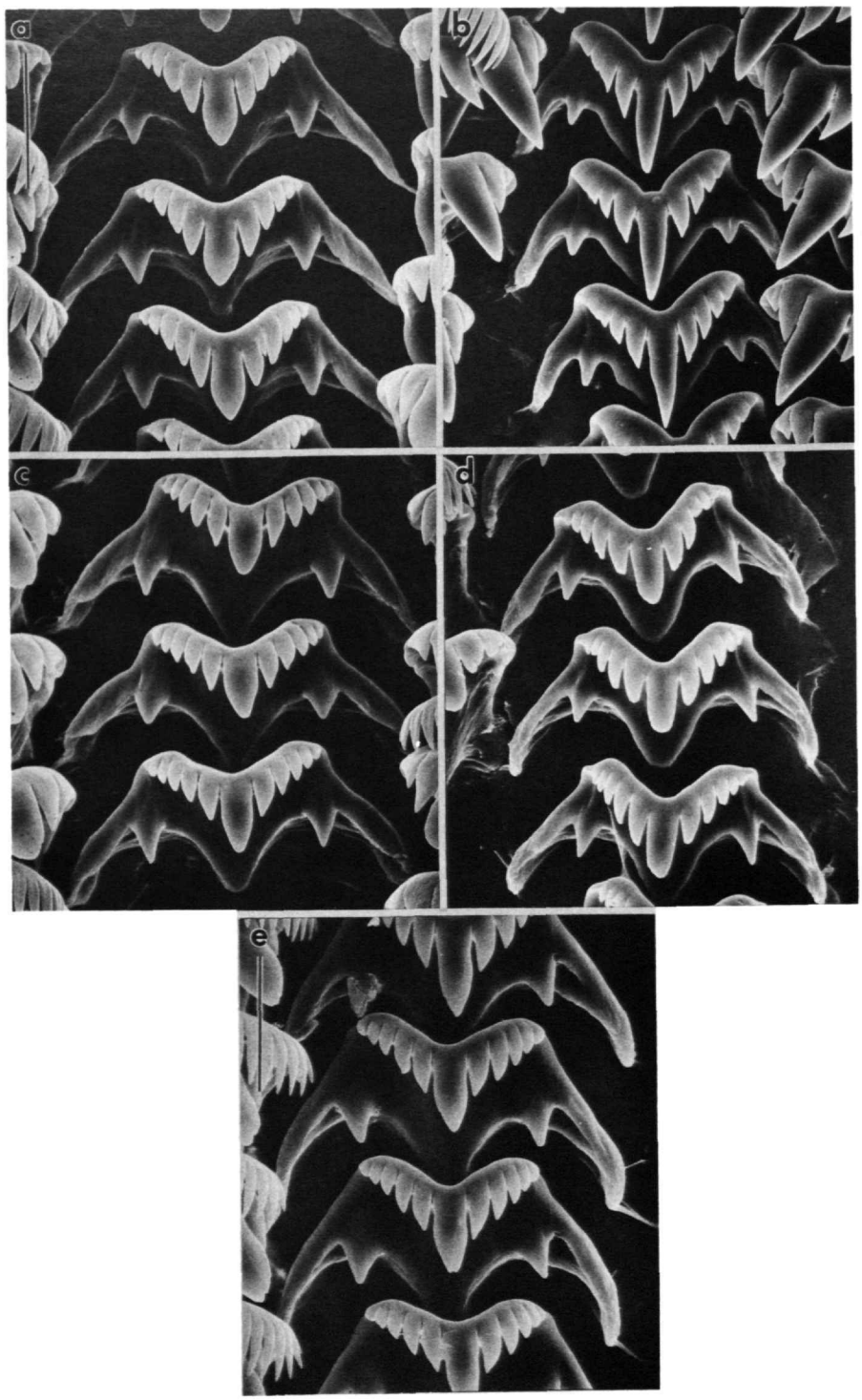

FIGURE 40.—Central radular teeth of western *Pyrgulopsis: a, P. stearnsiana*, USNM 873366 (bar = 12.0 μm); *b, P. thermalis*, USNM 873250 (scale as in *a*); *c, P. thompsoni*, USNM 847238 (scale as in *a*); *d, P. trivialis*, USNM 847234 (scale as in *a*); *e, P. wongi*, USNM 857941 (bar = 10.0 μm).

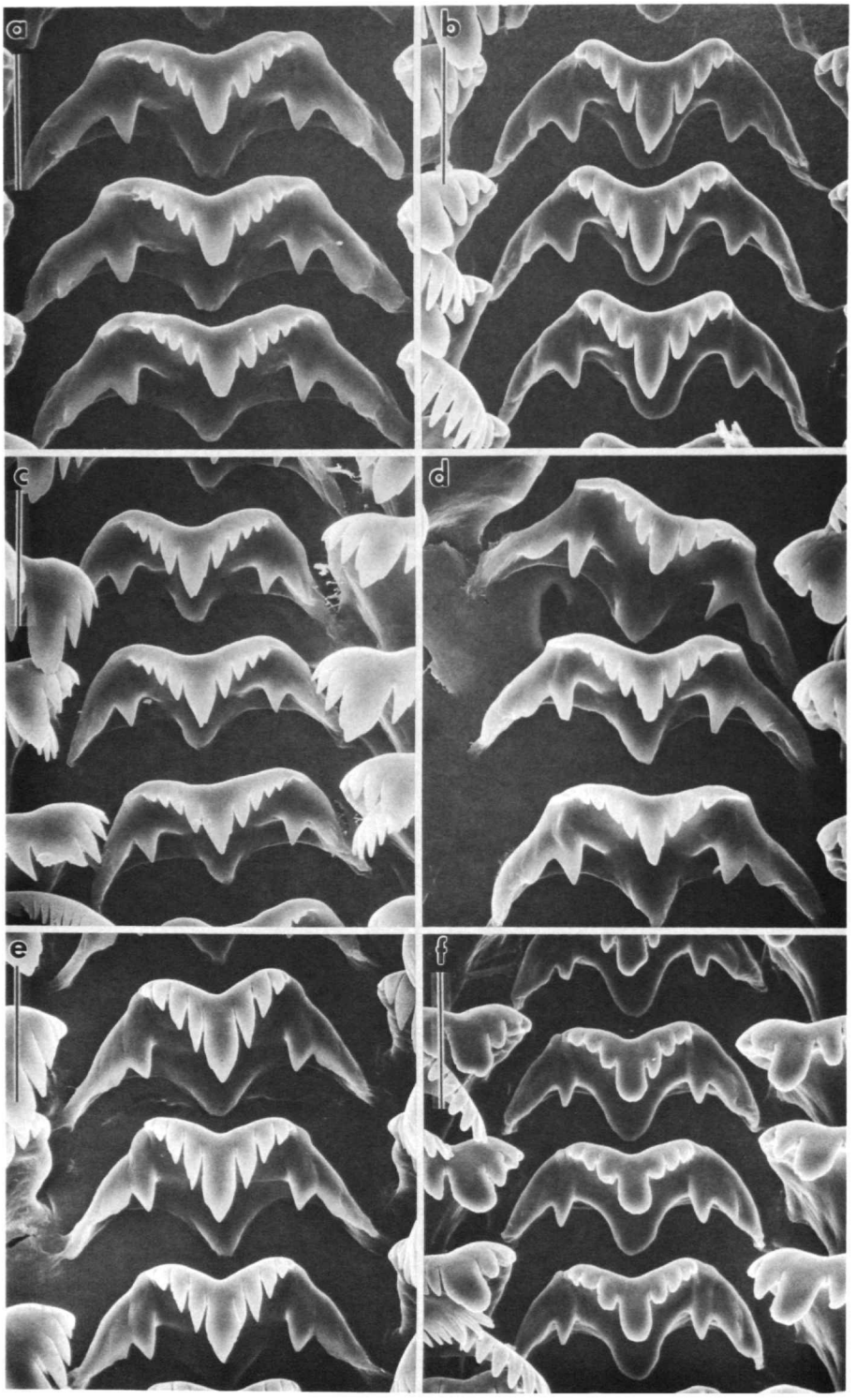

FIGURE 41.—Central radular teeth of eastern *Pyrgulopsis*: *a*, *P. agarhecta*, UF 193381 (bar = 8.6 µm); *b*, *P. arga*, UF uncat. (bar = 15.0 µm); *c*, *P. castor*, UF 189470 (bar = 10.0 µm); *d*, *P. halcyon*, UF 146698 (scale as in *a*); *e*, *P. letsoni*, UF 91727 (bar = 13.6 µm); *f*, *P. lustrica*, UF 22227 (bar = 17.6 µm).

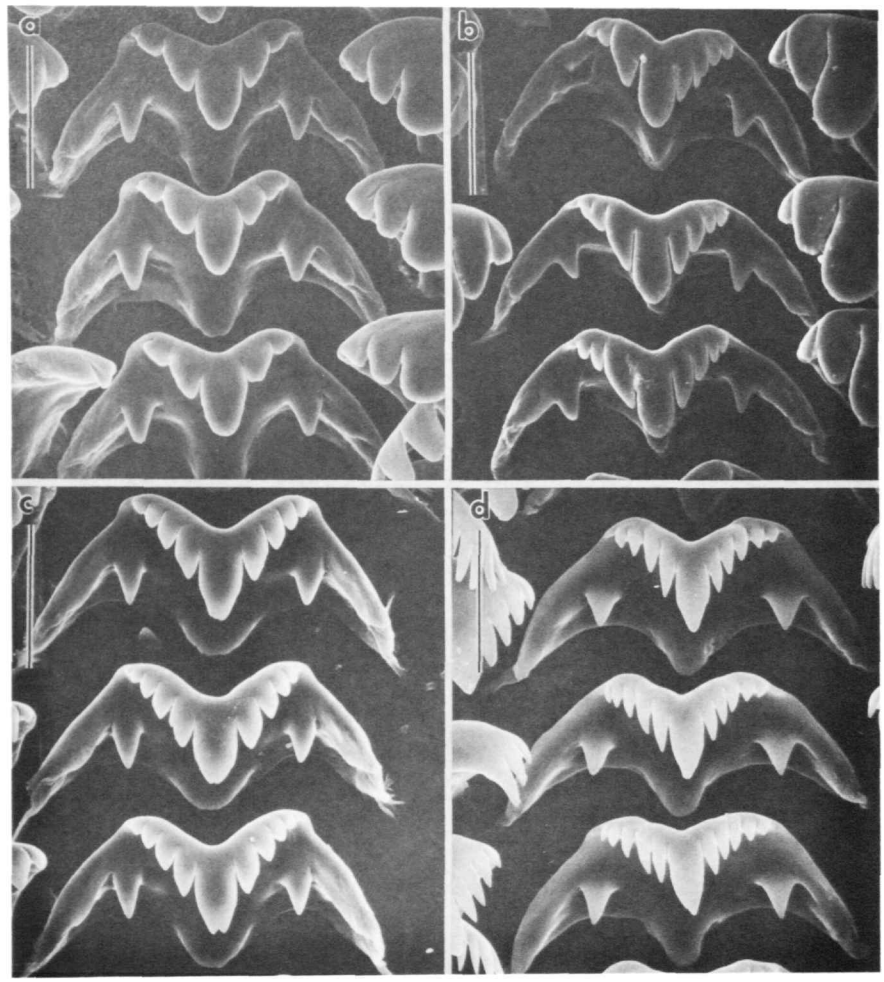

FIGURE 42.—Central radular teeth of eastern *Pyrgulopsis*: *a*, *P. ogmorphaphe*, UF 146697 (bar = 15.0 μm); *b*, *P. olivacea*, USNM 528038 (bar = 17.6 μm); *c*, *P. pachyta*, UF 189462 (bar = 12.0 μm); *d*, *P. scalariformis*, UF 91726 (bar = 8.6 μm).

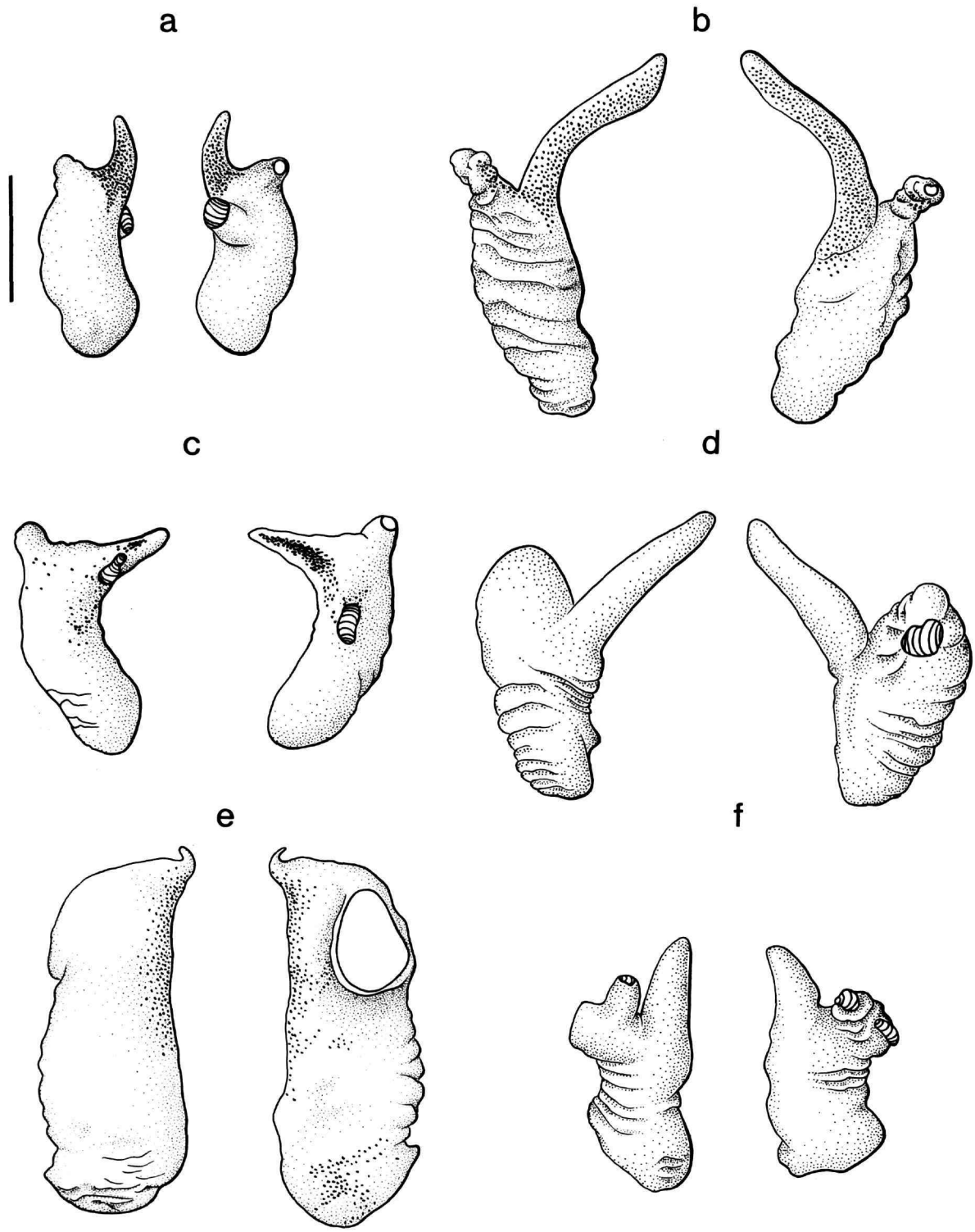

FIGURE 43.—Penes of western *Pyrgulopsis*: *a*, *P. aardahli*, USNM 857951; *b*, *P. amargosae*, USNM 857972; *c*, *P. archimedis*, USNM 874342; *d*, *P. arizonae*, USNM 847226; *e*, *P. avernalis*, USNM 874000; *f*, *P. bacchus*, USNM 847203. (Bar = 0.5 mm.)

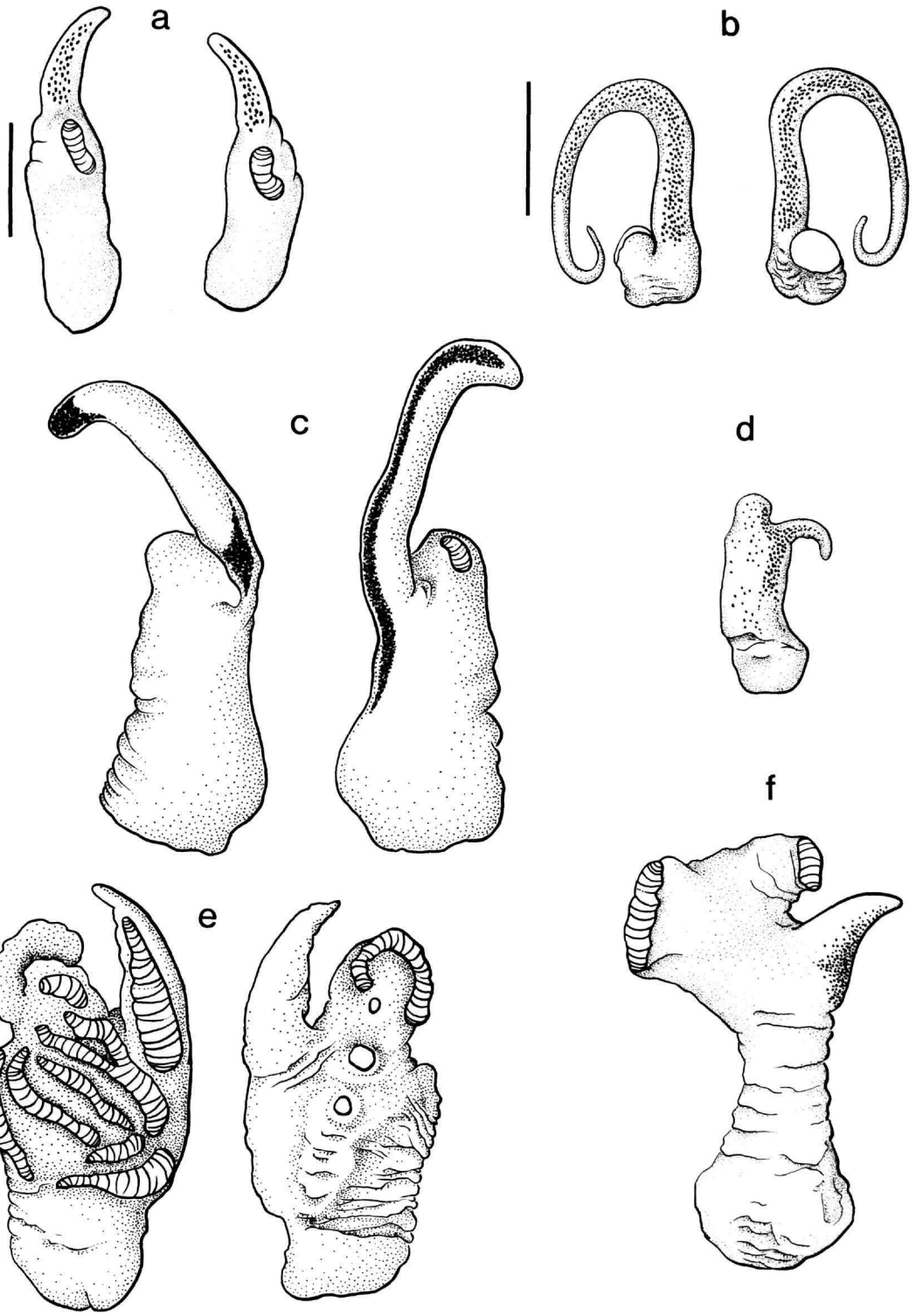

FIGURE 44.—Penes of western *Pyrgulopsis*: *a*, *P. bernardina*, USNM 847218 (bar = 0.25 mm); *b*, *P. brandi*, USNM 600499 (bar = 0.5 mm); *c*, *P. bruneauensis*, USNM 860509; *d*, *P. bryantwalkeri*, USNM 858278; *e*, *P. californiensis*, SBMNH uncat.; *f*, *P. carinifera*, USNM 874005. (Scale for *c*–*e* as in *b*.)

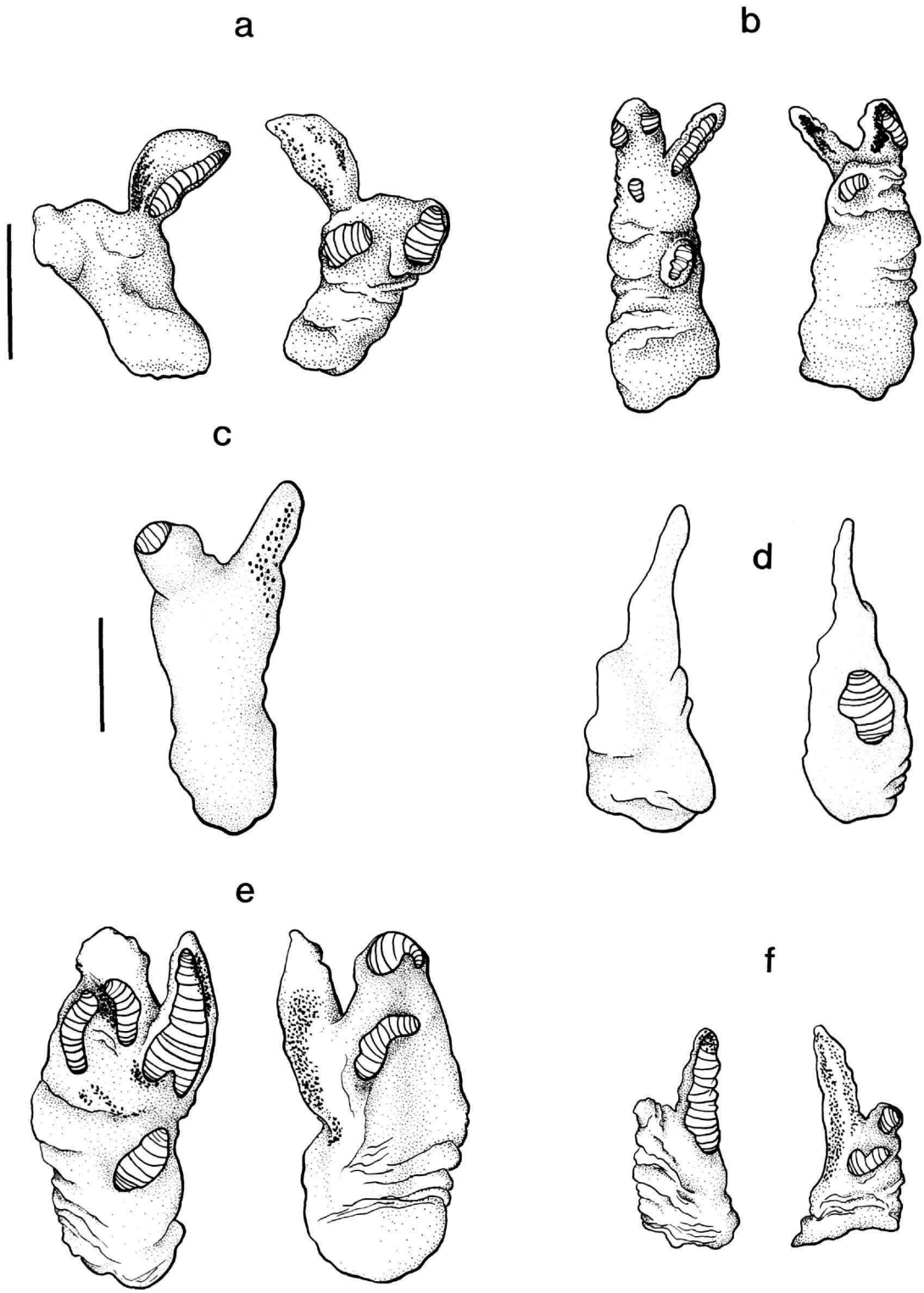

FIGURE 45.—Penes of western *Pyrgulopsis*: *a*, *P. chihuahua*, USNM 873296 (bar = 0.5 mm); *b*, *P. chupaderae*, USNM 873246; *c*, *P. conica*, USNM 847236 (bar = 0.25 mm); *d*, *P. crystalis*, USNM 850369; *e*, *P. davisi*, USNM 873427; *f*, *P. deserta*, USNM 847202. (Scale for *b* and *d*-*f* as for *a*.)

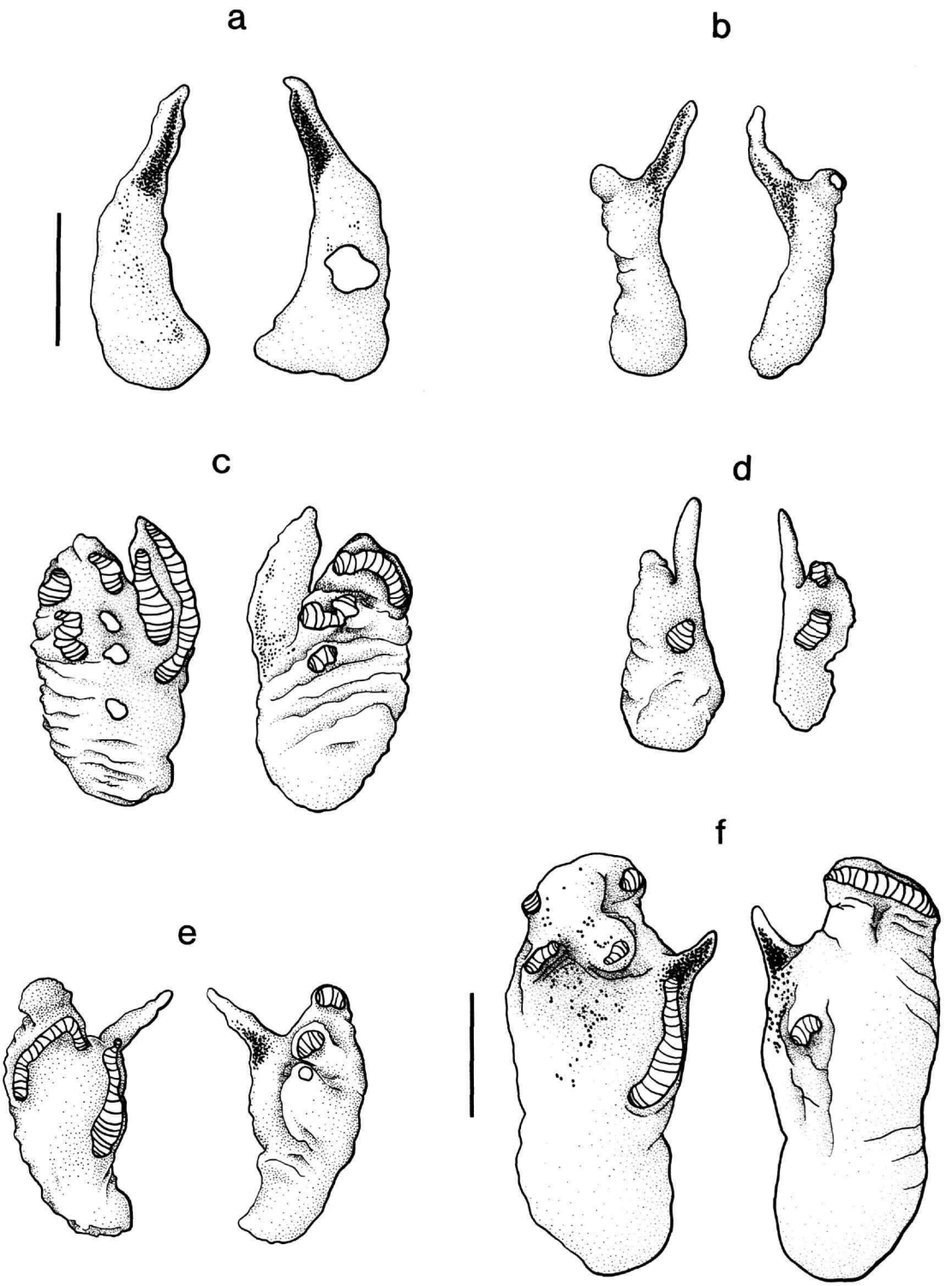

FIGURE 46.—Penes of western *Pyrgulopsis: a, P. erythropoma*, USNM 857862 (bar = 0.5 mm); *b, P. fairbanksensis*, USNM 850367; *c, P. gilae*, USNM 873211; *d, P. giulianii*, SBMNH uncat.; *e, P. glandulosa*, USNM 847205; *f, P. hendersoni*, USNM 874386 (bar = 1.0 mm). (Scale for *b–e* as for *a*.)

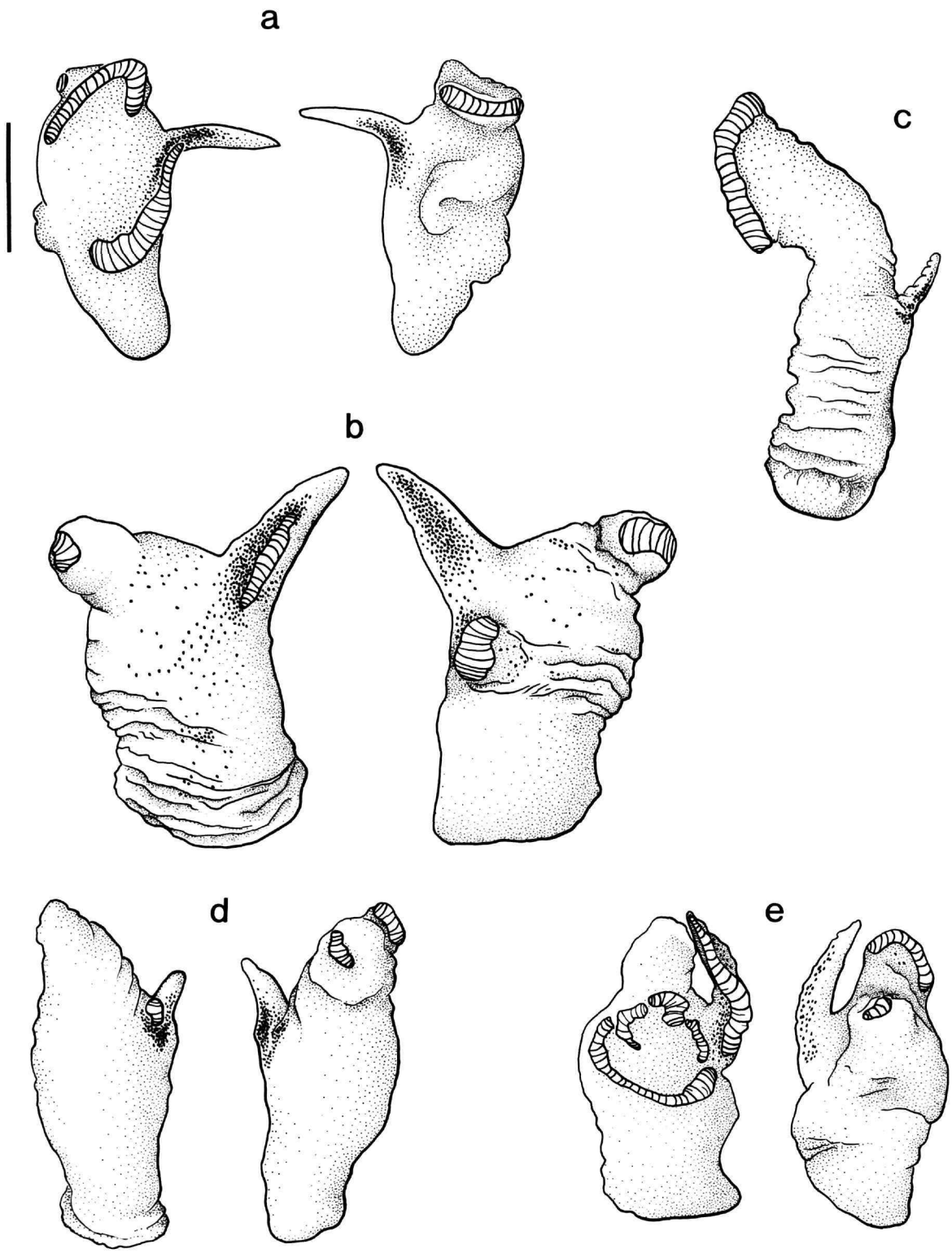

FIGURE 47.—Penes of western *Pyrgulopsis*: *a*, *P. idahoensis*, USNM 874698; *b*, *P. intermedia*, USNM 874195; *c*, *P. isolata*, USNM 850366; *d*, *P. kolobensis*, USNM 847249; *e*, *P. longinqua*, USNM 874104. (Bar = 0.5 mm.)

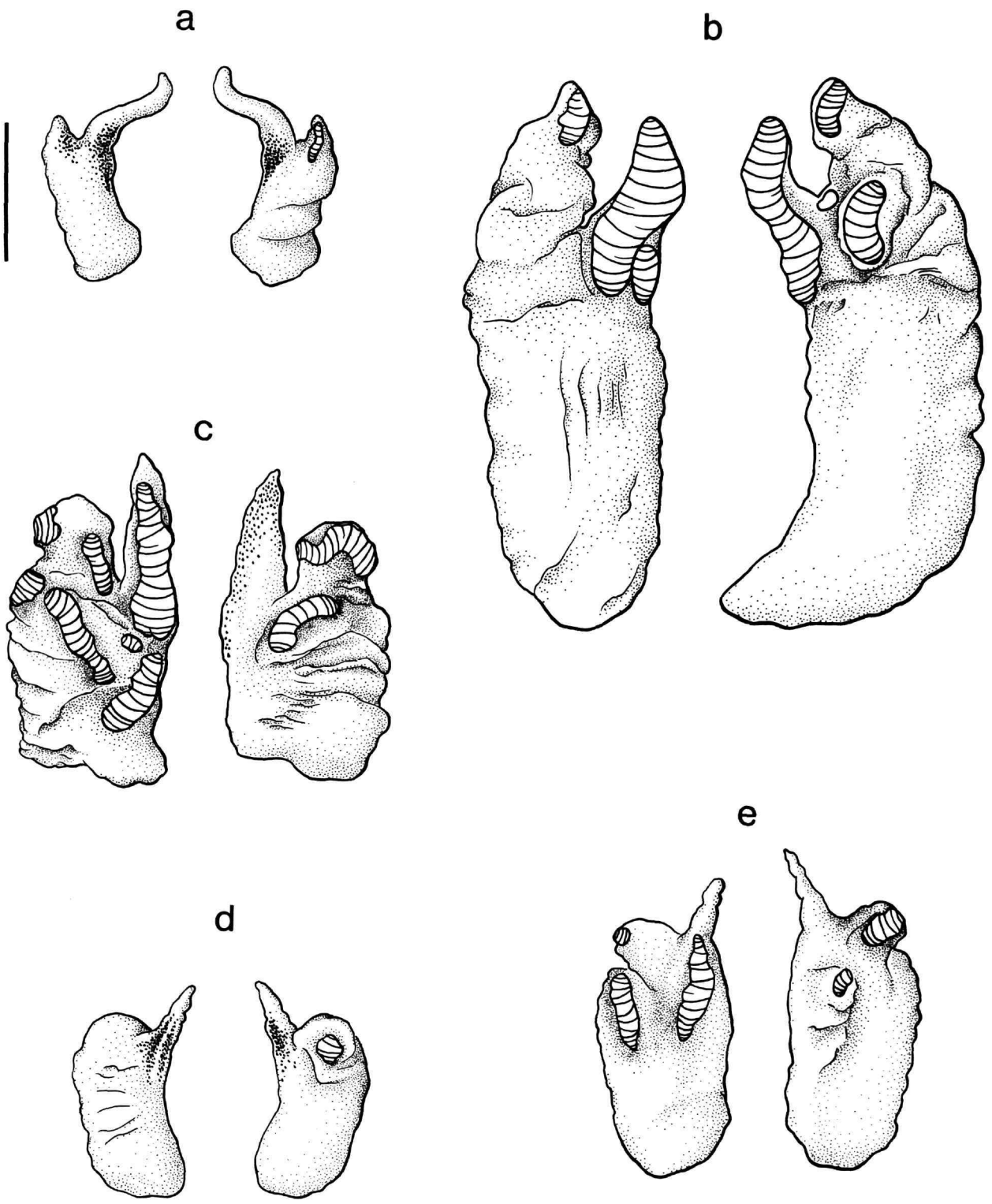

FIGURE 48.—Penes of western *Pyrgulopsis*: *a*, *P. manantiali*, ANSP A98881; *b*, *P. merriami*, USNM 873395; *c*, *P. metcalfi*, USNM 873301; *d*, *P. micrococcus*, USNM 850297; *e*, *P. montezumensis*, USNM 847233. (Bar = 0.5 mm.)

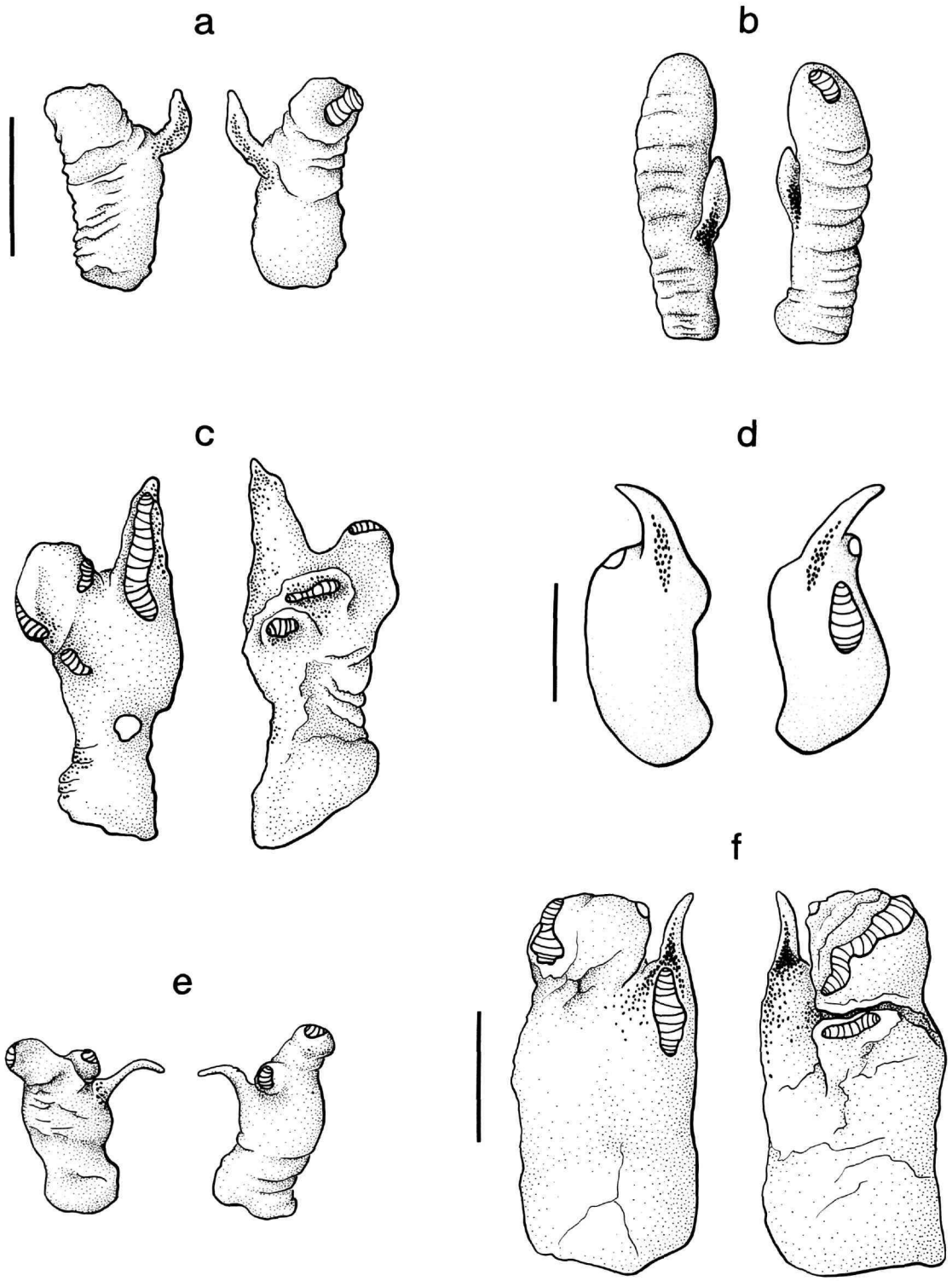

FIGURE 49.—Penes of western *Pyrgulopsis*: *a*, *P. morrisoni*, USNM 847231 (bar = 0.5 mm); *b*, *P. nanus*, USNM 850356; *c*, *P. neomexicana*, USNM 873227; *d*, *P. nevadensis*, USNM 63992 (bar = 0.25 mm); *e*, *P. owensensis*, USNM 857955; *f*, *P. pecosensis*, USNM 857131 (bar = 0.5 mm). (Scale for *b*,*c*,*d*,*e* as for *a*.)

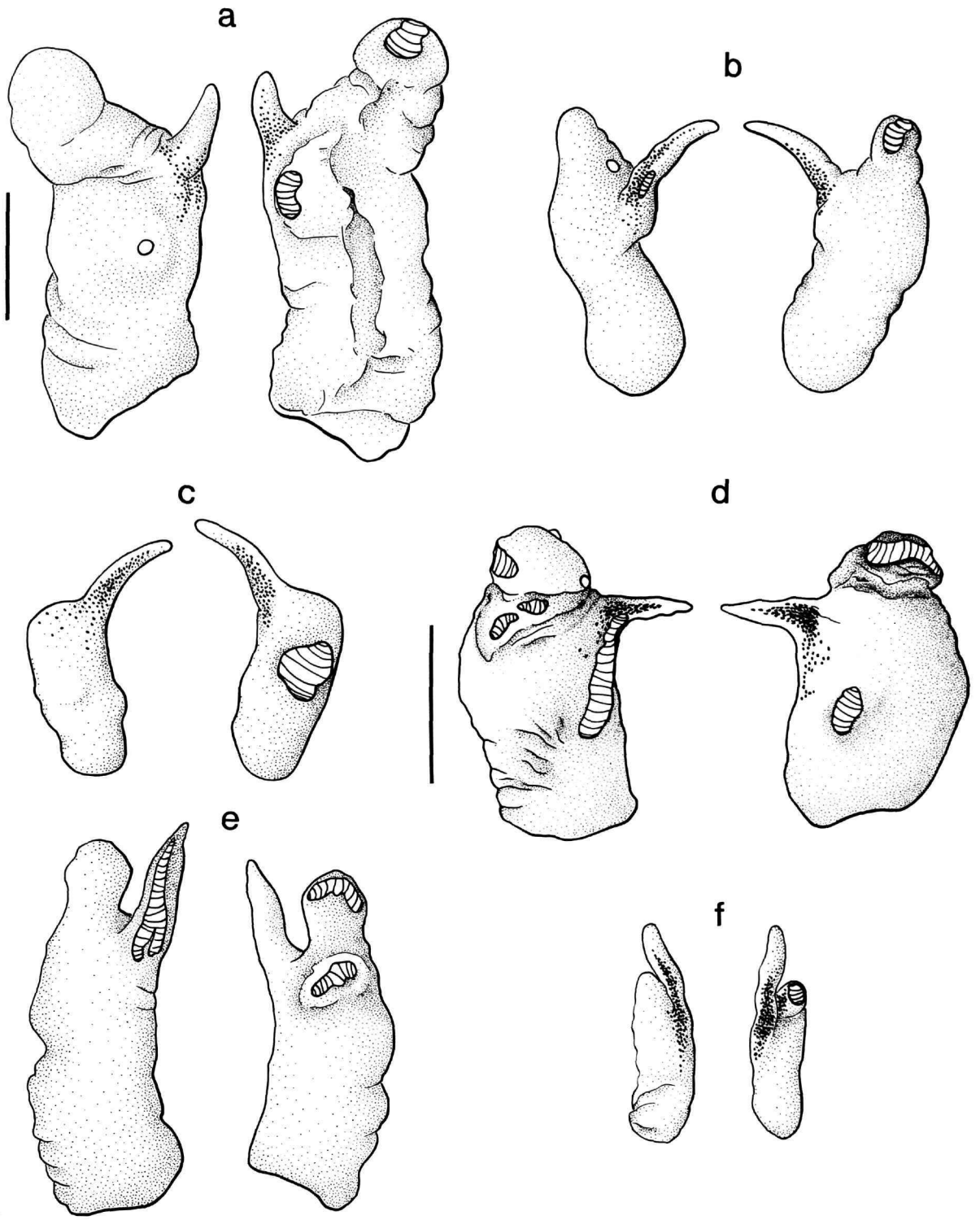

FIGURE 50.—Penes of western *Pyrgulopsis: a, P. perturbata*, USNM 857990 (bar = 0.5 mm); *b, P. pilsbryana*, USNM 858279; *c, P. pisteri*, USNM 850363; *d, P. robusta* (bar = 1.0 mm); *e, P. roswellensis*, USNM 873132; *f, P. simplex*, USNM 847230. (Scale for *b,c,e,f* as for *a*.)

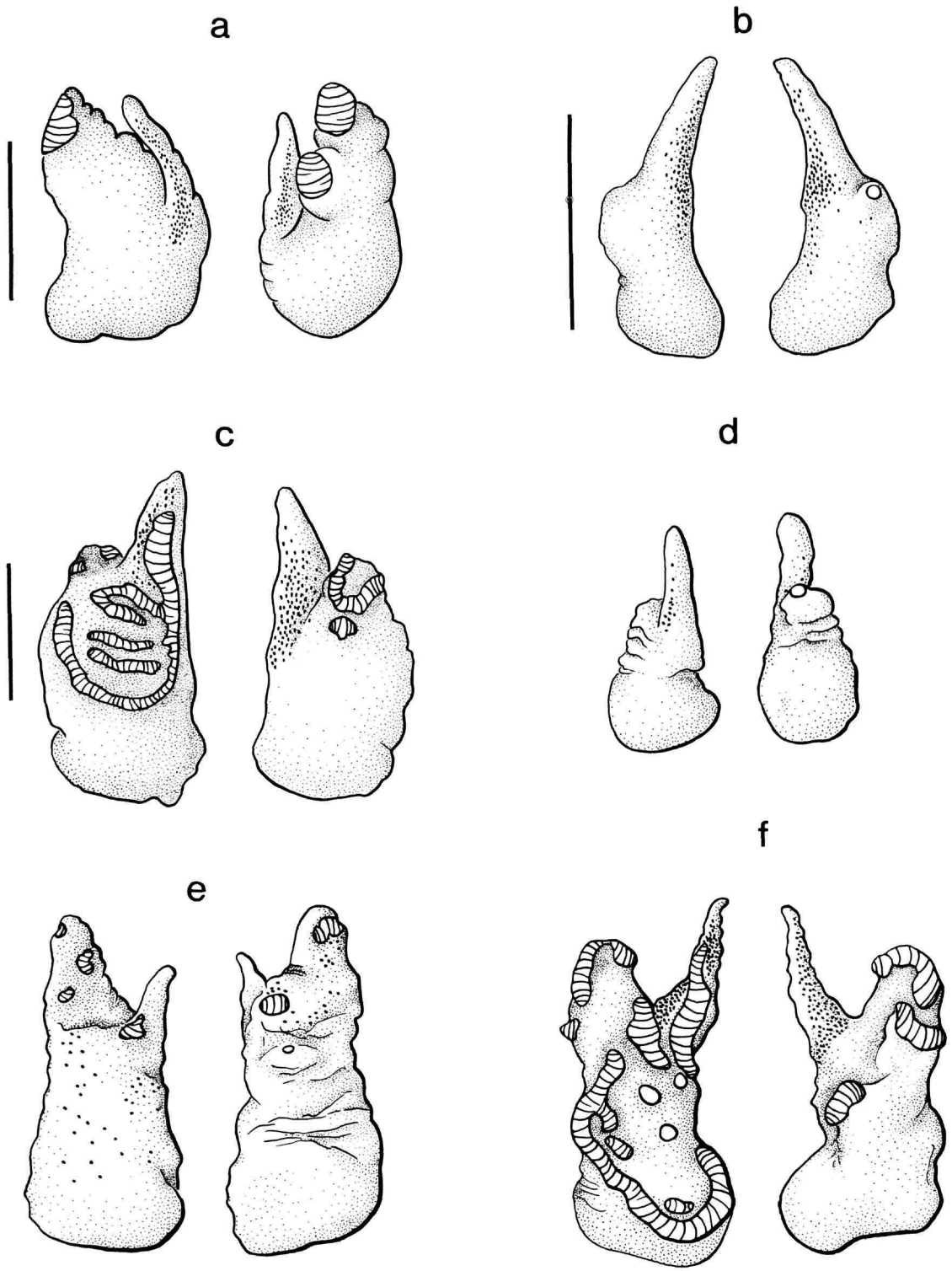

FIGURE 51.—Penes of western *Pyrgulopsis*: *a*, *P. sola*, USNM 850290 (bar = 0.25 mm); *b*, *P. stearnsiana*, USNM 874181 (bar = 1.0 mm); *c*, *P. thermalis*, USNM 873250 (bar = 0.5 mm); *d*, *P. thompsoni*, USNM 847238; *e*, *P. trivialis*, USNM 847234; *f*, *P. wongi*, USNM 857941. (Scale for *d*–*f* as for *b*.)

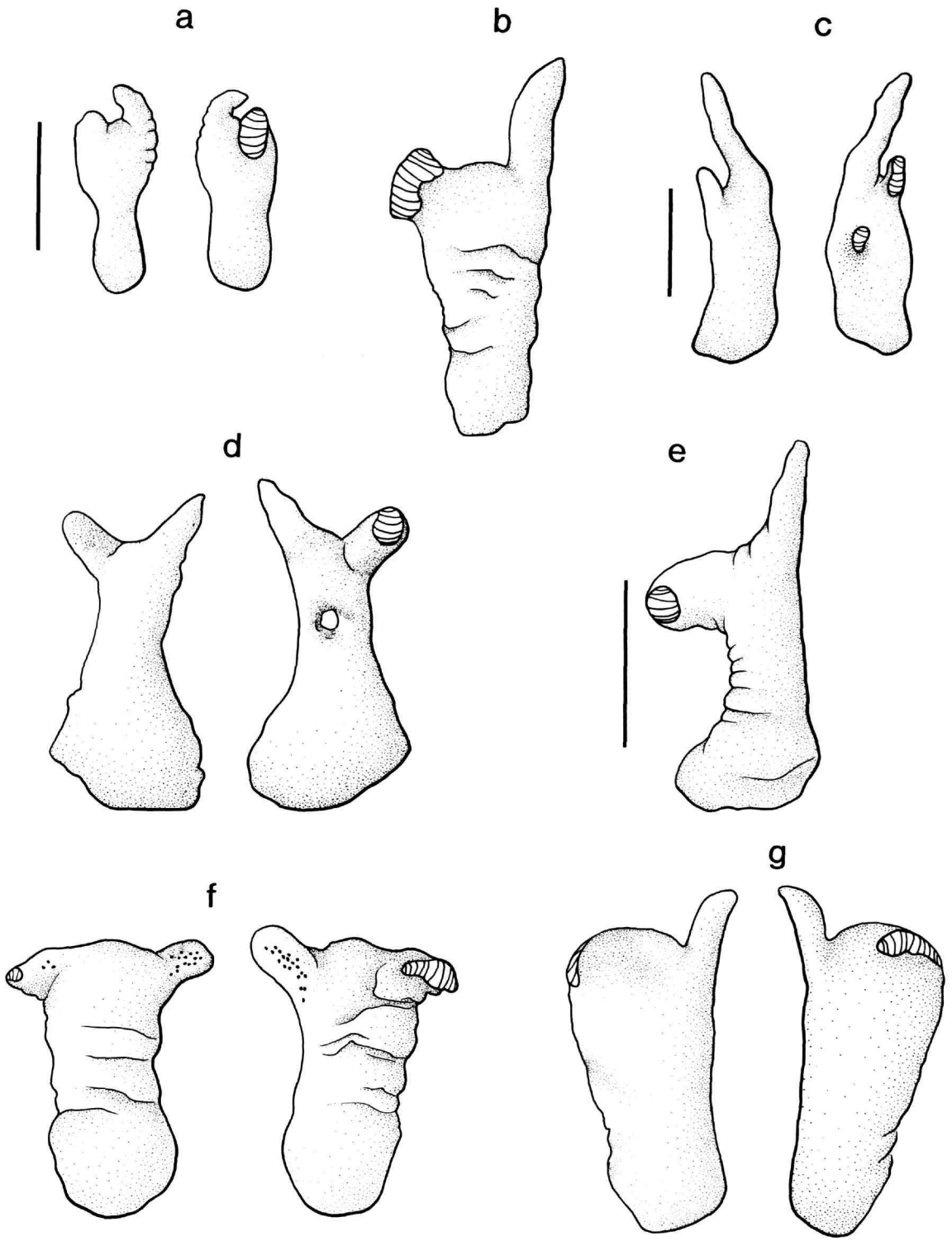

FIGURE 52.—Penes of eastern *Pyrgulopsis*: *a*, *P. agarhecta*, UF 189468 (bar = 0.5 mm); *b*, *P. arga*, UF uncat.; *c*, *P. castor*, UF 189470 (bar = 0.25 mm); *d*, *P. halcyon*, UF 146698; *e*, *P. letsoni*, UF 91727 (bar = 0.5 mm); *f*, *P. lustrica*, UF 22227; *g*, *P. ogmorphaphe*, UF 146697. (Scale for *b*,*d*,*f*,*g* as for *a*.)

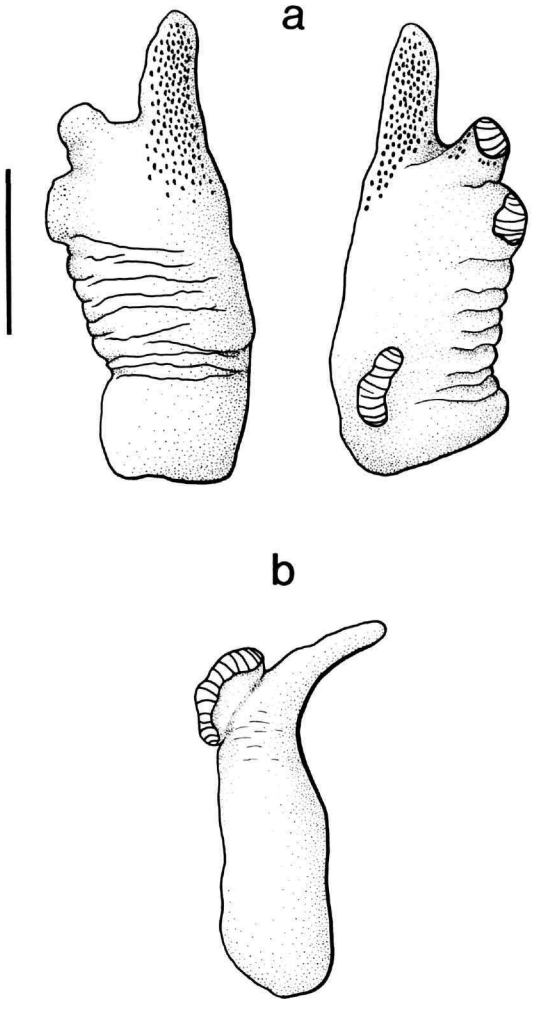

FIGURE 53.—Penes of eastern *Pyrgulopsis: a, P. pachyta*, UF 189462 (bar = 0.5 mm); *b, P. scalariformis*, UF 91726 (scale as for *a*).

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