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SPRINGSNAILS (GASTROPODA: HYDROBIIDAE) OF ASH MEADOWS, AMARGOSA BASIN, CALIFORNIA–NEVADA

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Abstract.—Aquatic snails of the family Hydrobiidae were sampled from numerous springs in Ash Meadows, California–Nevada, during 1985–1986. The fauna of this lush oasis is represented by at least three lineages and composed of 11 species in two genera, *Pyrgulopsis* Call and Pilsbry, 1886 and *Tryonia* Stimpson, 1865. Nine species are described herein as new. Nine species are locally endemic (three are restricted to single springs), while the remaining two are restricted to Amargosa River drainage. *Pyrgulopsis* species are well-differentiated in shell and anatomical features (mostly penial morphology), whereas *Tryonia* species show marked variation only in the former.

Stepwise discriminant analyses were done using shell morphometric data from three separate species groups in Ash Meadows. Separate analyses were done using standard measurements and Raupian parameters as a local test of their effectiveness in discriminating between closely related forms. Classification was uniformly high (86–93%) when the former data set was used, supporting taxonomy presented herein. Raupian parameters produced less successful classifications (48–71%), probably due to absence of shape diversity among similar-shelled members of species groups considered.

Ash Meadows springsnails parallel local fishes in having affinities with taxa from the Death Valley System and Colorado River drainages. Distributional evidence suggests that local differentiation of snails has primarily occurred within narrow ranges of altitude, in contrast to patterns documented for local fishes.

Gill-breathing springsnails (Gastropoda: Hydrobiidae) inhabiting the series of intermontane valleys that constitute the Death Valley System (Miller 1943) of southeastern California and southwestern Nevada are poorly known, as they are throughout the arid Southwest. While only two species have been described from this region, based on material collected by the United States Department of Agriculture 1891 Death Valley Expedition, unpublished data (see Taylor 1966, Landye 1973, Hershler 1985, Taylor in Williams et al. 1985) suggest that many additional species are present in the region, with diversity and localization of endemic taxa likely surpassing that documented for the region's well studied ichthyofauna (see Miller 1948, Soltz and Naiman 1978, Minckley et al. 1986).

An ongoing survey of the region's Hydrobiidae was initiated during 1985 by the senior author to obtain material for systematic study of the fauna. Fieldwork during 1985–1986 included survey of all known springs in Ash Meadows, a lush oasis renowned for its highly endemic biota (Beatley 1977, Soltz and Naiman 1978, Reveal 1979). We present herein a description of this faunule as the first of a series of papers on systematics of springsnails of the Death Valley System.

Eleven springsnail species are recognized,

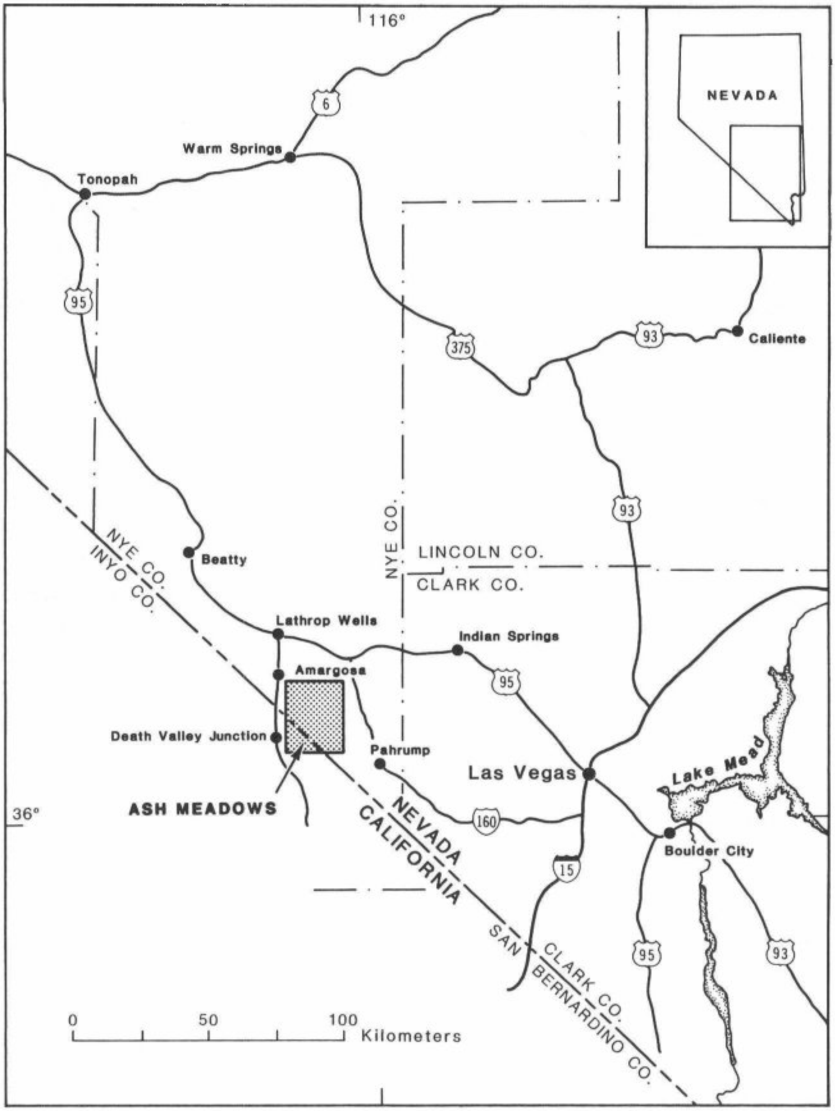


Fig. 1. Map showing location of Ash Meadows, Nevada–California.

representing two genera, *Pyrgulopsis* Call and Pilsbry, 1886, and *Tryonia* Stimpson, 1865. Nine species are new, and nine are endemic to Ash Meadows, three of which are restricted to single springs. Non-endemic forms are restricted to Amargosa River drainage in the eastern part of the Death Valley System. Both total and endemic diversity are striking, clearly cxceeding values for local fishes, and seldom matched by springsnail fauna of similarly sized regions (Taylor 1966). Three lineages are recognized in the fauna, which has affinities with springsnails from Death Valley System and Colorado River drainages. Shell morphometric data were gathered from selected populations and subjected to stepwise discriminant function analyses, with standard measurements and Raupian parameters (Raup 1966) used in separate analyses as a local test of relative effectiveness in discriminating between closely related taxa.

The taxonomic work presented herein is that of Hershler. Other parts of the paper were co-written.

Environmental Setting

Ash Meadows occupies ca. 25,000 ha in Amargosa Desert along the California–Nevada border 60 km W of Death Valley (Fig. 1). Local terrain slopes from neighboring hills of 1300 m elevation southwest to elevation of 560 m in Amargosa Valley. Mean annual temperature is 18.5°C (Dudley and Larson 1976), with summer highs often exceeding 40°C. Local rainfall is scant, averaging ca. 7.0 cm annually (Dudley and Larson 1976).

Shadscale (*Atriplex confertifolia*) and *Haplopapus acaradenius* dominate on xeric soils in Ash Meadows, and salt grass (*Distichlis spicata*) and rushes (*Juncus balticus* and *J. nodosus*) are spread over mesic areas where moisture is maintained by spring discharge or seasonal precipitation. Ash trees (*Fraxinus velutina* var. *coriacea*), mesquite (*Prosopis julifera* and *P. pubescens*), wild grape (*Vitus arizonica*), and salt grass are predominant riparian flora (Beatley 1971). The name "Ash Meadows" refers to local abundance of ash trees (Carlson 1974).

Approximately 50 springs are scattered throughout Ash Meadows, many emerging from old lake beds along a fault-controlled spring line in northern and eastern parts of the area. Springs (Figs. 2–4) vary in size from the large limnocrene, Crystal Pool, ca. 20 m in diameter and discharging 189 liters/sec, to seeps less than 1.0 m across and discharging only a few cc/sec (Dudley and Larson 1976, Garside and Schilling 1979). Total annual spring discharge is estimated as 671 liters/sec (Winograd and Thordarson 1975). Individual spring outflows extend 0.1–10 km before disappearing into soil. Springs are either isolated by expanses of arid terrain, or continuously or seasonally connected by confluence of outflows. Large springs are thermal (28–32°C). Typically lower temperatures of smaller springs may be due to rapid heat loss associated with small discharge. Springs along the eastern part of Ash Meadows are generally warmer than those to the west. All spring water is potable. Total dissolved solids range between 410 and 870 mg/liter (Dudley and Larson 1976), and specific conductivity ranges from 550–800 micromhos/cm (Winograd and Thordarson 1975). Sodium is the dominant cation, with concentrations ranging from 0.18–0.23 meq/liter; followed by magnesium and calcium. Bicarbonate ion is the most abundant anion, with typical concentration of 4.9 meq/liter (Dudley and Larson 1976, Garside and Schilling 1979). Local spring discharge is old water (ca. 10,000 years; Winograd and Thordarson 1975) transported to the area by deep carbonate aquifers draining about 7200 km^2 of southern Nevada (Winograd and Thordarson 1975). While currently endorheic, the area has had past connections with nearby Amargosa River, located a few km to the west (albeit intermittent at this point), which continues to the south before turning back north to terminate in Death Valley.

Ash Meadows is among the most significant endangered aquatic ecosystems in western North America (Williams et al. 1985). Including springsnails described herein, a total of 22 species-group aquatic or riparian taxa are considered local endemics, a total unmatched by any similar-sized area in the United States. Approximately 4000 ha. of the area (16% of total), including most springs, has been perturbed by mining, agriculture, and a municipal development. Establishment of a number of exotic species has further altered the ecosystem, with invading biota including bullfrogs (*Rana catesbeiana*), mosquito fish (*Gambusia affinis*), sailfin mollies (*Poecilia latipinna*), red-rim melania snail (*Melanoides tuberculata*),

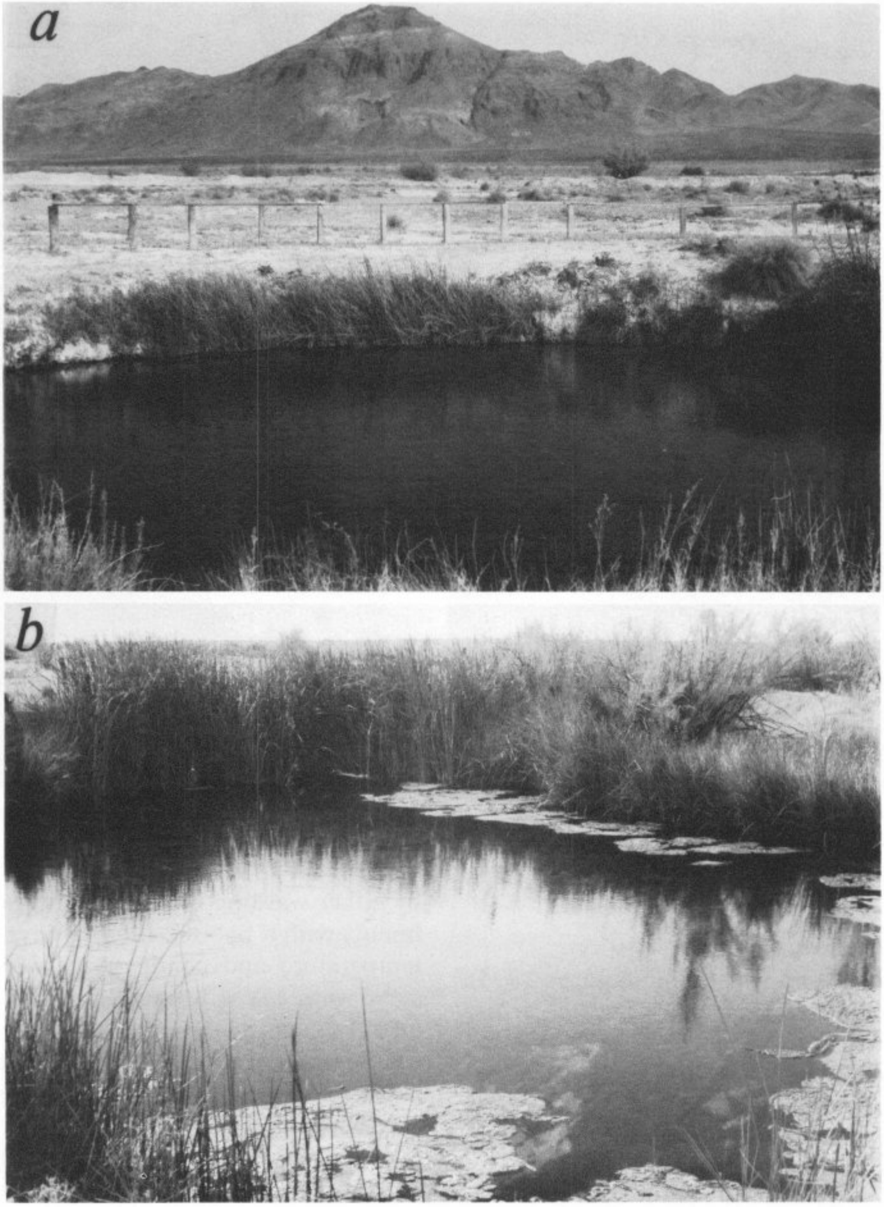


Fig. 2. Photographs of Ash Meadows springs: a, Big Spring (11/8/85); b, Crystal Pool (11/8/85).

crayfish (*Procambarus clarki*), and salt cedar (*Tamarisk* sp.). Perturbation has caused population decline of virtually all endemic taxa, 12 of which are federally listed as threatened or endangered (USDI 1986). All other endemic species, including most springsnails recognized herein, are candidates for future listing (USDI 1985a, b). There is, however, cause for optimism as The Nature Conservancy purchased the area in 1984 and sold it to U.S. Fish and Wildlife Service, which established the Ash Meadows National Wildlife Refuge (Sada and Mozejko 1984).

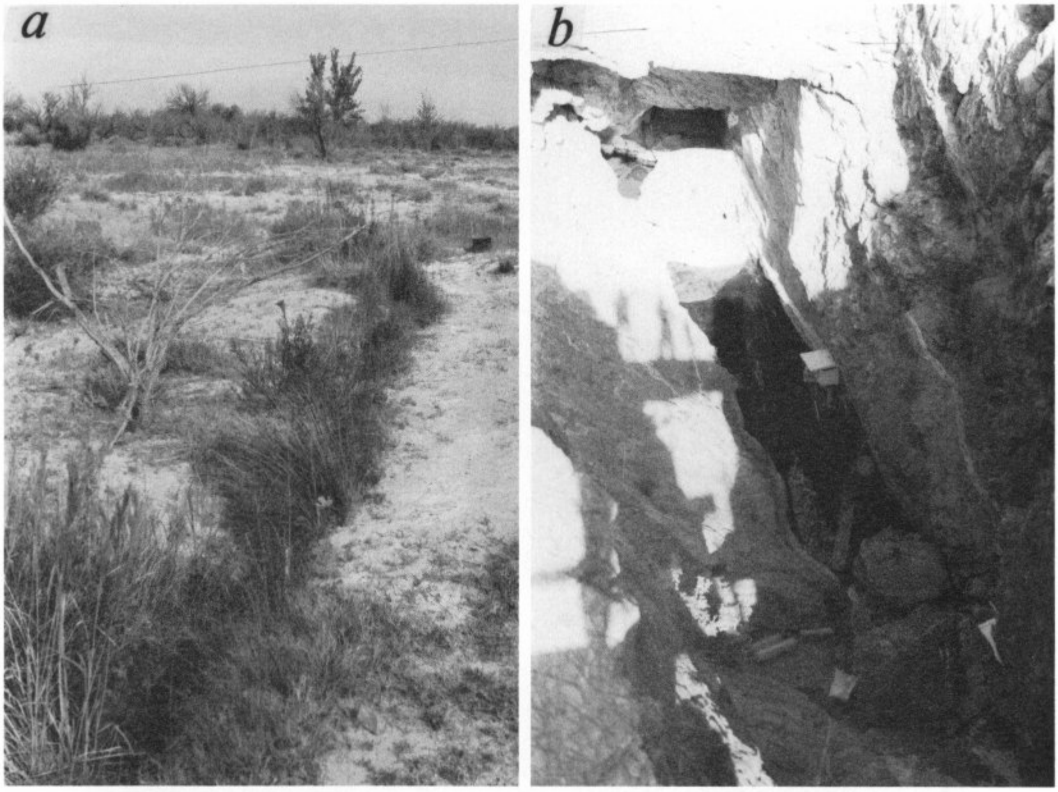


Fig. 3. Photographs of Ash Meadows springs: a, Outflow of North Indian Spring (11/10/85); b, Devils Hole (11/10/85).

List of Recognized Taxa

Pyrgulopsis micrococcus (Pilsbry).
P. erythropoma (Pilsbry, in Stearns 1893).
P. fairbanksensis Hershler and Sada, new species.
P. crystalis Hershler and Sada, new species.
P. isolatus Hershler and Sada, new species.
P. nanus Hershler and Sada, new species.
P. pisteri Hershler and Sada, new species.
Tryonia angulata Hershler and Sada, new species.
T. variegata Hershler and Sada, new species.
T. ericae Hershler and Sada, new species.
T. elata Hershler and Sada, new species.

Materials and Methods

Material examined.—Most localities visited, including all sites having snails, are shown in Figs. 5 and 6. Snails were collected by either washing rocks or sifting soft sediments with a fine-mesh hand sieve. Water temperature and conductivity were measured with a YSI Model 33, S-C-T meter. Dissolved oxygen concentrations were determined using a YSI 97 oxygen meter. Detailed descriptions of all localities visited in Ash Meadows are in Appendix 1. A few additional snailless sites were visited, including seeps by Crystal Pool. Collections often included shells of locally extinct springsnails that will be discussed further in a future publication. Distributions of species in Ash Meadows are shown in Figs. 16, 25, and 44.

Snails were relaxed with menthol crystals, fixed in 4% buffered formalin and preserved in 70% ethanol. This material is housed in the National Museum of Natural History, Smithsonian Institution (USNM) collec-

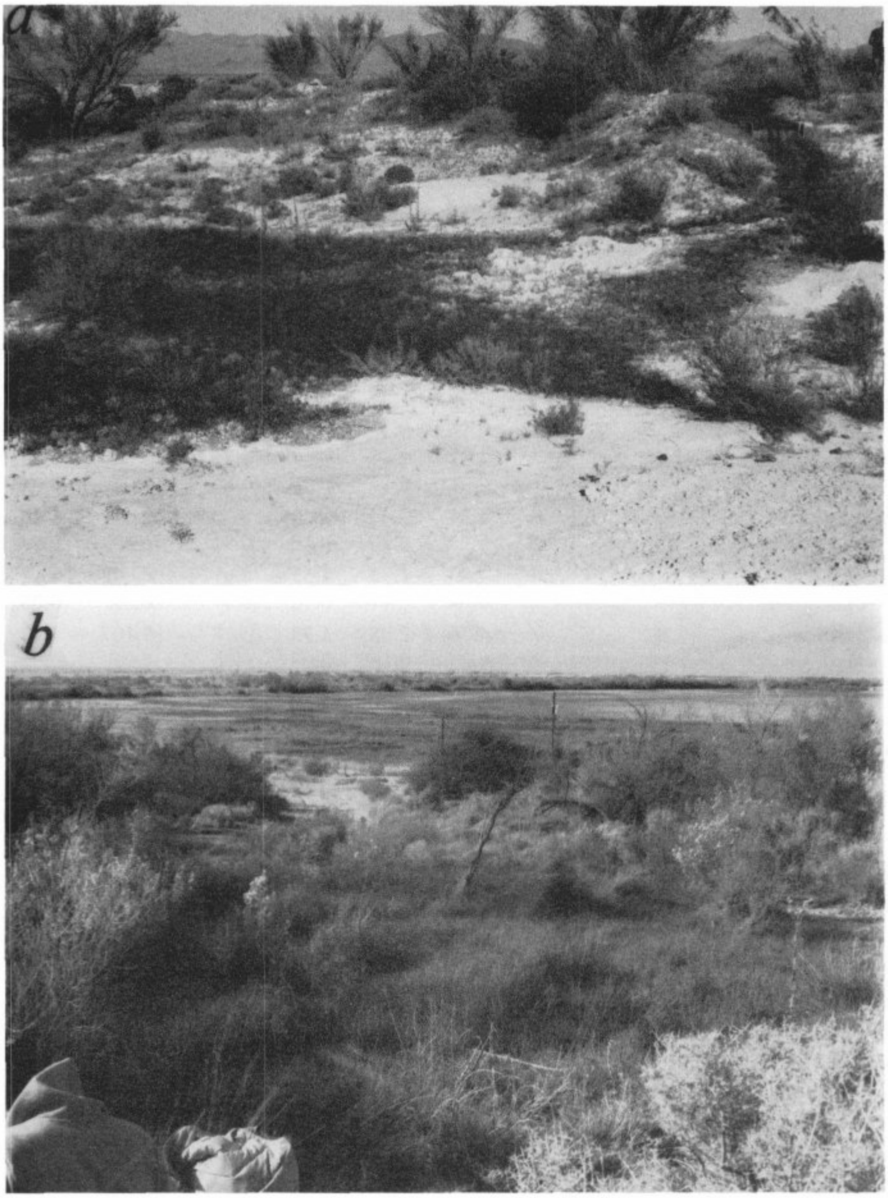


Fig. 4. Photographs of Ash Meadows springs: a, Outflow of Purgatory Spring (source at upper right corner) (11/6/85); b, Outflow of small spring at Point of Rocks (11/8/85).

tion, with paratypes of new species also deposited in the Florida State Museum (UF). Unless otherwise stated, catalog numbers in text refer to USNM material.

Morphologic study.—Shells, opercula, and radulae were photographed using a HITACHI S-570 scanning electron microscope (SEM). Generalized radular formulae were based on examination of SEM photos and are given in following order of tooth types: centrals, laterals, inner marginals, outer marginals. Intact bodies for dissection were obtained by decalcifying shells in concentrated Bouin's Solution and removing re-

Table 1.—Shell parameters for *Pyrgulopsis* species. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = apertural shape, W = whorl expansion rate.

Species and locality		Parameter						
		NW	SH	SW	T	D	AS	W
P. micrococcus								
Purgatory Spring	$\bar{x}$	4.35	2.51	1.69	4.77	−0.041	1.26	1.86
(n = 12)	s	0.23	0.18	0.09	0.55	0.05	0.06	0.32
Spring (N) S of Rogers Spring	$\bar{x}$	4.33	2.57	1.66	4.71	−0.001	1.24	1.60
(n = 15)	s	0.20	0.16	0.12	0.68	0.05	0.04	0.48
Spring (S) S of Rogers Spring	$\bar{x}$	4.36	2.59	1.68	4.42	−0.028	1.26	1.52
(n = 9)	s	0.18	0.14	0.08	0.37	0.04	0.05	0.25
Spring S of Five Springs	$\bar{x}$	4.30	2.32	1.53	4.67	−0.023	1.26	1.45
(n = 14)	s	0.18	0.15	0.10	0.94	0.06	0.07	0.33
Shaft Spring	$\bar{x}$	4.48	2.59	1.67	5.71	−0.043	1.24	1.79
(n = 11)	s	0.31	0.19	0.06	0.65	0.07	0.04	0.39
Springs (E) ncar Crystal Reservoir	$\bar{x}$	4.38	2.47	1.60	5.10	−0.099	1.33	2.42
(n = 15)	s	0.25	0.20	0.13	0.92	0.087	0.08	0.79
Spring at Clay Pits	$\bar{x}$	4.23	1.98	1.34	4.67	−0.049	1.19	1.45
(n = 10)	s	0.34	0.11	0.10	0.47	0.05	0.05	0.33
Springs S of Clay Pits	$\bar{x}$	4.36	2.08	1.33	5.78	−0.107	1.17	1.68
(n = 11)	s	0.23	0.15	0.08	0.66	0.05	0.06	0.39
Frenchy Springs (E)	$\bar{x}$	4.41	2.06	1.34	4.62	−0.017	1.20	1.23
(n = 11)	s	0.20	0.10	0.07	0.48	0.06	0.05	0.20
Frenchy Springs (W)	$\bar{x}$	4.03	1.70	1.21	4.08	−0.054	1.22	1.53
(n = 15)	s	0.19	0.09	0.07	0.71	0.04	0.03	0.31
Last Chance Spring	$\bar{x}$	4.23	2.36	1.53	4.84	−0.033	1.20	1.32
(n = 15)	s	0.18	0.14	0.11	0.44	0.05	0.10	0.23
P. fairbanksensis								
Fairbanks Spring	$\bar{x}$	3.29	2.84	2.56	3.13	−0.045	1.13	1.71
(n = 14)	s	0.34	0.24	0.17	0.59	0.07	0.07	0.36
P. crystalis								
Crystal Spring	$\bar{x}$	3.17	2.04	2.16	2.34	0.14	1.20	2.08
(n = 3)	s	0.29	0.20	0.22	0.06	0.05	0.12	0.95
P. erythropoma								
King's Pool	$\bar{x}$	3.41	2.28	2.13	3.60	−0.077	1.20	1.77
(n = 14)	s	0.23	0.20	0.14	0.78	0.06	0.05	0.66
Point of Rocks Springs (1)	$\bar{x}$	3.38	1.82	1.77	3.04	−0.066	1.21	2.79
(n = 12)	s	0.29	0.09	0.09	0.24	0.04	0.09	0.97
Point of Rocks Springs (2)	$\bar{x}$	3.60	2.38	2.13	3.58	−0.08	1.22	2.19
(n = 10)	s	0.13	0.12	0.15	0.42	0.04	0.06	0.38
Point of Rocks Springs (3)	$\bar{x}$	3.64	2.36	2.22	3.79	−0.08	1.17	2.44
(n = 16)	s	0.32	0.16	0.11	0.49	0.27	0.05	0.87
Point of Rocks Springs (4)	$\bar{x}$	3.30	1.66	1.61	3.06	−0.053	1.24	2.54
(n = 16)	s	0.14	0.12	0.14	0.28	0.04	0.05	1.14
P. pisteri								
Scruggs Spring	$\bar{x}$	4.03	2.50	2.23	3.46	−0.031	1.13	2.09
(n = 19)	s	0.20	0.17	0.12	0.56	0.05	0.05	0.53
Marsh Spring	$\bar{x}$	3.77	2.28	2.06	3.61	−0.081	1.11	2.19
(n = 12)	s	0.29	0.18	0.12	0.65	0.05	0.03	0.80

Table 1.—Continued.

Species and locality		Parameter						
		NW	SH	SW	T	D	As	W
P. nanus								
Five Springs	$\bar{x}$	3.50	1.72	1.64	3.22	0.002	1.16	2.51
(n = 14)	s	0.20	0.09	0.10	0.33	0.04	0.04	0.85
Mary Scott Spring	$\bar{x}$	3.66	2.04	1.78	3.60	−0.057	1.07	1.96
(n = 17)	s	0.28	0.20	0.15	0.53	0.06	0.11	0.64
Collins Ranch Spring	$\bar{x}$	3.50	1.62	1.49	3.18	−0.021	1.18	2.19
(n = 12)	s	0.21	0.12	0.12	0.29	0.03	0.07	0.45
P. isolatus								
Spring at Clay Pits	$\bar{x}$	4.00	2.94	2.39	3.53	−0.066	1.17	1.91
(n = 13)	s	0.14	0.14	0.11	0.31	0.05	0.04	0.47

maining pellicle. Selected animals were dried using a DENTON DCP-1 Critical Point Drier and then photographed using SEM.

Both standard measurements and Raupian parameters were obtained from selected series of adult specimens. While sexual dimorphism is common in hydrobiids, our intent was to characterize roughly typical adult form and therefore our measurements were based on randomly selected series of unsexed shells with complete and/or thickened inner lips (denoting adulthood). Shells were cleaned with CLOROX to remove surface deposits, and oriented in standard apertural aspect (Fig. 7) after counting of whorls (NW). Points and aspects of shell outline necessary for obtaining measurements, including position of coiling axis (Co, approximated as bisector of spire angle), were drawn on paper using camera lucida (12, 25 or 50×). Distances between points were then determined with a millimeter ruler. The following standard shell measurements were made (Fig. 7):

1) Shell Height (SH).

2) Shell Width (SW).

3) Length of Body Whorl (LBW).

4) Width of Body Whorl (WBW).

5) Aperture Length (AL) = length of line segment ab.

6) Aperture Width (AW) = length of line segment cd, perpendicular bisector of ab.

The following additional measurements were made in order to generate Raupian parameters:

1) Y = distance along coiling axis from apical tip to intersection (e) of line perpendicular to axis and passing through center of generating curve, approximated as intersection (f) of line segments ab and cd.

2) R = length of line segment ef, perpendicular distance from coiling axis to generating curve.

3) D1 = length of line segment ge, perpendicular distance from coiling axis to inner edge of aperture.

4) D2 = length of line segment eh, perpendicular distance from coiling axis to outer edge of aperture.

5) S1 = length of line segment ij, perpendicular distance from coiling axis to suture half a whorl back from aperture.

6) S2 = length of line segment kl, perpendicular distance from coiling axis to suture at posterior end of body whorl.

Raupian parameters (slightly modified from Raup 1966) were generated as follows:

1) Translation Rate (T) = Y/R.

2) Whorl Expansion Rate (W) = $(S1/S2)^2$. Note that W is approximated by measurements separated by a half whorl increment, hence the need to square the ratio. This is a crude approximation of W as only a single ratio was used, rather than the mean of (or preferably a function based on) a series of such measurements representing ontoge-

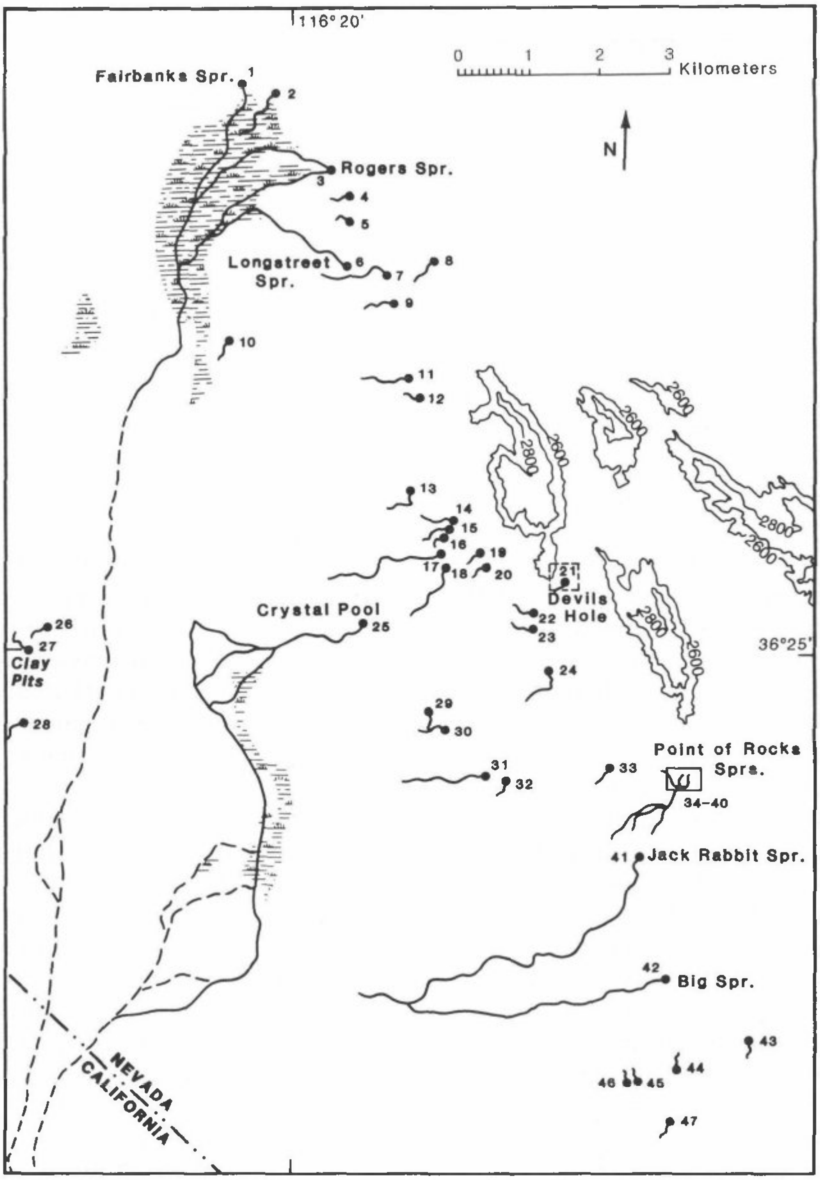


Fig. 5. Map of Ash Meadows, showing collecting localities. Adapted from Ash Meadows Quadrangle, Nevada–California (1952), USGS 15 minute series (topographic). Enclosed area at Point of Rocks enlarged in Fig. 6.

netic variation. The suture at posterior junction of aperture and body whorl was not used in this computation as hydrobiid shells typically have loosened coiling during the last quarter whorl of growth.

3) Distance from coiling axis to generating curve (D) = D1/D2.

4) Aperture Shape (AS) = AS/AW.

Data analysis. —Descriptive statistics were generated using SYSTAT (Wilkinson 1986) and are summarized in Tables 1 and 2.

Stepwise discriminant function (canonical variates) analyses were performed using SPSS-X (Klecka 1975). Since the goal of

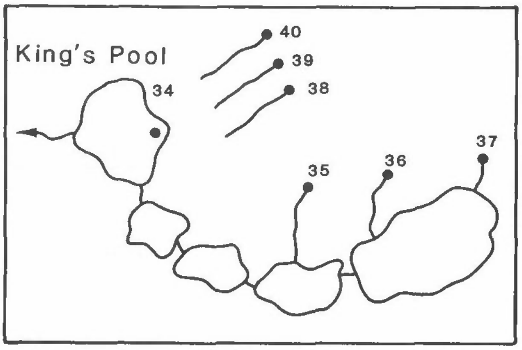


Fig. 6. Map of Point of Rocks area (enclosed by rectangle in Fig. 5), showing location of springs. Filled circle in King's Pool indicates location of spring orifice.

these analyses was to gauge distinctiveness of similar allopatric species, and as discriminant function analysis is most effective when the number of groups is small, separate analyses were done on each of three sets of three or four congeners considered closely related (Table 3). Note that the highly distinctive *P. micrococcus* was excluded. Discriminant analyses were constructed using all specimens measured for each species (considered as separate groups). Separate analyses using Raupian and standard shell parameters (excluding NW) were done to compare effectiveness of these data sets in discriminating species, yielding a total of six runs. Variables were selected in discriminant analyses on basis of providing the largest Mahalanobis distance between closest pairs of groups. In six of eight initial runs, continued selection of variables eventually resulted in decreased separation of closest groups. These were therefore rerun, using only variables providing continually increasing separation with each step. Pooled within-groups covariance matrix was used to compute probabilities of group membership.

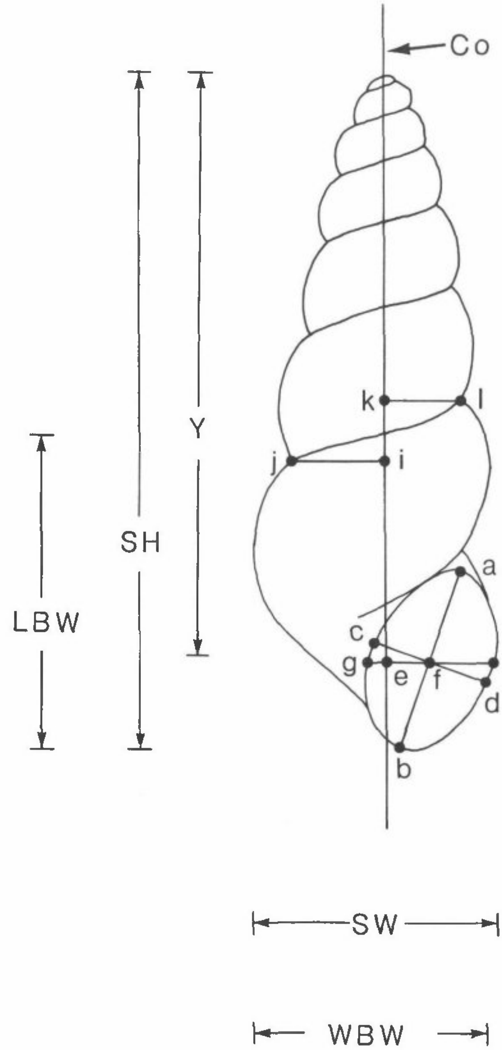


Fig. 7. Points and measurements used in morphometric analysis. Co, Coiling axis; LBW, Length of body whorl; SH, Shell height; SW, Shell width; WBW, Width of body whorl; Y, Translation along coiling axis. See text for explanation of points a–l.

Key to Ash Meadows Hydrobiidae

1. Penis simple or bilobed distally, with glandular ridge on surface (*Pyrgulopsis*) 2
– Penis with small, papillae-like lobes, glandular ridge absent (*Tryonia*) 8
2. Penis bilobed 3
– Penis simple, without lobes 6
3. Penial lobe much shorter than filament .... *Pyrgulopsis fairbanksensis*, new species
– Lobe about same length or longer than filament 4
4. Penial lobe about same length as

Table 2.—Shell parameters for *Tryonia* species. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = apertural shape, W = whorl expansion rate.

Species and locality		Parameter						
		NW	SH	SW	T	D	AS	W
T. angulata								
Fairbanks Spring	$\bar{x}$	5.98	3.56	1.72	6.40	−0.074	1.51	1.53
(n = 12)	s	0.27	0.24	0.07	0.53	0.02	0.08	0.30
Crystal Spring	$\bar{x}$	5.48	3.28	1.70	6.52	−0.009	1.45	1.23
(n = 12)	s	0.27	0.21	0.11	0.74	0.02	0.09	0.11
Big Spring	$\bar{x}$	5.65	3.08	1.52	5.98	−0.076	1.46	1.45
(n = 15)	s	0.72	0.30	0.11	0.59	0.04	0.06	0.34
T. variegata								
Five Springs	$\bar{x}$	6.20	3.73	1.71	7.74	−0.052	1.46	1.52
(n = 16)	s	0.75	0.82	0.12	1.86	0.06	0.13	0.33
Chalk Spring	$\bar{x}$	7.46	5.22	1.73	13.41	−0.056	1.58	1.38
(n = 14)	s	0.40	0.57	0.11	3.23	0.09	0.10	0.28
Mary Scott Spring	$\bar{x}$	6.75	5.15	1.81	12.17	−0.083	1.56	1.52
(n = 7)	s	0.43	0.29	0.12	0.46	0.03	0.10	0.29
Scruggs Spring (N)	$\bar{x}$	7.11	4.33	1.85	8.69	−0.047	1.57	1.44
(n = 11)	s	0.17	0.30	0.11	1.21	0.05	0.09	0.19
Scruggs Spring (S)	$\bar{x}$	7.08	4.42	1.75	8.28	−0.071	1.55	1.51
(n = 15)	s	0.31	0.18	0.07	0.69	0.03	0.08	0.26
Marsh Spring	$\bar{x}$	7.16	4.51	1.81	10.42	−0.080	1.62	1.62
(n = 16)	s	0.27	0.22	0.07	1.28	0.06	0.08	0.31
Indian Spring (N)	$\bar{x}$	7.17	4.82	1.86	10.48	−0.078	1.51	1.50
(n = 15)	s	0.50	0.32	0.11	0.90	0.04	0.06	0.25
School Spring	$\bar{x}$	6.44	4.24	1.76	9.46	−0.063	1.53	1.66
(n = 9)	s	0.21	0.23	0.18	0.88	0.04	0.06	0.28
Devils Hole	$\bar{x}$	6.67	3.44	1.69	6.38	0.067	1.33	1.31
(n = 13)	s	0.66	0.20	0.08	0.84	0.05	0.06	0.21
Collins Ranch Spring	$\bar{x}$	5.96	2.90	1.29	6.86	−0.112	1.48	1.61
(n = 11)	s	0.19	0.10	0.08	0.30	0.05	0.17	0.22
Springs (W) near Crystal Reservoir	$\bar{x}$	7.59	5.61	2.06	9.63	−0.082	1.57	1.36
(n = 14)	s	0.52	0.38	0.15	1.32	0.04	0.08	0.18
Springs (E) near Crystal Reservoir	$\bar{x}$	8.66	6.41	2.04	14.05	−0.137	1.51	1.48
(n = 17)	s	0.66	0.58	0.14	3.06	0.07	0.21	0.37
Point of Rocks Springs (4)	$\bar{x}$	7.03	4.08	1.73	9.51	−0.069	1.63	1.41
(n = 10)	s	0.46	0.27	0.08	1.50	0.08	0.07	0.21
Point of Rocks Springs (5)	$\bar{x}$	6.19	3.74	1.69	7.83	−0.073	1.61	1.43
(n = 12)	s	0.39	0.41	0.13	0.99	0.06	0.06	0.16
T. ericae								
Scruggs Spring	$\bar{x}$	5.19	1.57	0.87	6.41	−0.026	1.28	1.49
(n = 9)	s	0.58	0.19	0.05	1.23	0.06	0.08	0.27
Springs (N) N of Collins Ranch	$\bar{x}$	4.28	1.37	0.76	5.15	−0.093	1.33	1.57
(n = 10)	s	0.34	0.16	0.04	0.59	0.05	0.07	0.24
T. elata								
Point of Rocks Springs (1)	$\bar{x}$	6.37	1.88	0.83	9.00	−0.068	1.38	1.43
(n = 15)	s	0.27	0.11	0.06	1.23	0.07	0.06	0.29
Point of Rocks Springs (4)	$\bar{x}$	5.62	2.31	0.94	8.89	−0.056	1.39	1.42
(n = 15)	s	0.45	0.25	0.06	1.89	0.07	0.10	0.27

filament, glandular ridge elongated along long axis of lobe ....
.... *Pyrgulopsis micrococcus* (Pilsbry)
- Lobe longer than filament, glandular ridge elongated along distal edge of lobe 5

5. Shell <2.4 mm high; penis extending only slightly anterior to mantle collar ....
...... *Pyrgulopsis nanus,* new species
- Shell >2.6 mm high; penis extending well anterior to mantle collar .. *Pyrgulopsis isolatus,* new species

6. Distal penis much wider than filament ....
...... *Pyrgulopsis pisteri,* new species
- Distal penis only slightly wider than filament 7

7. Aperture ovate, adnate to or slightly separated from body whorl; glandular ridge small, circular ...
... *Pyrgulopsis erythropoma* (Pilsbry)
- Aperture greatly enlarged, very broadly ovate, well separated from body whorl; glandular ridge enlarged, elongate ....
.... *Pyrgulopsis crystalis,* new species

8. Whorls angled well below sutures; outer apertural lip strongly sinuate
...... *Tryonia angulata,* new species
- Subsutural angulations absent; outer apertural lip straight to moderately sinuate 9

9. Shell typically <2.0 mm tall, elongate-conic ....
.... *Tryonia ericae,* new species
- Shell typically >2.0 mm tall, turriform to aciculate 10

10. Shell 1.8–2.9 mm tall, with moderately rounded and slightly shouldered whorls ....
.... *Tryonia elata,* new species
- Shell 2.8–7.5 mm tall; whorls well-rounded and typically unshouldered *Tryonia variegata,* new species

Systematics

Family Hydrobiidae Troschel, 1857
Genus *Pyrgulopsis* Call and Pilsbry, 1886

Fluminicola Stimpson, 1865:52 [in part].
Pyrgulopsis Call and Pilsbry, 1886:9.—Hershler and Thompson, 1987:28 [with references].

Diagnosis.—Shell globose to conical, 1.2–8.0 mm tall. Aperture simple, often loosened from body whorl, inner lip often thickened. Umbilicus absent to open. Protoconch usually covered with wrinkled pits. Teleoconch smooth or unicarinate on periphery, growth lines often prominent. Taenioglossate radula with basal cusps on central teeth. Head/foot, mantle, and penis often with distinctive pigmented (melanin) regions. Penis with small distal lobe (reduced or absent in a few species) and narrow filament of varying length. Penial surface typically having one to fifteen glandular ridges, sometimes borne on fleshy crests. Females oviparous. Capsule gland with 2 tissue sections and near-terminal opening. Bursa copulatrix often partly posterior to albumen gland. Seminal receptacle relatively small (absent in one species).

Comparisons.—*Fluminicola erythropoma* Pilsbry and similar Ash Meadows taxa described below have globose-neritiform shells characteristic of the genus. However, they are much smaller than typical *Fluminicola* and have smooth protoconchs and penial glandular ridges, features seen in neither *F. nuttalliana* (Lea), the generic type species, nor in any other lithoglyphine examined by Thompson (1984). Possession of penial glandular ridges in these taxa indicates that they are nymphophilines (see Thompson 1979 for subfamilial diagnosis) convergent upon *Fluminicola.* Unusual character states (i.e., *Fluminicola*-like shell, unlobed penis, dark body pigmentation) occur among these species, suggesting that they comprise a distinctive species group. However, variation indicates gradation toward states typical of *Pyrgulopsis*, to which they are therefore assigned. *Fluminicola avernalis* Pilsbry and *F. merriami* Pilsbry and Beecher from southern Nevada, which also have penial glandular ridges (Hershler, pers. obs.), are also transferred to *Pyrgulopsis*.

Remarks.—Congeners differ primarily in shell features, penial form and pattern of glandular ridge positioning. An expanded description is given below for *P. erythropoma* as representative of the *Fluminicola*-like group.

Pyrgulopsis micrococcus (Pilsbry)
Oasis Valley springsnail
Figs. 8a, 9–16

Amnicola micrococcus Pilsbry in Stearns, 1893:277.

Fontelicella micrococcus.—Gregg and Taylor, 1965:109.—Landye, 1973:18.—Taylor, 1975:123.—USDI, 1984b:21673.

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

Material examined.—NEVADA, NYE COUNTY: small spring in Oasis Valley ANSP 67279 (holotype, 123622 (paratypes from type lot).—Spring in Oasis Valley (Thirsty Canyon), Nye County, Nevada, T10S, R47E, SE ¼ sec. 32, 850297, 18 Nov 1985.—Spring 0.2 km S of Rogers Spring, 850334, 859180, 7 Nov 1985.—Spring 0.3 km S of Rogers Spring, 850336, 859181, 7 Nov 1985; 850335, 7 Jul 1986.—Purgatory Spring, 850333, 859179, 6 Nov 1985.—Spring 1.0 km S of Five Springs, 850338, 859182, 8 Nov 1985; 850337, 7 Jul 1985.—Shaft Spring, 850331, 859183, 10 Nov 1985.—Chalk Spring, 850340, 10 Nov 1985.—Spring (southern) N of Collins Ranch Spring, 850342, 859195, 9 Nov 1985; 850341, 8 Jul 1986.—Spring N of Clay Pits, 850343, 859184, 11 Nov 1985; 850344, 8 Jul 1986.—Spring at Clay Pits, 850345, 859185, 11 Nov 1985; 850346, 8 Jul 1986.—Spring S of Clay Pits, 850347, 859186, 11 Nov 1985; 850348, 8 Jul 1986.—Spring (western) near Crystal Reservoir, 850349, 10 Nov 1985.—Spring (eastern) near Crystal Reservoir, 850350, 859187, 10 Nov 1985.—Frenchy Springs (western), 850352, 859189, 10 Nov 1985.—Frenchy Springs (eastern), 850351, 859188, 10 Nov 1985.—Last Chance Spring, 850353, 859190, 10 Nov 1985. CALIFORNIA, INYO COUNTY: Shoshone Spring (Shoshone), T22N, R7E, NW corner sec. 30, 12 Mar 1985.—Tecopa Hot Springs (Tecopa), T21N, R7E, NE corner sec. 33, 12 Mar 1985.—Spring by Grimshaw Lake (Tecopa), T21N, R7E, NE corner sec. 9, 13 Mar 1985.—Springs in Amargosa Gorge (Tecopa), T21N, R7E, SE corner sec. 9, 13 Mar 1985.

Diagnosis.—A small-sized species, with moderate-spired, globose to ovate-conic shell. Penis with single glandular ridge on ventral surface of moderate-sized lobe.

Description.—Shell (Figs. 8a, 9, 10) 1.6–2.8 mm high, up to one and a half times taller than wide. Whorls, 3.75–5.0, well-rounded, with impressed sutures and slight sutural shelving. Spire convex, often irregularly so due to bulging of whorls. Body whorl 63–80% of shell height. Shell colorless, transparent; periostracum light brown. Aperture ovate-pyriform, usually separated from body whorl in adult specimens. Inner lip moderately thickened and slightly reflected; outer lip thin. Umbilicus chink-like to open. Growth lines moderately pronounced.

Visceral coil usually darkly pigmented, especially on stomach. Melanic pigmentation of head/foot variable; ranging from absent to sparse covering of light brown pigment to near uniform (except for central portion on sides) black. Dense, dark, subepithelial pigment granules sometimes present in sides of head/foot. Penial filament usually with dark subepithelial pigment along much of length (Figs. 12–14).

Radular (Fig. 11) formula: 5-1-5/1-1, 3-1-4, 20–26, 31; width of central tooth, 0.023 mm. Cusps on central teeth dagger-like. Stomach slightly longer than style sac. Posterior stomach edge with small caecum.

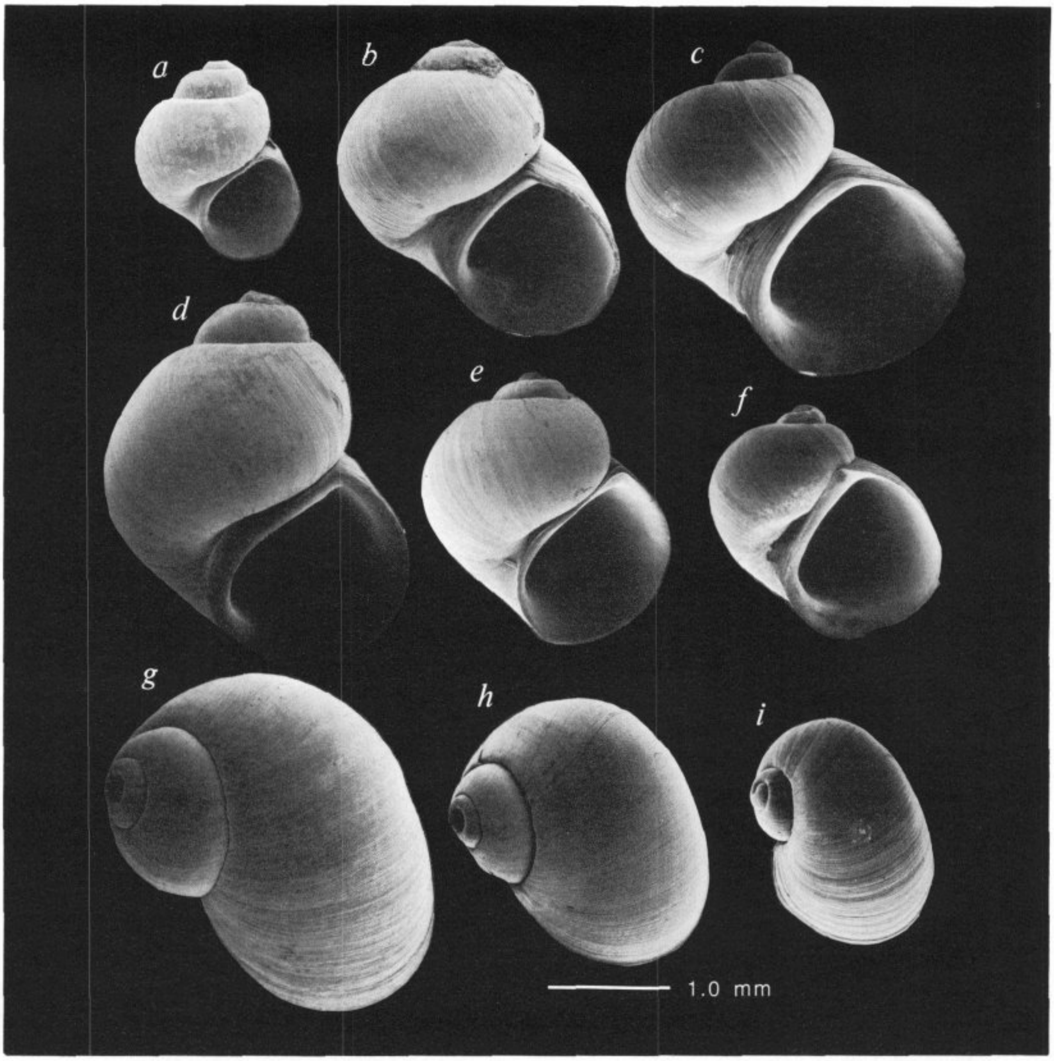


Fig. 8. SEM micrographs of shells of *Pyrgulopsis* spp.: a, *P. micrococcus*, paratype, USNM 123622, spring in Oasis Valley; b, e, h, *P. erythropoma*, King's Pool (b, paratype, ANSP 73667; e, h, USNM 859207); c, f, i, *P. crystalis*, Crystal Pool (c, holotype, USNM 859205; f, i, paratypes, USNM 859206); d, g, *P. fairbanksensis*, Fairbanks Spring (d, holotype, USNM 859203; g, paratype, USNM 859204).

Kidney relatively elongate. Ctenidium with up to 20 triangular filaments. Anterior fifth (ca.) of prostate gland pallial. Penis (Figs. 12–14) small, barely extending anterior to mantle collar, near-straight, thickened, 2 or more times longer than wide. Vas deferens located along outer edge of penis (not figured). Filament thickened and short. Penial lobe simple, rarely extending distal to tip of filament. Glandular ridge usually occupying most of penial lobe, but sometimes reduced or absent. Pallial oviduct complex (Fig. 15) typical of genus. Capsule gland opening slit-like. Posterior section of capsule gland somewhat longer than anterior section. Albumen gland slightly longer than capsule

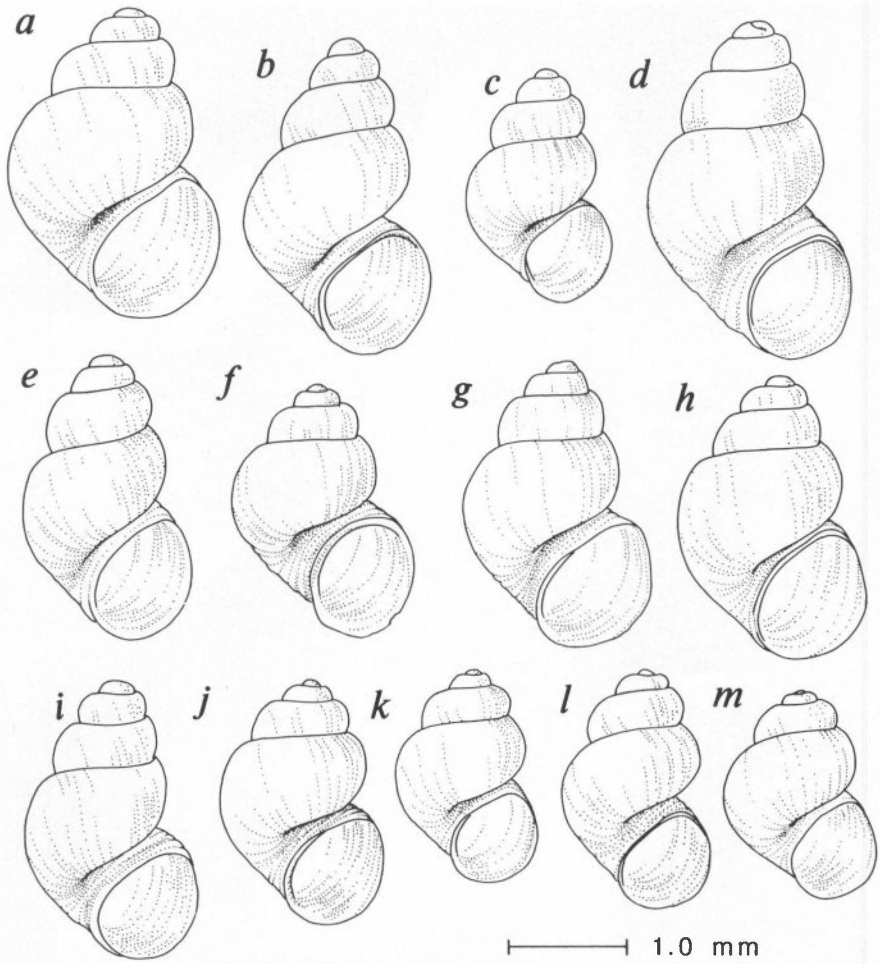


Fig. 9. Shells of *P. micrococcus*: a, b, USNM 850297, spring in Oasis Valley; c, d, USNM 859180, spring 0.2 km S of Rogers Spring; e, f, USNM 859181, spring 0.3 km S of Rogers Spring; g, h, USNM 859179, Purgatory Spring; i, j, USNM 859182, spring 1.0 km S of Five Springs; k, USNM 859195, spring (southern) N of Collins Ranch Spring; l, USNM 859184, spring N of Clay Pits; m, USNM 859185, spring at Clay Pits.

gland. Oviduct looping twice before receiving duct of seminal receptacle. Bursa copulatrix club-shaped, variable in size, but always larger than seminal receptacle. Bursa partly posterior to albumen gland.

Type locality.—Small spring in Oasis Valley, Nye County, Nevada (precise location unknown).

Distribution and habitat.—Restricted to Amargosa River drainage: Oasis Valley (several springs) and Ash Meadows (15 sites, Fig. 16) in Nye County, Nevada; and Shoshone Spring and numerous springs in vicinity of Tecopa in Inyo County, California. Typically common in soft sediments in upper segments of small springbrooks.

Syntopic with *P. nanus,* n. sp. (described below) in spring north of Collins Ranch Spring, and with *P. isolatus,* n. sp. (described below) in spring S of Clay Pits.

Comparisons.—Distinguished from several Arizona species possessing single glan-

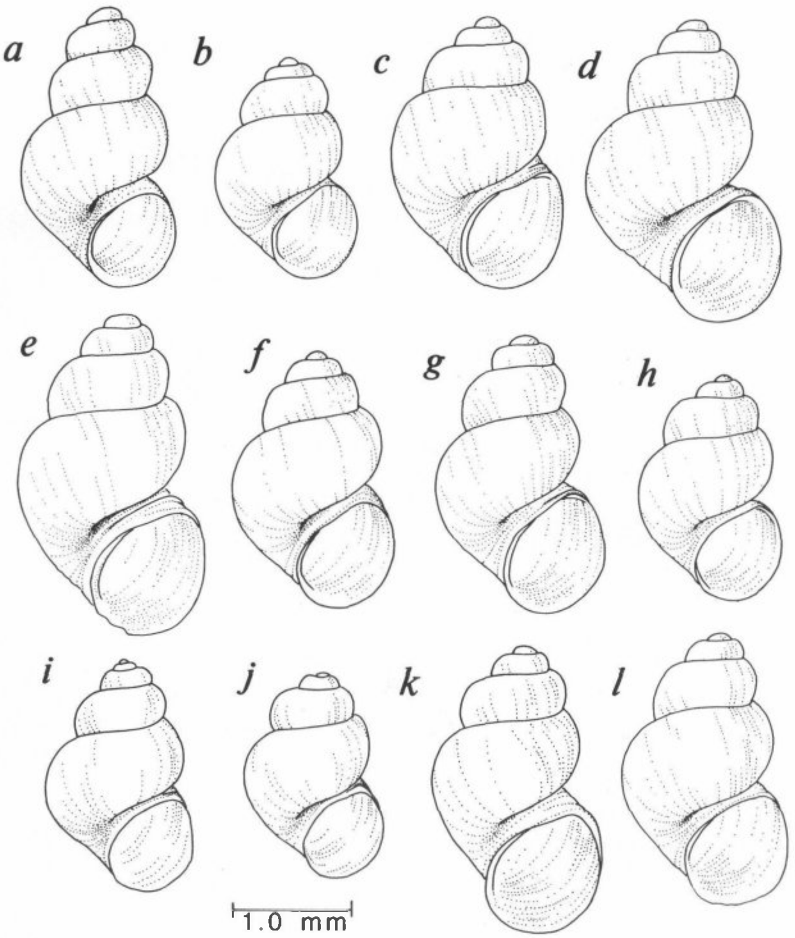


Fig. 10. Shells of *P. micrococcus*: a, b, USNM 859186, spring S of Clay Pits; c, d, USNM 859187, spring (eastern) near Crystal Reservoir; e, f, USNM 859183, Shaft Spring; g, h, USNM 859188, Frenchy Springs (eastern); i, j, USNM 859189, Frenchy Springs (western); k, l, USNM 859190, Last Chance Spring.

dular ridge on penial lobe (Hershler and Landye 1988) by narrower shell and invariant location of glandular ridge on ventral surface of penial lobe. Additional study is needed to determine status of similar forms occurring in springs in Death Valley and adjacent basins to the west. Specimens collected by Nelson and Bailey in 1891 from Saratoga Spring in Death Valley (USNM 123904) and referred to *P. micrococcus* by Pilsbry (in Stearns 1893) represent an undescribed congener belonging to the *Fluminicola*-like group.

Additional descriptive information for this species is provided by Gregg and Taylor (1965), and Hershler and Thompson (1987).

Pyrgulopsis erythropoma (Pilsbry)
Ash Meadows pebblesnail
Figs. 8b, e, h, 17, 18d–i, 19b, c, 20–22, 23a–c, 24a, c, 25

Fluminicola fusca Haldeman var. *minor*.— Pilsbry in Stearns, 1893:282.
Fluminicola erythropoma Pilsbry, 1899:125.

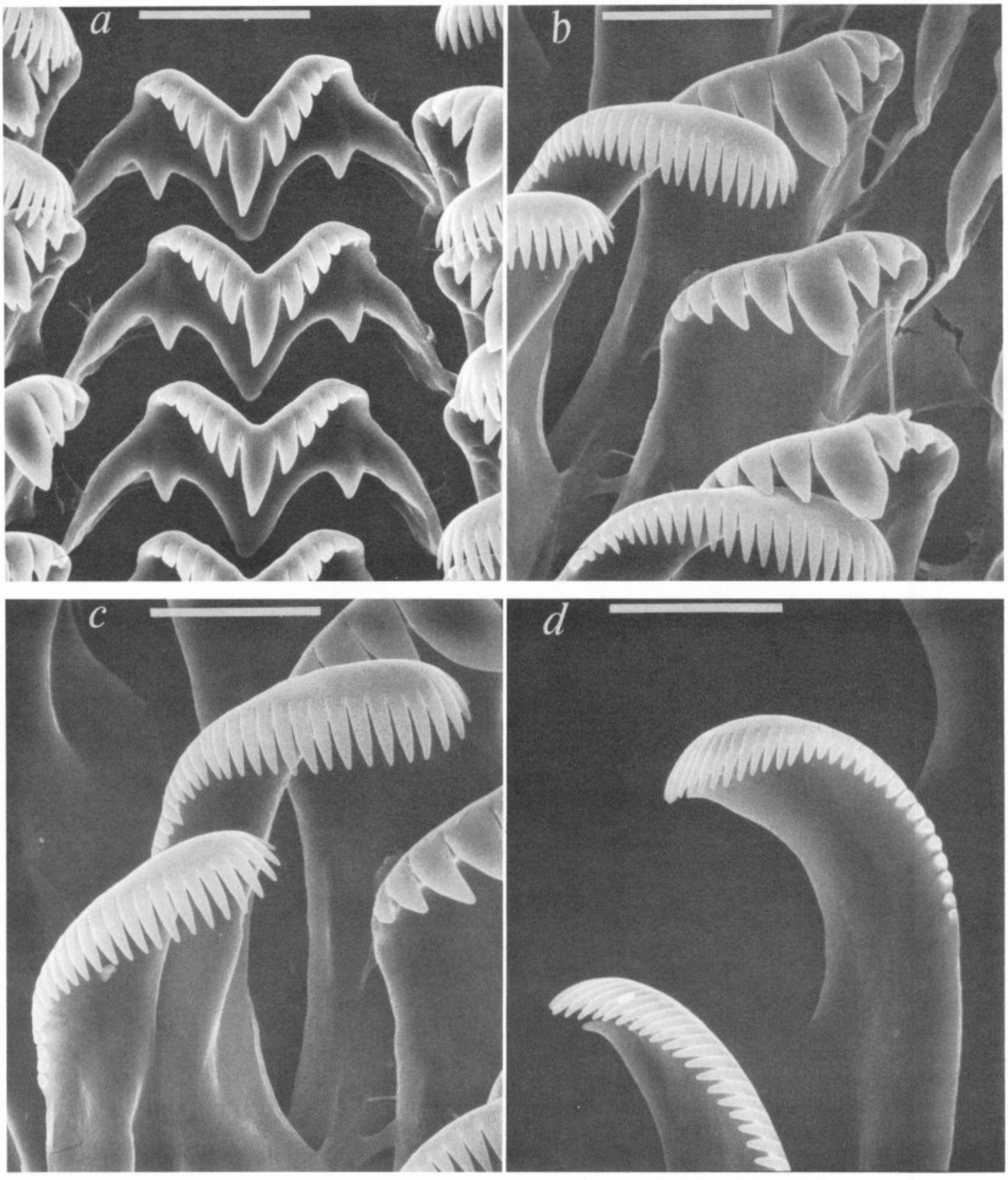


Fig. 11. SEM micrographs of radula of *P. micrococcus*, USNM 850297, spring in Oasis Valley, showing the four tooth types: a, Centrals (bar = 12 μm); b, Laterals (bar = 10 μm); c, Inner marginals (bar = 8.6 μm); d, Outer marginals (bar = 6.0 μm).

"*Fluminicola*" *erythropoma*.—Landye, 1973:15.—Taylor, 1975:79.

Fluminicola erythropoma.—Sada and Mozejko, 1984:A-1 (Appndx.).—USDI, 1984b:21673.

Point-of-Rocks Springs snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Point of Rocks Springs, King's

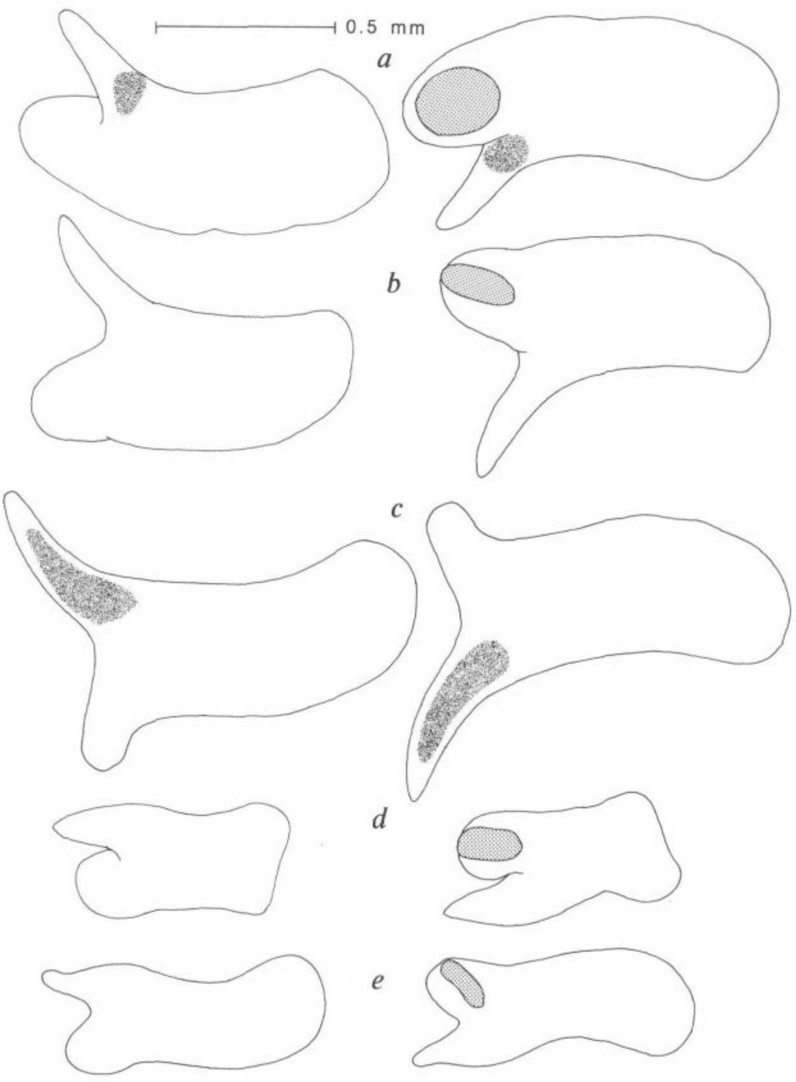


Fig. 12. Penes of *P. micrococcus*: a, b, USNM 850297, spring in Oasis Valley; c, USNM 850334, spring 0.2 km S of Rogers Spring; d, USNM 850333, Purgatory Spring; e, USNM 850338, spring 1.0 km S of Five Springs. Dorsal aspects to left, ventral aspects to right; light screened areas indicate glandular ridges, darker screened areas indicate melanic pigment.

Pool, ANSP 73607 (holotype), ANSP 73667 (paratypes from type lot); 850371, 859207, 8 Nov 1985; 857861, 8 Jul 1986.—Point of Rocks Springs (Locality 35), 850372, 859208, 8 Nov 1985.—Point of Rocks Springs (Locality 36), 857862, 859209, 8 Nov 1985; 857863, 8 Jul 1986.—Point of Rocks Springs (Locality 37), 857864, 859210, 8 Nov 1985.—Point of Rocks Springs (Locality 38), 857865, 8 Nov 1985.—Point of Rocks Springs (Locality 39), 857866, 9 Nov 1985.—Point of Rocks Springs (Locality 40), 856867, 859211, 9 Nov 1985.

Diagnosis.—A small-sized species with very short-spired, globose-turbinate shell. Penis simple, with small glandular ridge near base on dorsal surface.

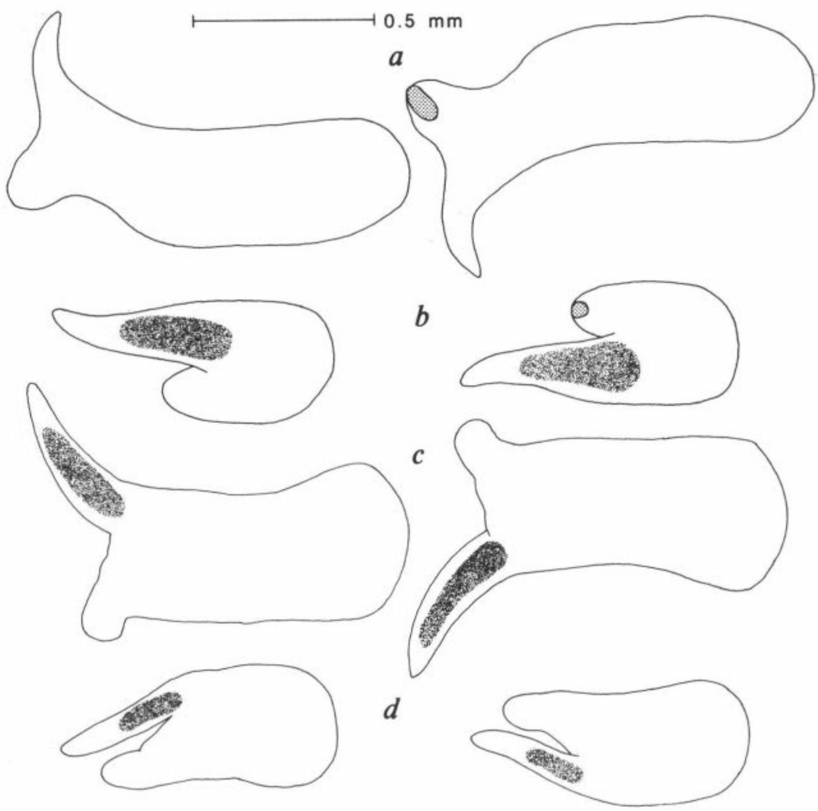


Fig 13. Penes of *P. micrococcus*: a, USNM 850331, Shaft Spring; b, USNM 850344, spring N of Clay Pits; c, USNM 850346, spring at Clay Pits; d, USNM 850348, spring S of Clay Pits.

Description.—Shell (Figs. 8b, e, h, 17, 18d–i) 1.6–2.4 mm high, slightly taller than wide. Whorls, 3.0–4.0, well-rounded, with impressed sutures. Spire convex, with apex often highly eroded. Body whorl ca. 90% of shell height. Shell transparent when fresh; periostracum thin, amber-colored, sometimes absent. Aperture broadly ovate, angulate above. Inner lip moderately thickened, slightly reflected, narrowly adnate above (rarely free). Outer lip fairly thin. Umbilicus broadly open. Protoconch (Fig. 17) surface slightly wrinkled; teleoconch with pronounced growth lines and faint spiral striations.

Visceral coil uniformly dark brown. Head/foot, including snout and distal parts of tentacles, usually covered with very dark brown epithelial pigment, with central areas on sides of head/foot somewhat lighter. Sole of foot unpigmented. Dark internal pigment filling much of penial filament, sometimes extending into proximal penis (Fig. 23a–c).

Radular (Fig. 20) formula: 7-1-7/1-1, 4-1-5, 26–28, 27–28; width of central tooth, 0.029 mm. Cusps on central teeth narrow, dagger-like. Head/foot morphology as for genus although foot relatively broad and thickened. Ciliation on cephalic tentacles sparse, irregular (Fig. 19b). Ctenidium with about 15 filaments. Testis a single, lobate mass filling most of digestive gland and partly overlapping posterior stomach (Fig. 21). Prostate gland longer than wide, with small pallial portion. Vas deferens extending along outer edge of penis without coiling; exiting slightly distal to penis base (Fig. 22). Penis (Figs. 19c, 22, 23a–c) small, blade-like, much longer than wide, tapering distally so that base of filament indistinct.

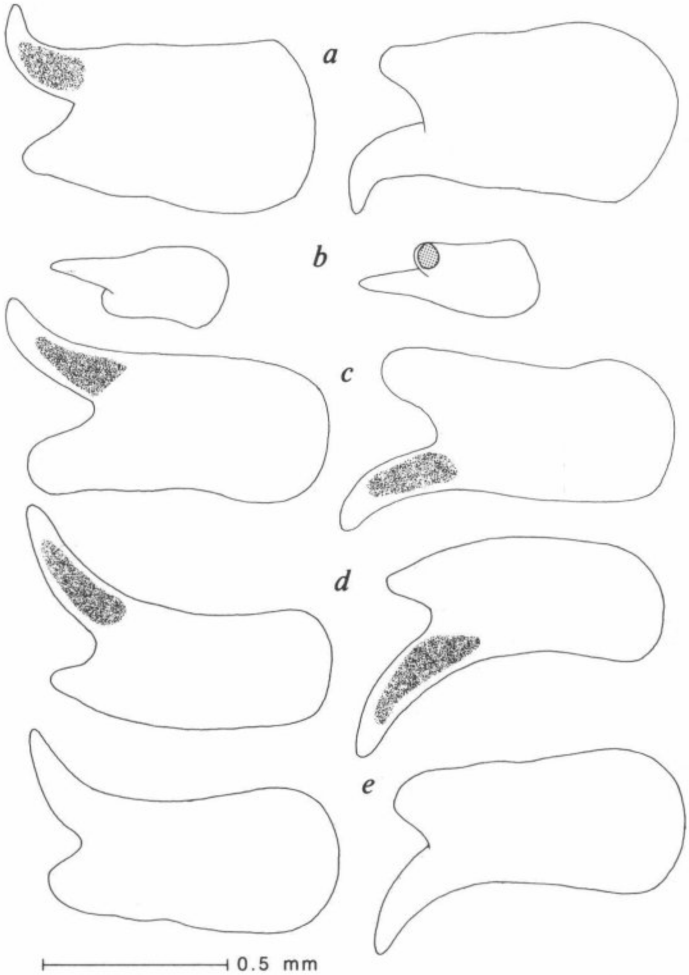


Fig. 14. Penes of *P. micrococcus*: a, USNM 850349, spring (western) near of Crystal Reservoir; b, USNM 850350, spring (eastern) near Crystal Reservoir; c, USNM 850351, Frenchy Springs (eastern); d, USNM 850352, Frenchy Springs (western); e, USNM 850353, Last Chance Spring.

Glandular ridge circular to somewhat elongate, positioned at one-third to one-half of length of penis from base. Pallial oviduct complex (Fig. 24a, c) as for genus. Capsule gland opening slit-like. Anterior capsule gland section much longer than posterior section. Capsule gland slightly longer than albumen gland. Oviduct looping once lateral to albumen gland. Seminal receptacle very small relative to bursa copulatrix. Club-shaped bursa copulatrix partly posterior to albumen gland; width of bursa duct variable.

Type locality.—King's Pool at Point of Rocks, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to six springs at Point of Rocks near eastern end of spring line in Ash Meadows (Fig. 25). Springs all within 0.5 km of one another at 702–707 m elevation. In King's Pool, species restricted to opening of large orifice, where large numbers of snails were clinging to travertine and were abundant. Also found in five small springbrooks in area (common in three), on stones and travertine in swift current.

Comparisons.—Similar to other Ash

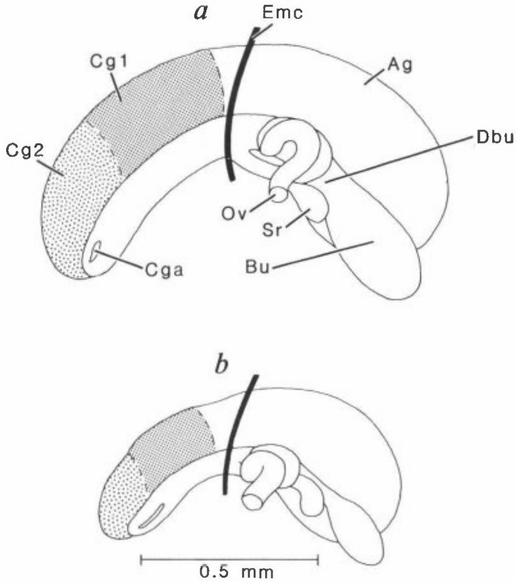


Fig. 15. Pallial oviducts of *P. micrococcus,* viewed from left side: a, USNM 850297, spring in Oasis Valley; b, USNM 850350, spring (eastern) near Crystal Reservoir. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; Ov = oviduct; Sr = seminal receptacle.

Meadows congeners found in large spring pools as all have globose-neritiform shell with very reduced spire. These differ from *P. avernalis* and *P. merriami* by lacking penial crests. Distinguished from *P. fairbanksensis,* n. sp. (described below) by smaller size, thinner inner shell lip and unlobed penis. Separated from *P. crystalis,* n. sp. (described below), a probable sister species, by globose (versus neritiform) shell and thicker penial filament. Distinguished from both of above by narrower, more numerous cusps on radular teeth.

Pyrgulopsis fairbanksensis, new species
Fairbanks springsnail
Figs. 8d, g, 18a, b, 19a, 24d, 25–27

Material examined.—NEVADA, NYE COUNTY: Fairbanks Spring, 859203 (holotype), 859204 (paratypes), UF 93955 (paratypes), 850369, 7 Nov 1985; 850367, 7 Jul 1986.

Diagnosis.—A moderate-sized species with very short-spired, globose-turbinate shell having especially thickened inner lip. Penis with small lobe bearing single glandular ridge ventrally.

Description.—Shell (Figs. 8d, g, 18a, b) 2.5–3.4 mm high, slightly taller than wide. Whorls, 3.0–4.0, well-rounded. Sutures impressed. Spire convex, apex usually eroded. Body whorl ca. 90% of shell height. Shell transparent when fresh; amber periostracum very thin or absent. Aperture broadly ovate, angulate above. Inner lip well thickened and reflected above, adnate to or slightly separated from body whorl above. Outer lip thin. Umbilicus chink-like, umbilical area often eroded. Growth lines pronounced on teleoconch; spiral striations faint. Paucispiral operculum, typical of genus, shown in Fig. 19a.

Visceral coil dark brown. Head/foot variably covered with grey-brown pigment. Small pigment patch on base of penial filament.

Radular (Fig. 26) formula: 3(4)-1-4/1-1, 3-1-4(5), 16–18, 20–25; width of central tooth, 0.053 mm. Central cusps on central and lateral teeth broad. Dimorphism of cusp size on lateral teeth pronounced (Fig. 26c). Heavy wear evident on ribbons. Ctenidial filaments, ca. 20. Penis (Fig. 27) small, elongate, with relatively small, blunt distal lobe. Filament elongate, tapering. Glandular ridge small, circular, located along or just proximal to tip of lobe. Albumen gland longer than capsule gland, with significant pallial portion (Fig. 24d). Seminal receptacle minute. Bursa copulatrix partly posterior to albumen gland.

Type locality.—Fairbanks Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to type locality, a large spring at relatively low elevation (695 m) in northern part of Ash Meadows (Fig. 25). Common on travertine at spring orifice.

Etymology.—Named for Fairbanks Spring.

Comparisons.—Separated from similar

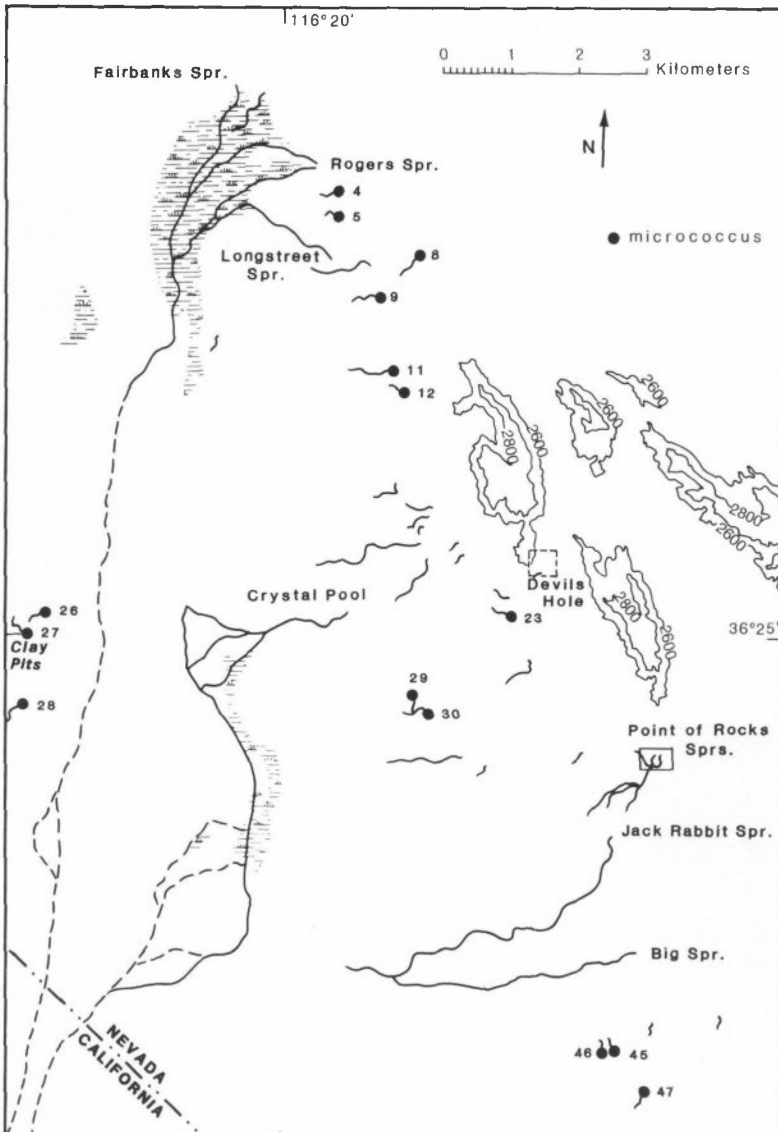


Fig. 16. Map showing distribution of *P. micrococcus* in Ash Meadows.

Ash Meadows *Pyrgulopsis* by highly thickened inner shell lip and unique penis, elongate with small lobe and long filament.

Pyrgulopsis crystalis, new species
Crystal springsnail
Figs. 8c, f, i, 18c, 23d, 24b, 25, 28

Material examined.—NEVADA, NYE COUNTY: Crystal Spring, 859205 (holotype), 859206 (paratypes), UF 93956 (paratypes), 850368, 8 Nov 1985; 850370, 7 Jul 1986.

Diagnosis.—A small-sized species, with globose-neritiform shell. Spire very short; aperture broad and enlarged. Penis simple, with narrow filament and large glandular ridge.

Description.—Shell (Figs. 8c, f, i, 18c) 1.8–2.6 mm high; width typically slightly ex-

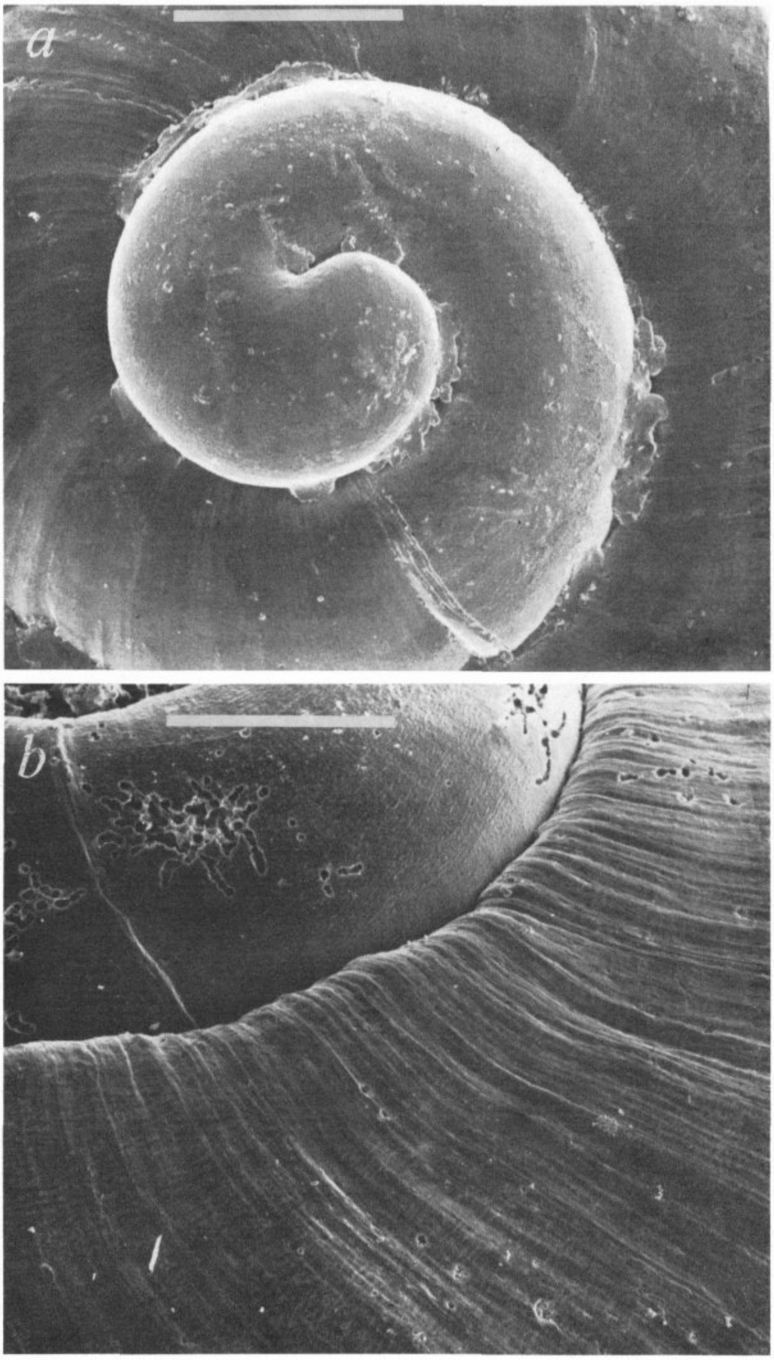


Fig. 17. SEM micrographs of shells of *P. erythropoma*: a, Protoconch (bar = 120 μm), USNM 857863, Point of Rocks Springs (Locality 36); b, Close-up showing strong growth lines on teleoconch (bar = 86 μm), USNM 857864, Point of Rocks Springs (Locality 37).

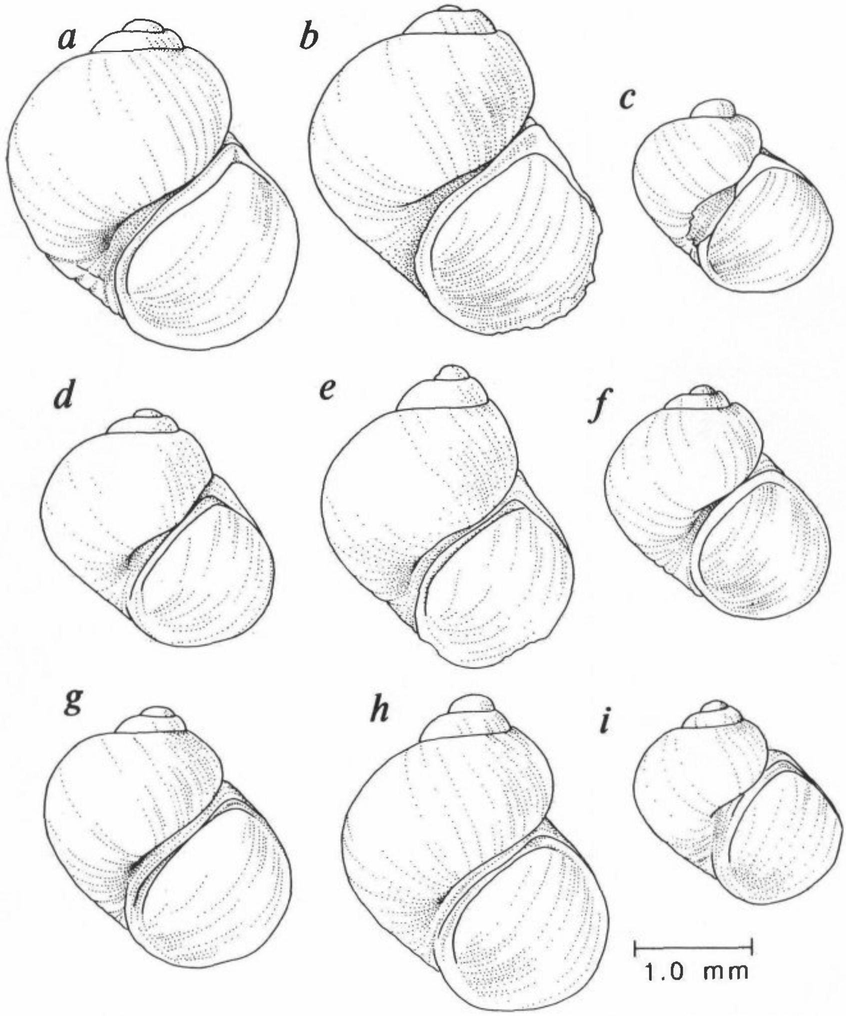


Fig. 18. Shells of *Pyrgulopsis* spp.: a, b, Paratypes, *P. fairbanksensis*, USNM 859204, Fairbanks Spring; c, Paratype, *P. crystalis*, USNM 859206, Crystal Spring; d–i, *P. erythropoma* (d, e, USNM 859207, King's Pool; f, USNM 859208, Point of Rocks Springs [Locality 35]; g, h, USNM 859210, Point of Rocks Springs [Locality 37]; i, USNM 859211, Point of Rocks Springs [Locality 40]).

ceeding length. Whorls, 3.0–3.5, highly convex, with deeply impressed sutures. Spire outline concave due to greatly expanded body whorl, which gives shell neritiform appearancc. Apex often uneroded; protoconch somewhat tilted relative to subsequent whorls (Fig. 8c). Body whorl ca. 90% of shell height. Shell colorless, transparent, quite thin; periostracum very light brown. Aperture very broadly ovate (near-circular), only slightly angled above, well separated from body whorl in largest specimens. Inner lip moderately thickened and slightly reflected above; outer lip thin. Umbilicus broadly open. Growth lines prominent; spiral lines very weak–absent.

Visceral coil dark brown. Head/foot variably dusted with grey-brown melanin. Penial filament with small pigment patch proximally (Fig. 23d).

Radular (Fig. 28) formula: 3(4)-1-3(4)/1-1, 2(3)-1-3, 14, 16–18; width of central tooth,

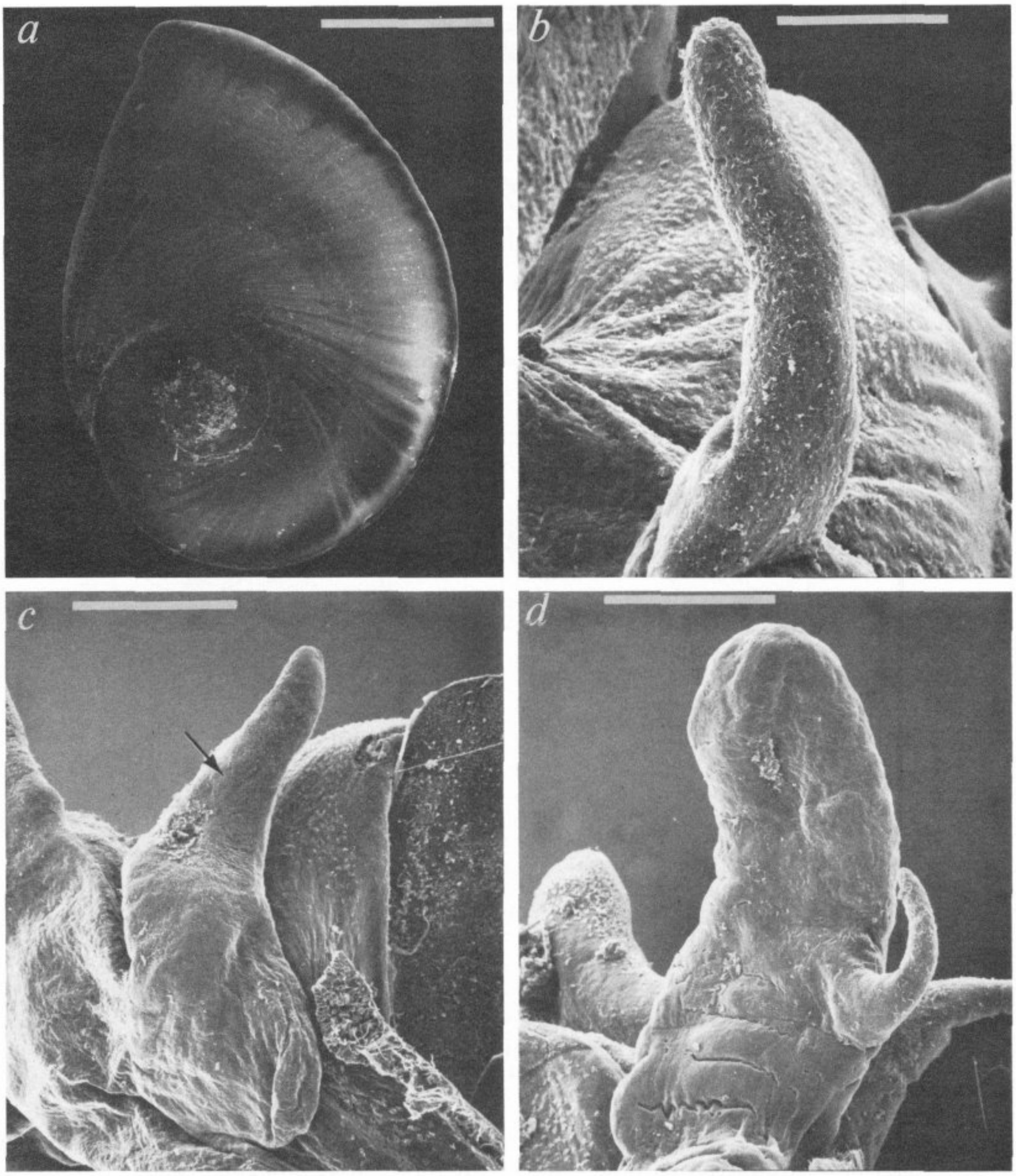


Fig. 19. SEM micrographs of operculum, cephalic tentacles, and penes of *Pyrgulopsis* spp.: a, Operculum of *P. fairbanksensis* (bar = 0.43 mm), USNM 850368, Fairbanks Spring; b, c, *P. erythropoma*, USNM 857863 (b, left cephalic tentacle showing irregular patches of cilia [bar = 150 μm]; c, penis [indicated by arrow] [bar = 0.3 mm]); d, penis of *P. isolatus* (bar = 0.3 mm), USNM 850366, spring S of Clay Pits.

0.047 mm. Cusps on central and lateral teeth fairly broad. Heavy wear apparent on ribbons. Ctenidium with 15–20 filaments. Prostate gland small, ca. 25% of length pallial. Small penis (Fig. 23d) longer than wide, tapering distally. Filament narrow, elongate. Glandular ridge elongate and large, filling much of ventral surface of penis. Cap-

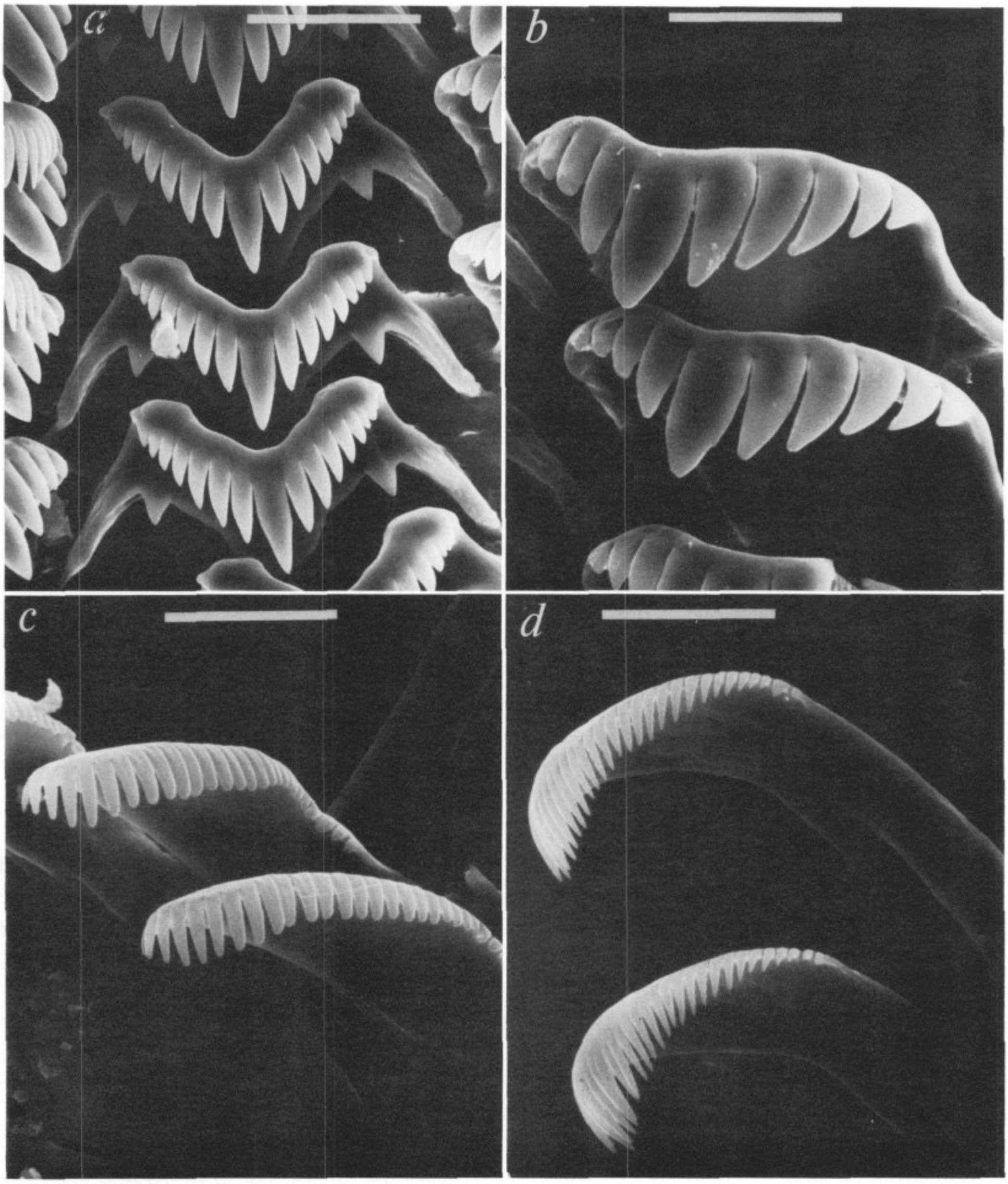


Fig. 20. Radula of *P. erythropoma,* USNM 857864, Point of Rocks Springs (Locality 37): a, Centrals (bar = 12 μm); b, Laterals (bar = 8.6 μm); c, Inner marginals (bar = 8.6 μm); d, Outer marginals (bar = 8.6 μm).

sule gland opening broad. Albumen and capsule glands near-equal in length (Fig. 24b). Seminal receptacle minute. Distal edge of bursa copulatrix even with posterior end of albumen gland.

Type locality.—Crystal Pool, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to and rare in type locality, a large, low elevation (668 m) spring in Ash Meadows (Fig.

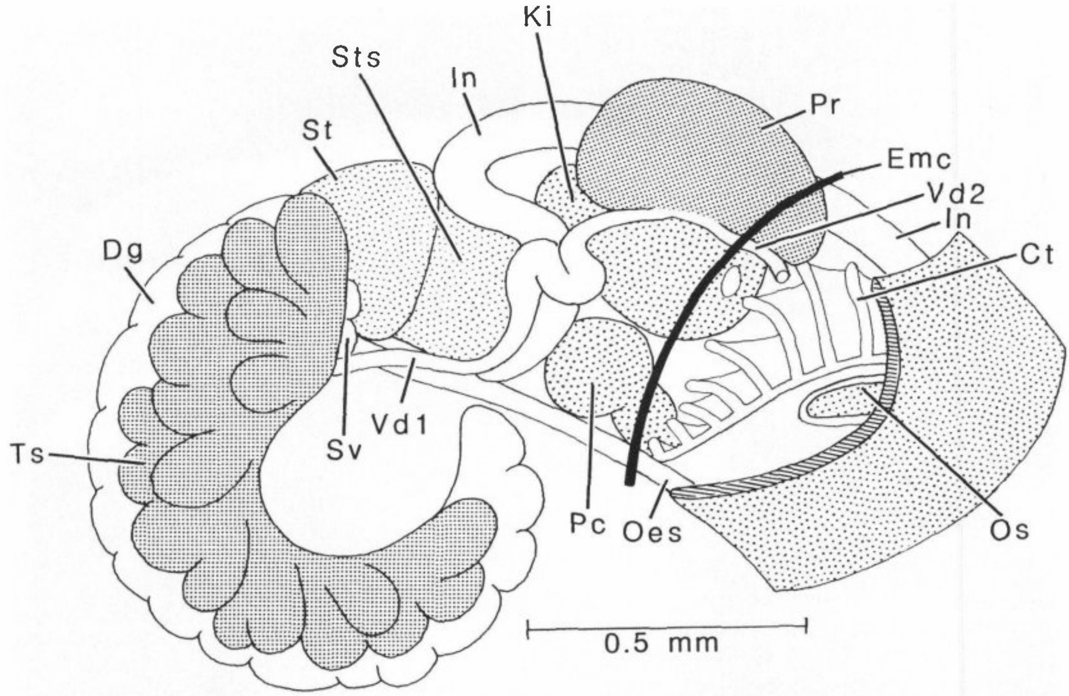


Fig. 21. Male anatomy (minus head) of *P. erythropoma*, USNM 857861, King's Pool. Pallial roof cut away to expose contents of posterior portion of cavity; prostate gland (Pr) lifted (dorsally) slightly to expose kidney. Ct = ctenidium; Dg = digestive gland; Emc = posterior end of pallial cavity; In = intestine; Ki = kidney; Oes = oesophagus; Os = osphradium; Pc = pericardium; Pr = prostate gland; St = stomach; Sts = style sac; Sv = seminal vesicle; Ts = testis; Vd1 = posterior vas deferens; Vd2 = anterior vas deferens.

25). Snails only found clinging to travertine walls of chasm-like orifices in deepest (>four meters) part of spring.

Etymology.—Named after Crystal Pool.

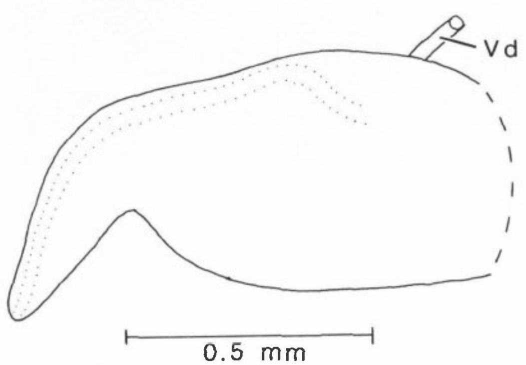


Fig. 22. Penis of *P. erythropoma*, USNM 857851, King's Pool, showing location of vas deferens (dotted line in penis). Vd = vas deferens.

Comparisons.—Neritiform shell and simple penis with slender filament and large glandular ridge distinguish this from other *Fluminicola*-like *Pyrgulopsis*.

Pyrgulopsis nanus, new species
Distal-gland springsnail
Figs. 25, 29a, d, 30–32, 33a, b

Large gland Nevada springs snail.—Sada and Mozejko, 1984: fig. 5.
"*Fluminicola*" sp.—USDI, 1984b:21673.
Large gland Nevada spring snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Five Springs, 859191 (holotype), 859192 (paratypes), UF 93957 (paratypes), 850354, 7 Nov 1985.—Mary Scott Spring, 850355, 859113, 9 Nov 1985; 850356, 8 Jul 1986.—Collins Ranch Spring,

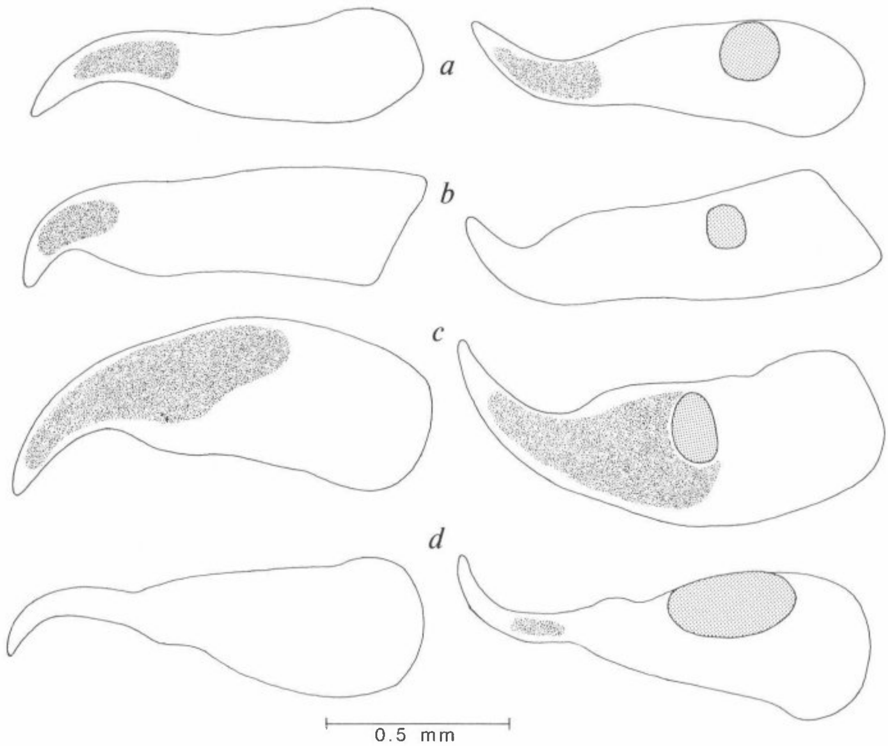


Fig. 23. Penes of *P. erythropoma* and *P. crystalis*: a–c, *P. erythropoma* (Pilsbry) (a, USNM 857861, King's Pool; b, USNM 857863, Point of Rocks Springs [Locality 36]; c, USNM 857864, Point of Rocks Springs [Locality 37]); d, *P. crystalis* new species, USNM 850370, Crystal Pool.

850357, 859194, 9 Nov 1985; 850360, 8 Jul 1986.—Spring (northern) N of Collins Ranch Spring, 850359, 859196, 9 Nov 1985; 850360, 8 Jul 1986.

Diagnosis.—A small-sized species with globose, short-spired shell. Penis with short filament and large lobe bearing glandular ridge along distal edge.

Description.—Shell (Figs. 29a, d, 30) 1.5–2.4 mm high, slightly taller than broad. Whorls, 3.0–4.0, convex and inflated, with impressed sutures. Spire straight or slightly convex. Body whorl ca. 83% of shell height. Shell colorless, transparent; amber periostracum thin. Aperture broadly ovate, pyriform above. Inner lip slightly thickened and reflected, narrowly adnate to or slightly separated from body whorl. Outer lip thin. Umbilicus chink-like to broadly open. Growth lines pronounced; spiral striae weakly developed.

Visceral coil typically uniformly dark brown. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Proximal half of penial filament usually darkly pigmented externally (Fig. 32).

Radular (Fig. 31) formula: 4(5)-1-4(5)/1-1, 2-1-3, 20–22, 21; width of central tooth, 0.035 mm. Central tooth broadly trapezoidal, cusps fairly narrow. Penis (Fig. 32) longer than wide. Elongate lobe characteristic; width of lobe variable but typically subequal to width of penis near base. Filament short, rarely exceeding lobe in length, narrow compared to lobe. Glandular ridge typically located at or just proximal to tip of lobe; ridge size and shape variable, ranging from small and circular to thickened and elongate. Albumen gland somewhat longer than capsule gland; posterior section of latter sometimes greatly reduced (Fig. 33a, b).

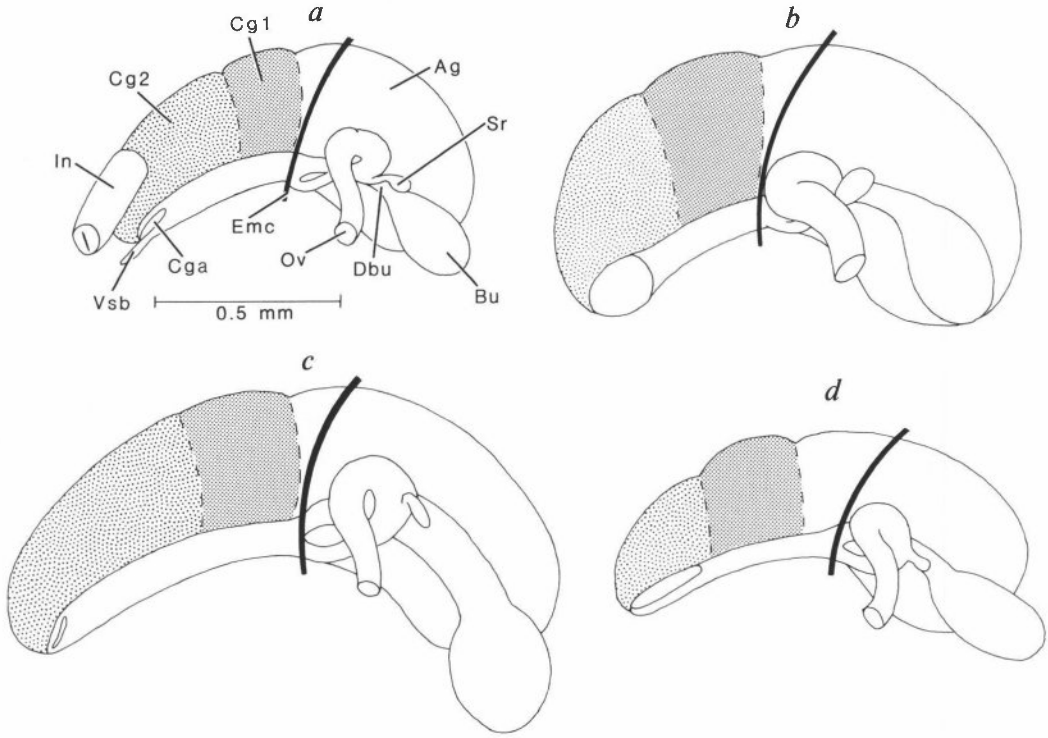


Fig. 24. Pallial oviducts of *Pyrgulopsis* spp., viewed from left side: a, c, *P. erythropoma* (a, USNM 857867, King's Pool; c, USNM 857863, Point of Rocks Springs [Locality 36]); b, *P. crystalis*, USNM 850370, Crystal Pool; d, *P. fairbanksensis*, USNM 850368, Fairbanks Spring. Capsule gland vestibule (Vsb) and position of intestine (In) shown only in a. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; In = intestine; Ov = oviduct; Sr = seminal receptacle; Vsb = capsule gland vestibule.

Seminal receptacle minute. Bursa copulatrix small, club-shaped to near-spherical, partly posterior to albumen gland.

Type locality.—Five Springs, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Restricted to four small Ash Meadows springbrooks within 10 km of one another at or above 700 m elevation (Fig. 25). Common in upper segments of streams on soft sediment and loose travertine.

Etymology.—From Latin *nanus*, a dwarf, referring to small size of species.

Comparisons.—Unusual penial morphology shared by *P. isolatus*, n. sp. (described below). Separable from this probable sister species by smaller size, smaller penis (relative to body size), more globose shell, and narrower cusps on central radular teeth.

Pyrgulopsis pisteri, new species
Median-gland springsnail
Figs. 29b, e, 33c, 34a–e, 35, 36

Median-gland Nevada spring snail.—Sada and Mozejko, 1984: fig. 5.
"*Fluminicola*" sp.—USDI, 1984:21673.
Median-gland Nevada spring snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Marsh Spring, 859197 (holotype), 859198 (paratypes), UF 94958 (paratypes), 850364, 10 Nov 1985.—North

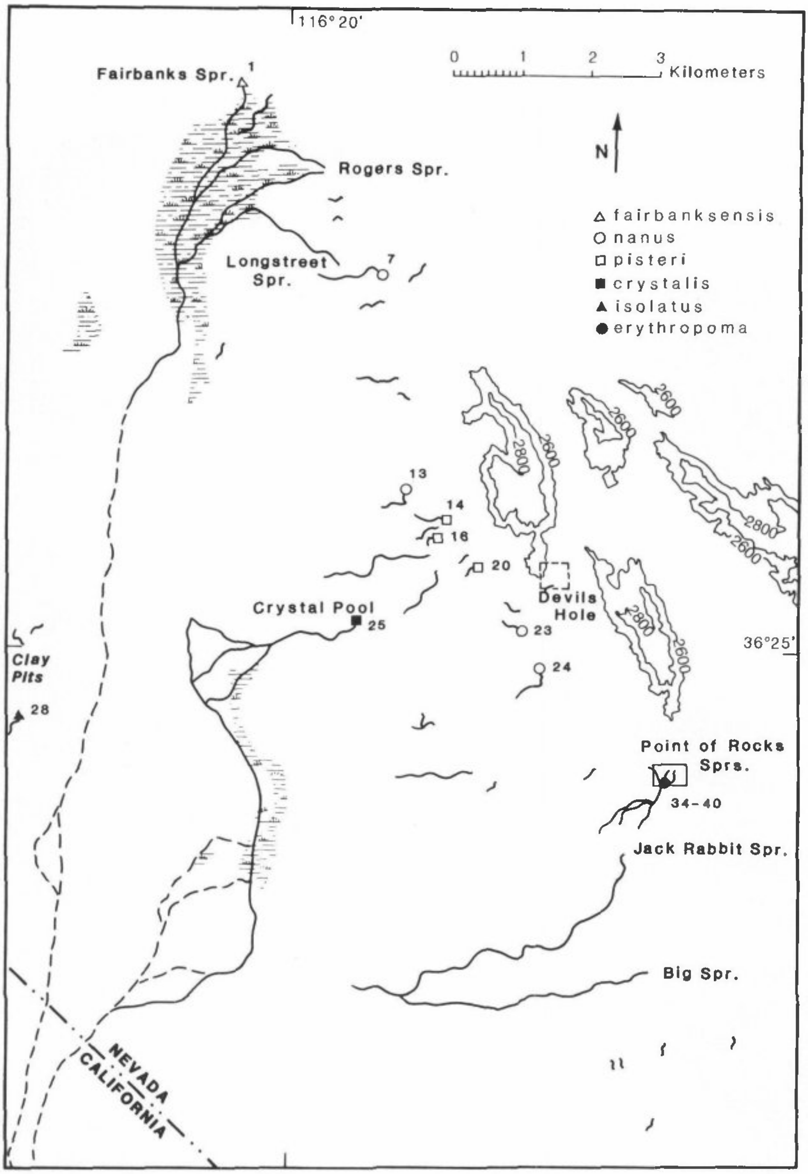


Fig. 25. Map showing distribution of *Pyrgulopsis* spp. in Ash Meadows.

Scruggs Spring, 850362, 859199, 10 Nov 1985; 850361, 8 Jul 1986.—Observation pond below School Spring, 850365, 859200, 10 Nov 1985.

Diagnosis.—A small-sized species with globose shell with short spire. Penis simple, nontapering, with glandular ridge positioned ventrally near mid-point.

Description.—Shell (Figs. 29b, e, 34a–e) 1.8–2.7 mm high, slightly taller than broad. Whorls, 3.25–4.50, convex and inflated. Sutures impressed. Spire slightly convex. Body whorl ca. 83% of shell height. Shell colorless, transparent, with very thin, light brown periostracum (sometimes absent). Aperture broadly ovate, somewhat angled above. Inner lip slightly thickened and reflected; narrowly adnate to or slightly separated from

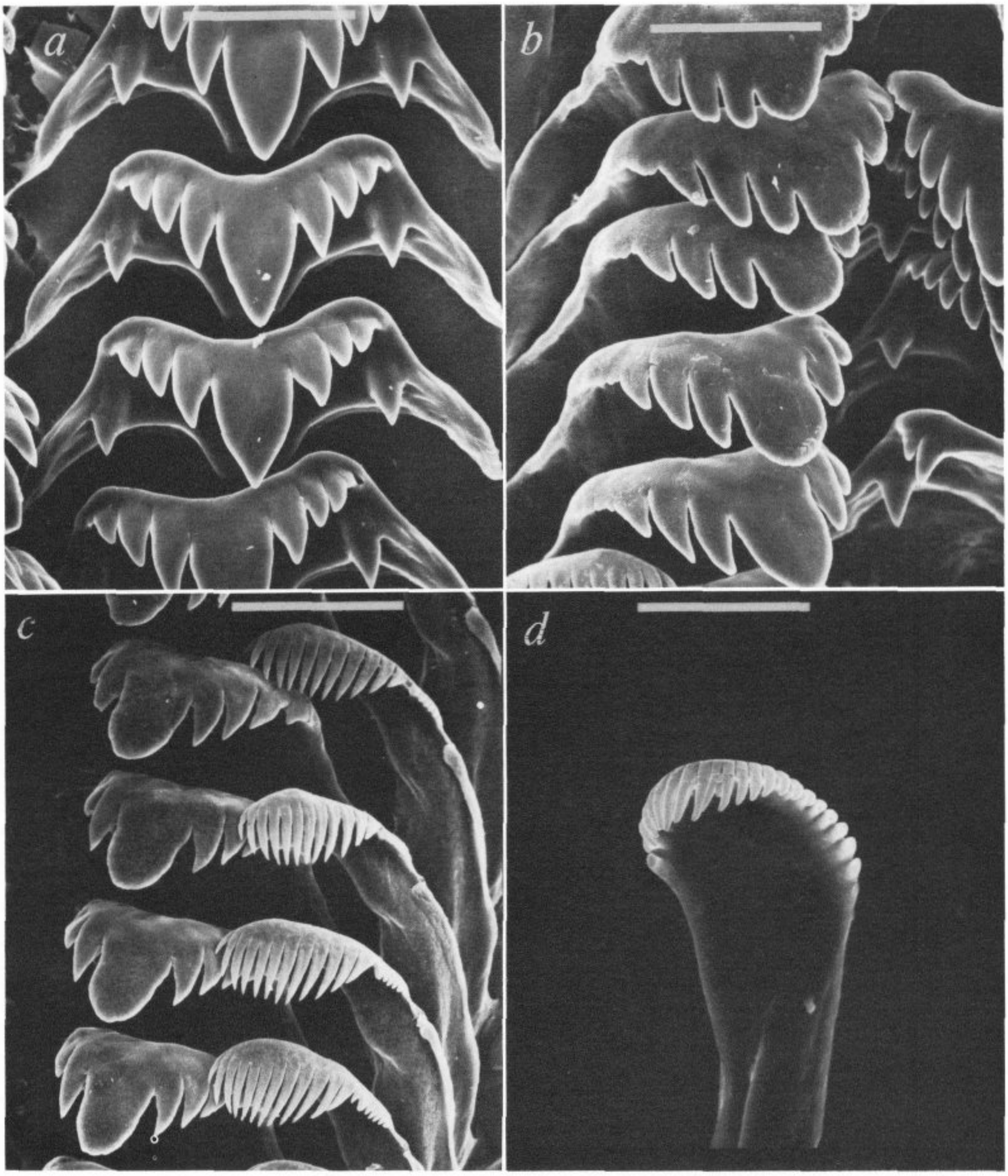


Fig. 26. Radula of *P. fairbanksensis*, USNM 850368, Fairbanks Spring. a, Centrals (bar = 20 μm); b, Laterals (bar = 23.1 μm); c, Laterals and inner marginals (bar = 27 μm); d, Outer marginal (bar = 10 μm).

body whorl. Outer lip thin. Umbilicus chink-like to broadly open. Growth lines pronounced, often somewhat elevated near end of body whorl. Spiral striae moderately pronounced.

Visceral coil typically uniform dark brown or black. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Proximal half of penial filament darkly pigmented, with pigment often extending into distalmost penis (Fig. 36).

Radular (Fig. 35) formula: 3(4)-1-3(4)/1-1, 3-1-3(4), 16–17, 14; width of central tooth, 0.045 mm. Cusps on central teeth moderately wide. Ctenidial filaments, ca. 20. Pros-

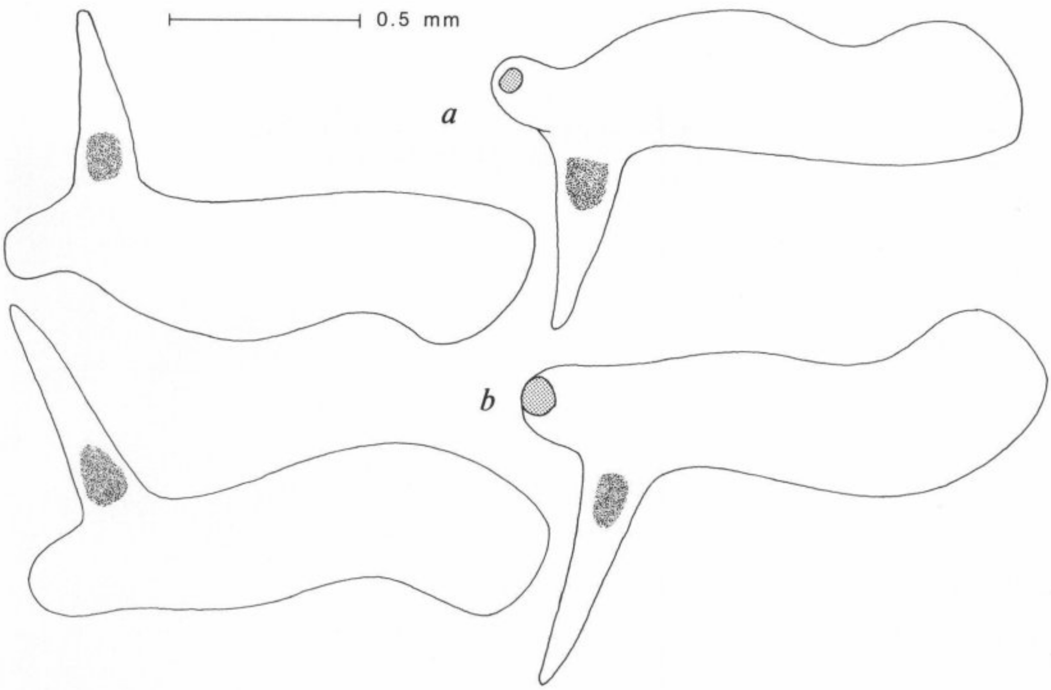


Fig. 27. Penes of *P. fairbanksensis,* USNM 850368, Fairbanks Spring.

tate gland small, largely pallial. Penis (Fig. 36) near-rectangular, with narrow filament arising from broad distal end. Filament less than half of penis length. Glandular ridge typically large and circular, positioned at or near inner edge of penis. Albumen gland slightly longer than capsule gland (Fig. 33c). Seminal receptacle minute. Bursa copulatrix quite small, near-spherical, partly posterior to albumen gland; duct of bursa narrow.

Type locality.—Marsh Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Restricted to small-sized Marsh and North Scurggs Springs, and an observation pond below School Spring, all within two km of one another above 702 m elevation in Ash Meadows. Common in springpools and outflows of former two springs, on aquatic macrophytes, and travertine. Rare in observation pond, on soft, detritus-covered substrate.

Etymology.—Named after E. P. Pister, in recognition of his tremendous effort over the past 20 years to preserve native aquatic fauna of the Death Valley System.

Comparisons.—Shell similar to that of *P. nanus* and *P. isolatus,* n. sp. (described below), but species separable from above by absence of penial lobe and position of glandular ridge. Simple penis having glandular ridge near mid-point of ventral surface similar to those of *P. erythropoma* and *P. crystalis,* but species distinguished from above by high-spired shell, untapered shape of penis, and habitat of small springs (compared to large spring pools).

Pyrgulopsis isolatus, new species
Elongate-gland springsnail
Figs. 19d, 25, 29c, f, 33d, 34f, g, 37, 38

Material examined.—NEVADA, NYE COUNTY: Spring S of Clay Pits, 859201 (holotype), 859202 (paratypes), UF 93959 (paratypes), 850366, 8 Jul 1986.

Diagnosis.—A large-sized species, with

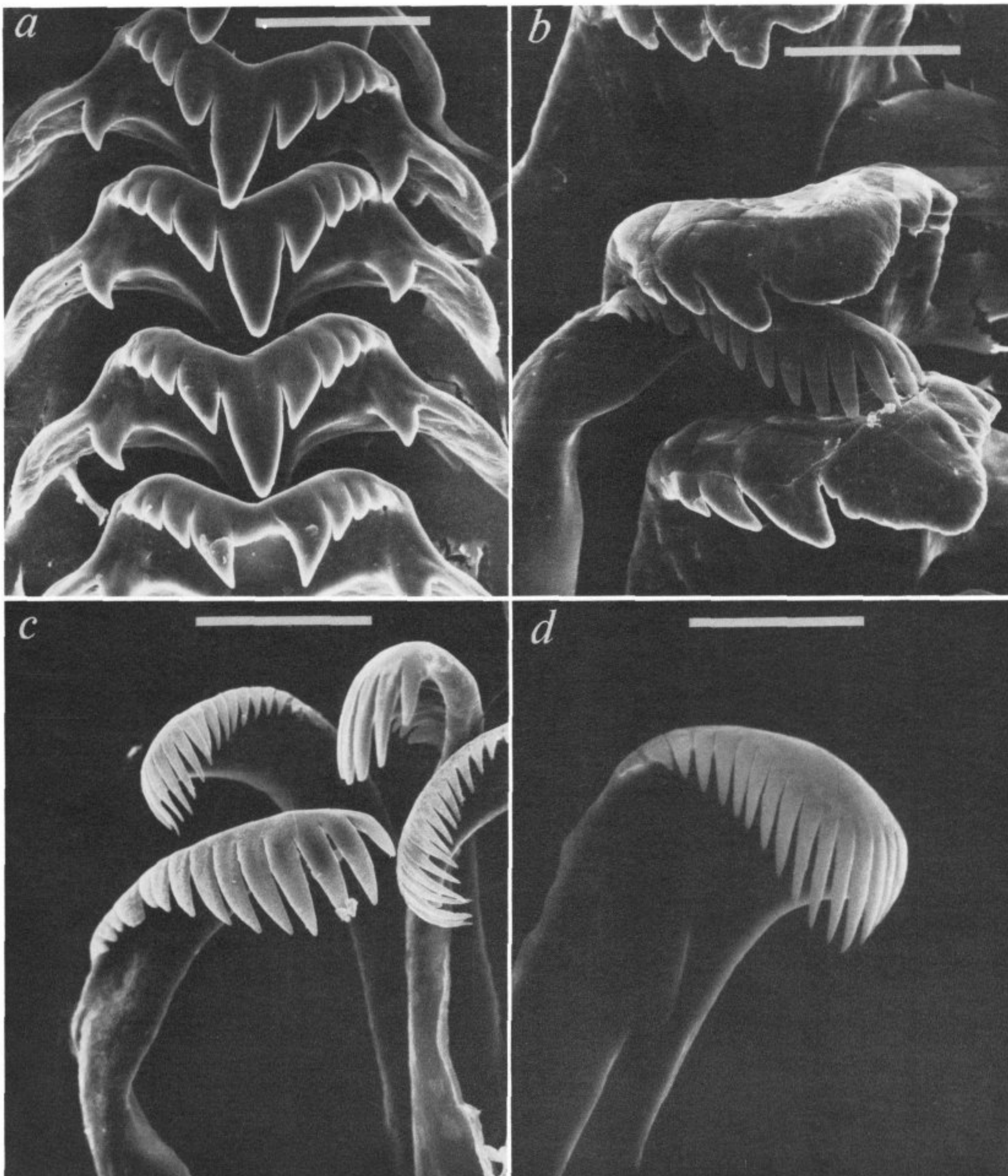


Fig. 28. Radula of *P. crystalis,* USNM 850370, Crystal Pool. a, Centrals (bar = 17.6 μm); b, Laterals and inner marginal (bar = 17.6 μm); c, Inner marginals (bar = 15.0 μm); d, Outer marginal (bar = 8.6 μm).

broadly conical shell having moderate spire. Penis enlarged, rectangular, with enlarged lobe bearing elongate glandular ridge distally.

Description.—Shell (Figs. 29c, f, 34f, g) 2.6–3.1 mm high, ca. one-fifth taller than wide. Whorls 3.75–4.25, convex and inflated, with impressed sutures. Spire straight or

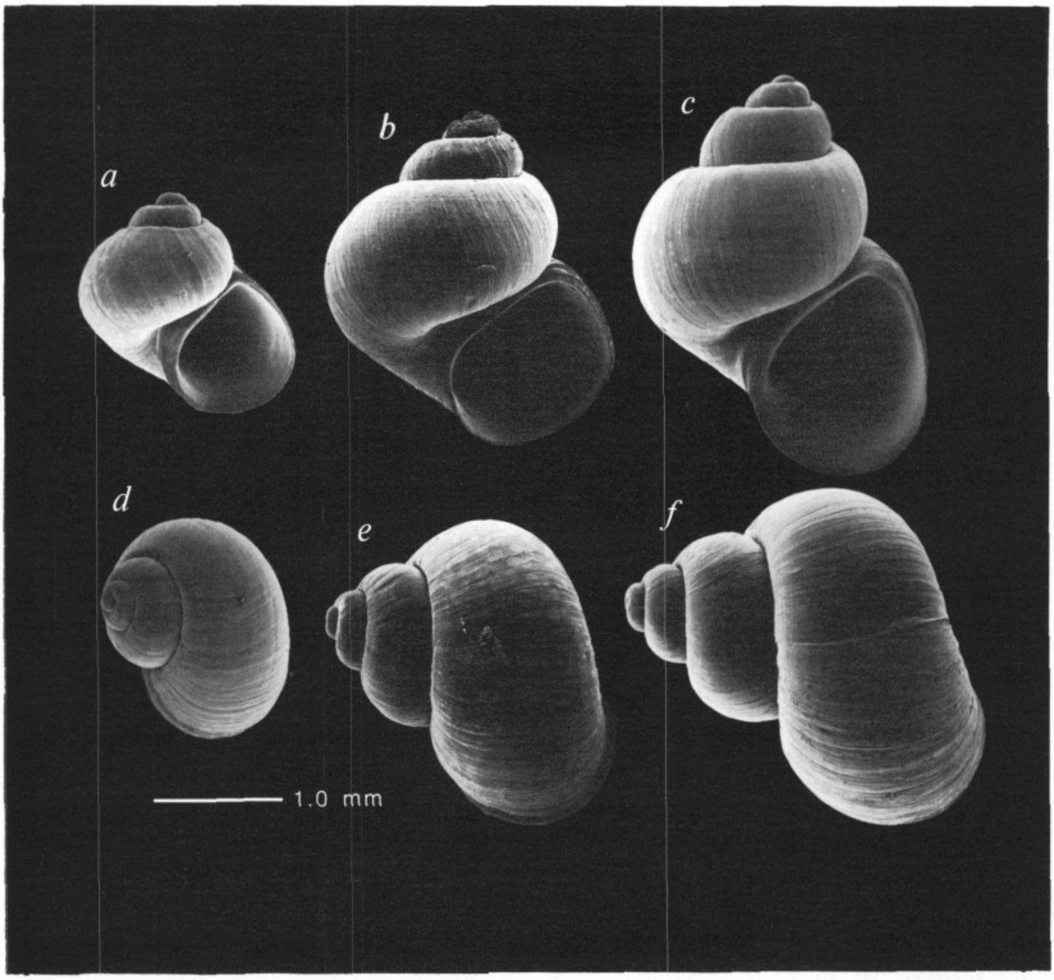


Fig. 29. SEM micrographs of shells of *Pyrgulopsis* spp.: a, d, *P. nanus,* Five Springs (a, holotype, USNM 859191; d, Paratype, USNM 859192); b, e, *P. pisteri,* Marsh Spring (b, holotype, USNM 859197; e, paratype, USNM 859198); c, f, *P. isolatus,* spring S of Clay Pits (c, holotype, USNM 859201; f, paratype, USNM 859202).

slightly convex. Body whorl ca. 80% of shell height. Shell colorless, transparent; periostracum light brown. Aperture ovate, slightly angular above. Inner lip slightly thickened and reflected; often slightly separated from body whorl. Outer lip thin. Umbilicus chink-like to broadly open. Growth lines pronounced; spiral striae weakly developed.

Visceral coil typically uniformly dark brown. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Virtual entirety of penial filament usually darkly pigmented (Fig. 38).

Radular (Fig. 37) formula: 4-1-4/1-1, 3-1-3(4), 22–24, 24–27; width of central tooth, 0.044 mm. Central cusps of central and lateral teeth broad. Ctenidial filaments, ca. 20. Prostate gland large, with very small pallial portion. Penis (Figs. 19d, 38) extending well anterior to mantle collar, nontapering, with deep folds along much of length. Lobe often as long as distal penis, nontapering or even expanding distally. Fil-

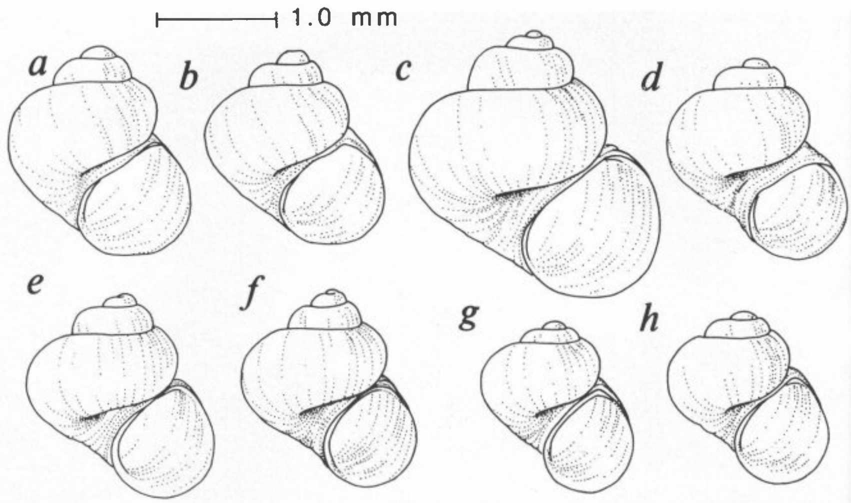


Fig. 30. Shells of *P. nanus*: a, b, Paratypes, USNM 859192, Five Springs; c, d, USNM 859193, Mary Scott Spring; e, f, USNM 859194, Collins Ranch Spring; g, h, USNM 859196, spring 1.0 km N of Collins Ranch Spring.

ament very short relative to penis length. Glandular ridge narrowly elongate, typically extending along entire distal edge of lobe. Albumen gland longer than capsule gland (Fig. 33d). Seminal receptacle minute. Bursa copulatrix enlarged, more than half of length posterior to albumen gland.

Type locality.—Spring at Clay Pits, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to type locality W of Carson Slough, Ash Meadows (Fig. 25). Most common in small stream outflow from marsh.

Etymology.—From New Latin *isolatus,* detached or separate, referring to endemism in area disjunct from most other Ash Meadows waters.

Comparisons.—Most similar to *P. nanus* (see above).

Genus *Tryonia* Stimpson, 1865

Tryonia Stimpson, Hershler and Thompson, 1987:26 [with references].

Diagnosis.—Shell elongate-conic to turreted, 1.2–7.0 mm tall. Aperture simple, unthickened. Umbilicus narrow or absent. Sexual dimorphism often pronounced (males smaller). Protoconch smooth or with slight wrinkling. Teleoconch smooth or with spiral lines and/or axial striations or varices; growth lines often prominent. Operculum paucispiral. Central radular teeth dagger-like; basal cusps present. Penis flattened, elongate, with varying numbers of papillae at base and along inner curvature. Females ovoviviparous. Capsule gland reflected posteriorly; albumen gland greatly reduced. Spermathecal duct opens posterior to capsule gland opening.

Remarks.—Congeners differ mostly in subtle shell features, with number and location of penial papillae sometimes varying. Additional study will be necessary to confirm our impression that detailed anatomy of Ash Meadows *Tryonia* varies little from that described below for *T. angulata,* n. sp.

Tryonia angulata, new species
Sportinggoods Tryonia
Figs. 39a, 40, 41, 42a, d, 43, 44

Sportinggoods Tryonia.—Sada and Mozejko, 1984: fig. 5.
Tryonia sp.—USDI, 1984:21673.

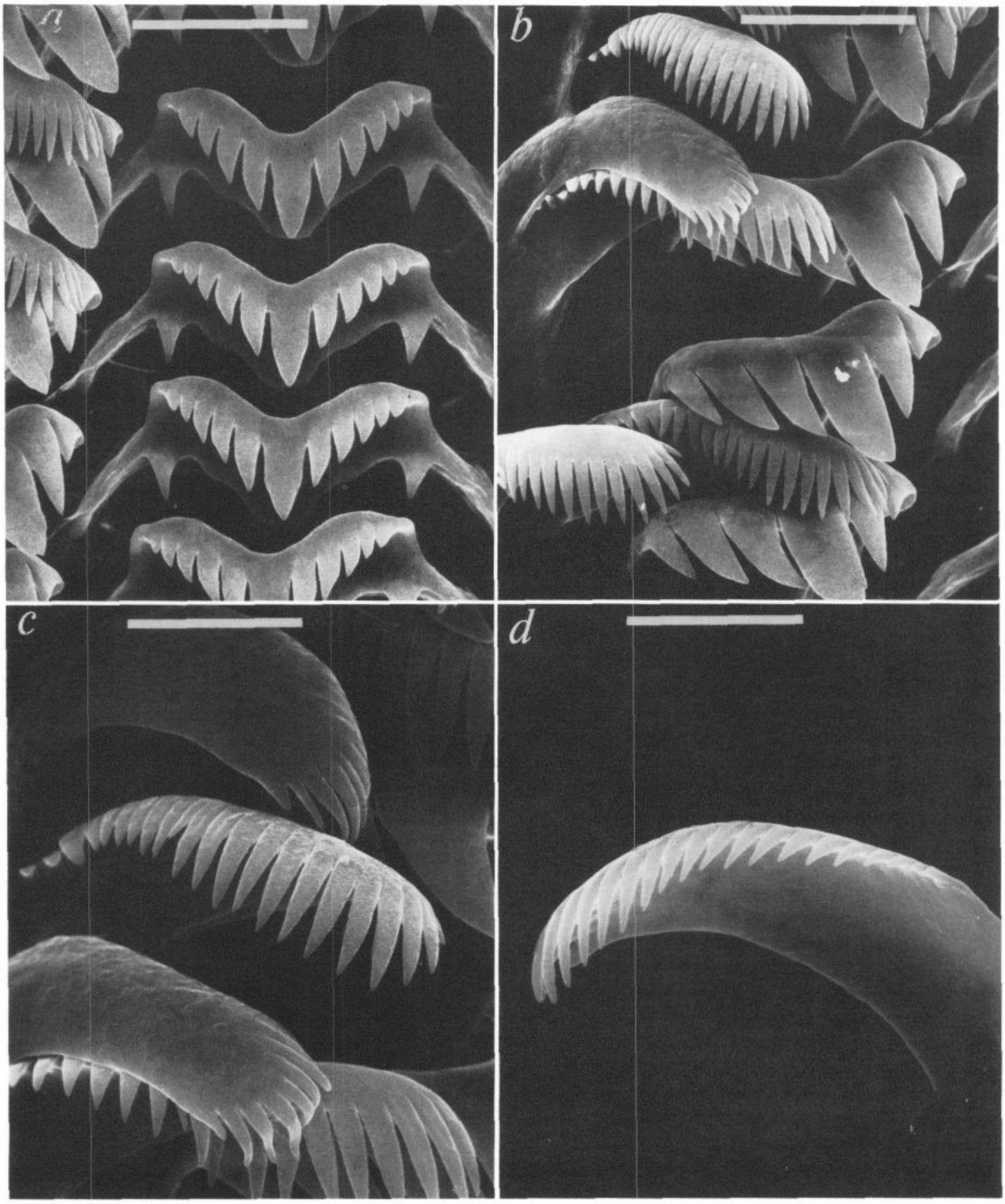


Fig. 31. Radula of *P. nanus,* USNM 850354, Five Springs. a, Centrals (bar = 15 μm); b, Laterals and inner marginals (bar = 13.6 μm); c, Inner marginals (bar = 7.5 μm); d, Outer marginal (bar = 6 μm).

Sportinggoods tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Fairbanks Spring, 859151 (holotype), 859152 (paratypes), UF 93960 (paratypes), 850298, 7 Nov 1985; 850299, 7 Jul 1986.—Crystal Pool, 850300, 859153, 8 Nov 1985.—Big Spring, 850302, 859212, 8 Nov 1985; 850301, 8 Jul 1986.

Diagnosis.—A fairly large-sized species, with elongate-conic shell. Whorls with sub-

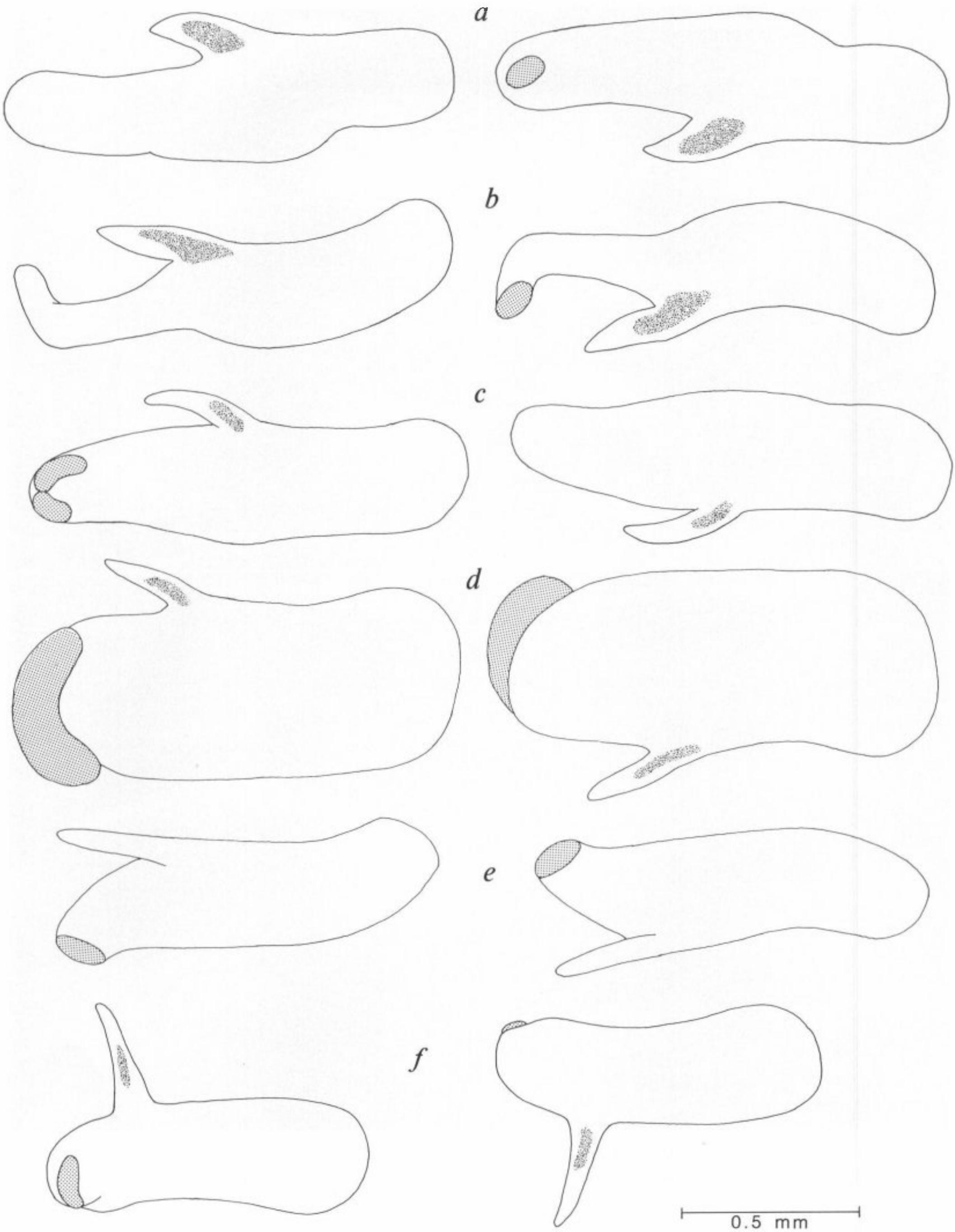


Fig. 32. Penes of *P. nanus*: a, b, USNM 850354, Five Springs; c, d, USNM 850356, Mary Scott Spring; e, USNM 850360, spring (southern) N of Collins Ranch Spring; f, USNM 850358, Collins Ranch Spring.

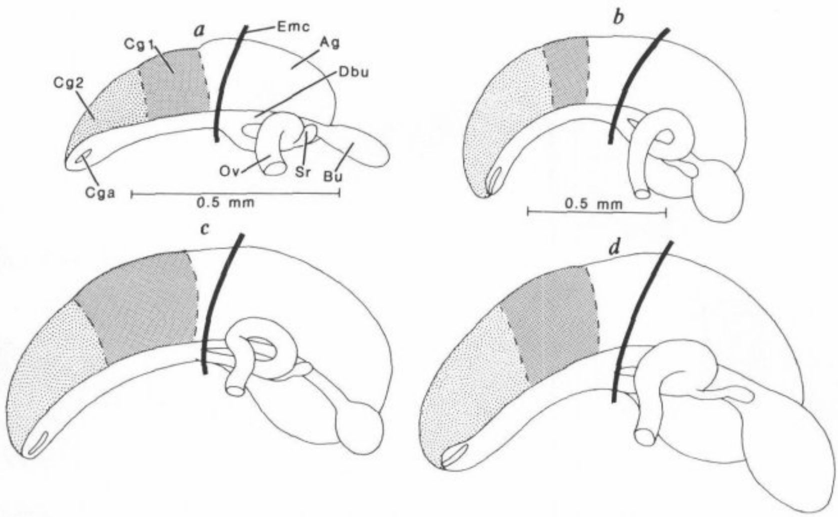


Fig. 33. Pallial oviducts of *Pyrgulopsis* spp., viewed from left side: a, b, *P. nanus* (a, USNM 850354, Five Springs; b, USNM 850356, Mary Scott Spring); c, *P. pisteri,* USNM 850364, Marsh Spring; d, *P. isolatus,* USNM 850366, spring S of Clay Pits. "c" and d drawn to same scales as a and b, respectively. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; Ov = oviduct; Sr = seminal receptacle.

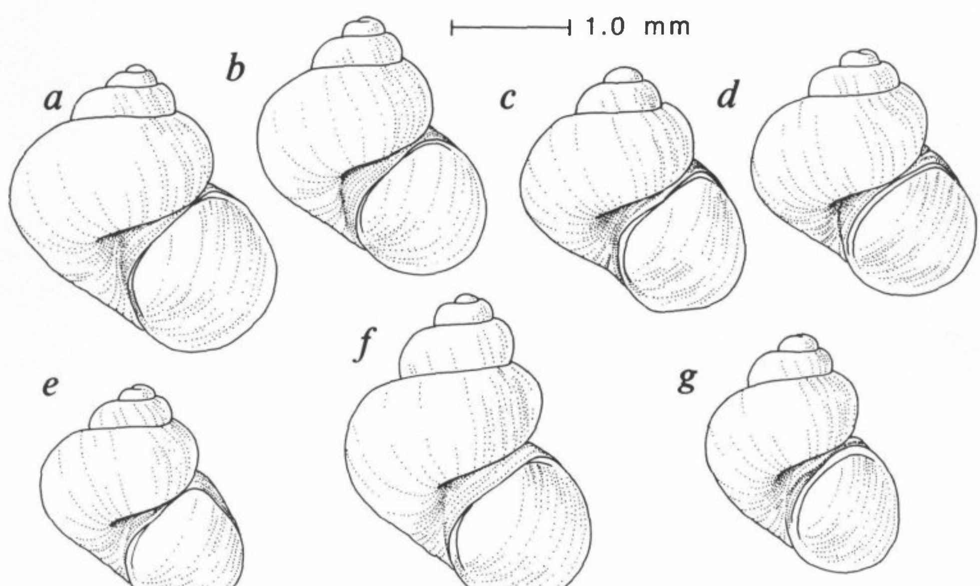


Fig. 34. Shells of *P. pisteri* and *P. isolatus*: a–e, *P. pisteri* (a, b, USNM 859199, North Scruggs Spring; c, d, paratypes, USNM 859198, Marsh Spring; e, USNM 859200, observation pond below School Spring); f, g, *P. isolatus,* paratypes, USNM 859202, spring S of Clay Pits.

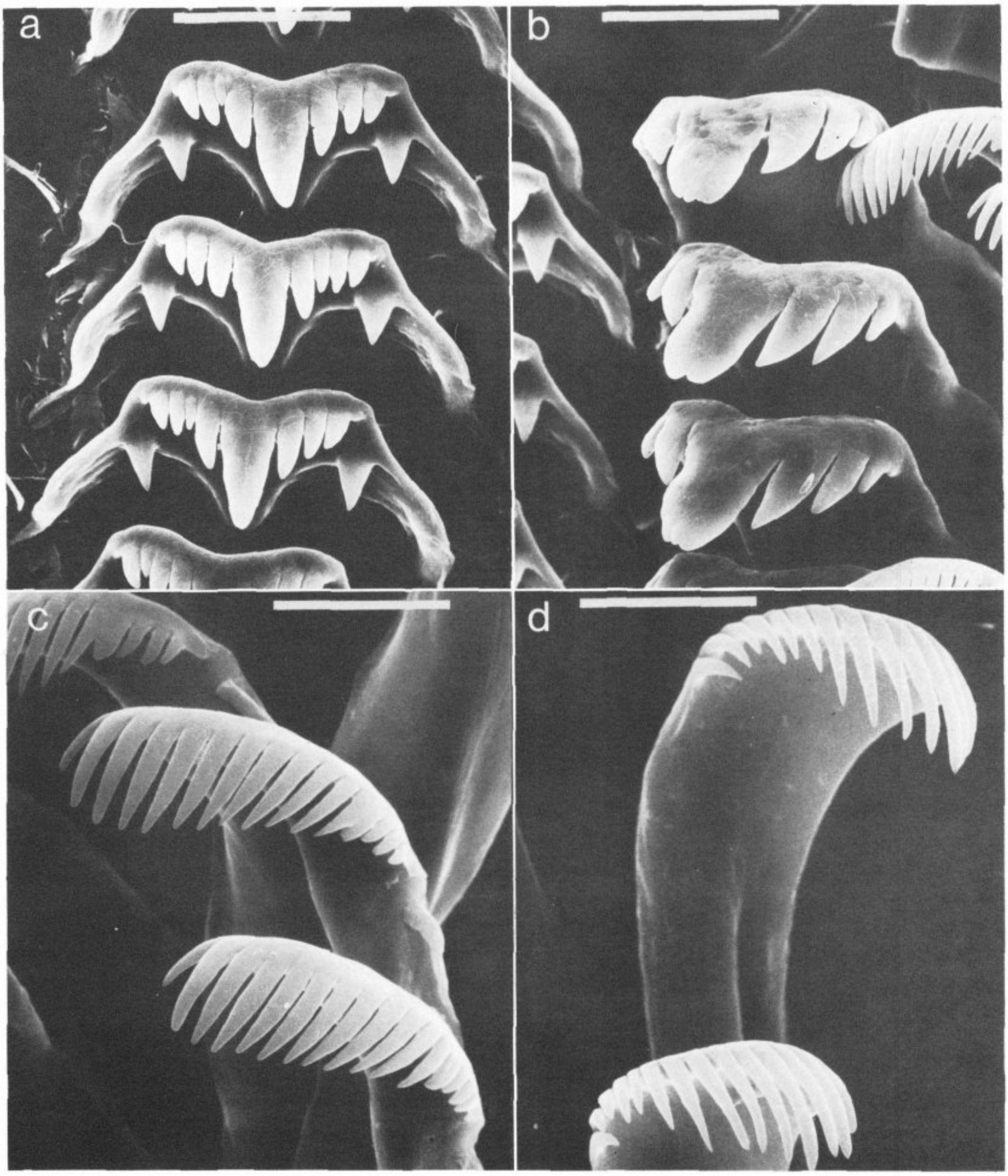


Fig. 35. Radula of *P. pisteri*, USNM 850364, Marsh Spring. a, Centrals (bar = 20 μm); b, Laterals (bar = 20 μm); c, Inner marginals (bar = 12 μm); d, Outer marginals (bar = 6.7 μm).

sutural angulations; outer apertural lip strongly sinuate. Central radular teeth with 2 pairs of basal cusps. Penis with 3 papillae on inner curvature (2 distal); outer curvature often with papilla at base.

Description.—Shell (Figs. 39a, 40) 2.7–4.0 mm high, about twice as tall as wide. Whorls, 5.0–7.0, well-rounded, fairly rapidly cxpanding, with impressed sutures. Translation rate (T) moderate, 5.2–7.9. Spire

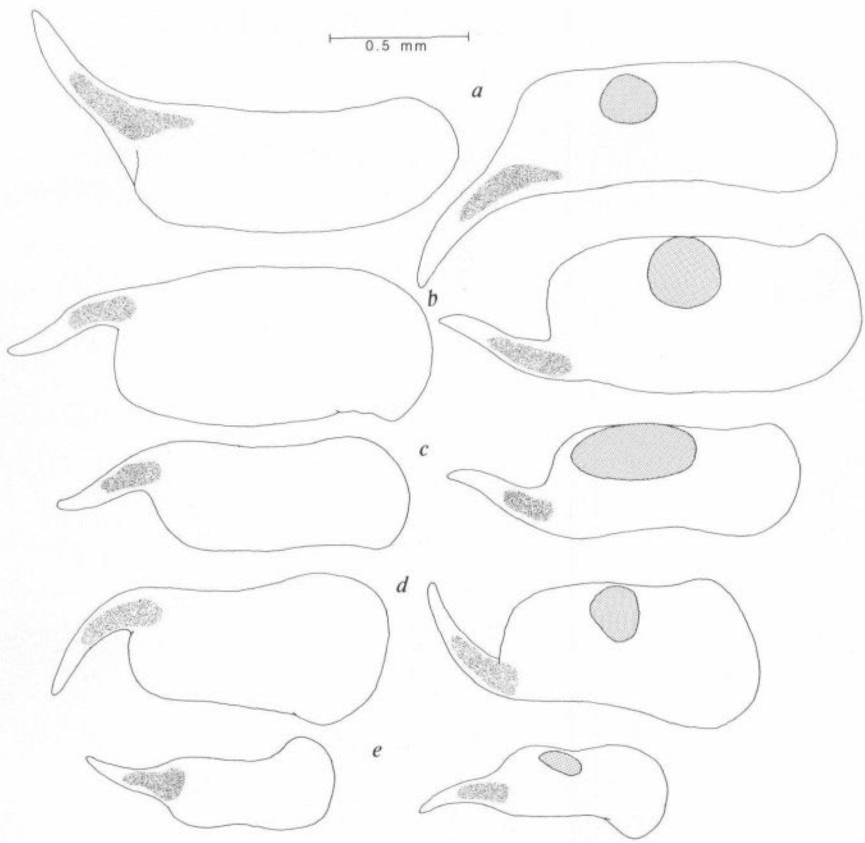


Fig. 36. Penes of *P. pisteri*: a, b, USNM 850362, North Scruggs Spring; c, d, USNM 850364, Marsh Spring; e, USNM 850365, observation pond below School Spring.

slightly convex; apex often eroded. Body whorl ca. 60% of shell height. Shell colorless, transparent (although eroded apex whitened); periostracum light brown. Aperture narrowly ovate, slightly angled above, usually fairly broadly adnate to body whorl above. Inner lip slightly thickened, reflected below; outer lip thin. Umbilicus chink-like. Growth lines moderately pronounced.

Visceral coil darkly pigmented with melanin, especially on digestive gland and stomach. Snout and sides of head/foot variably dusted with grey or brown pigment. Operculigerous lobe darkly pigmented internally. Penis frequently with small, distal pigment patch. Proximal papillae often darkly pigmented and bases of distal papillae sometimes streaked with melanin.

Radular (Fig. 41) formula: 5-1-5/2-2, 3-1-4, 22, 34; width of central tooth, 0.025 mm. Cusps on outer marginals (Fig. 41d) relatively numerous. Ctenidium with up to 25 small filaments. Prostate gland (Fig. 42a) bean-shaped, with more than one-third of length pallial. Posterior vas deferens (Vd1) enters left side of prostate gland, near posterior edge; anterior vas deferens (Vd2) exits from anterior tip of gland as thickened tube. Vas deferens only slightly looping in penis. Penis elongate, projecting well anterior to mantle collar, coiling counter-clockwise. Distal edge of penis blunt, with slight bulge on inner side. Penis with 2 distal, flask-shaped papillae on inner curvature; usually closely spaced near distal tip; and single papilla at base on inner curvature. Single, enlarged papilla often present at base on outer curvature. General organization of pallial

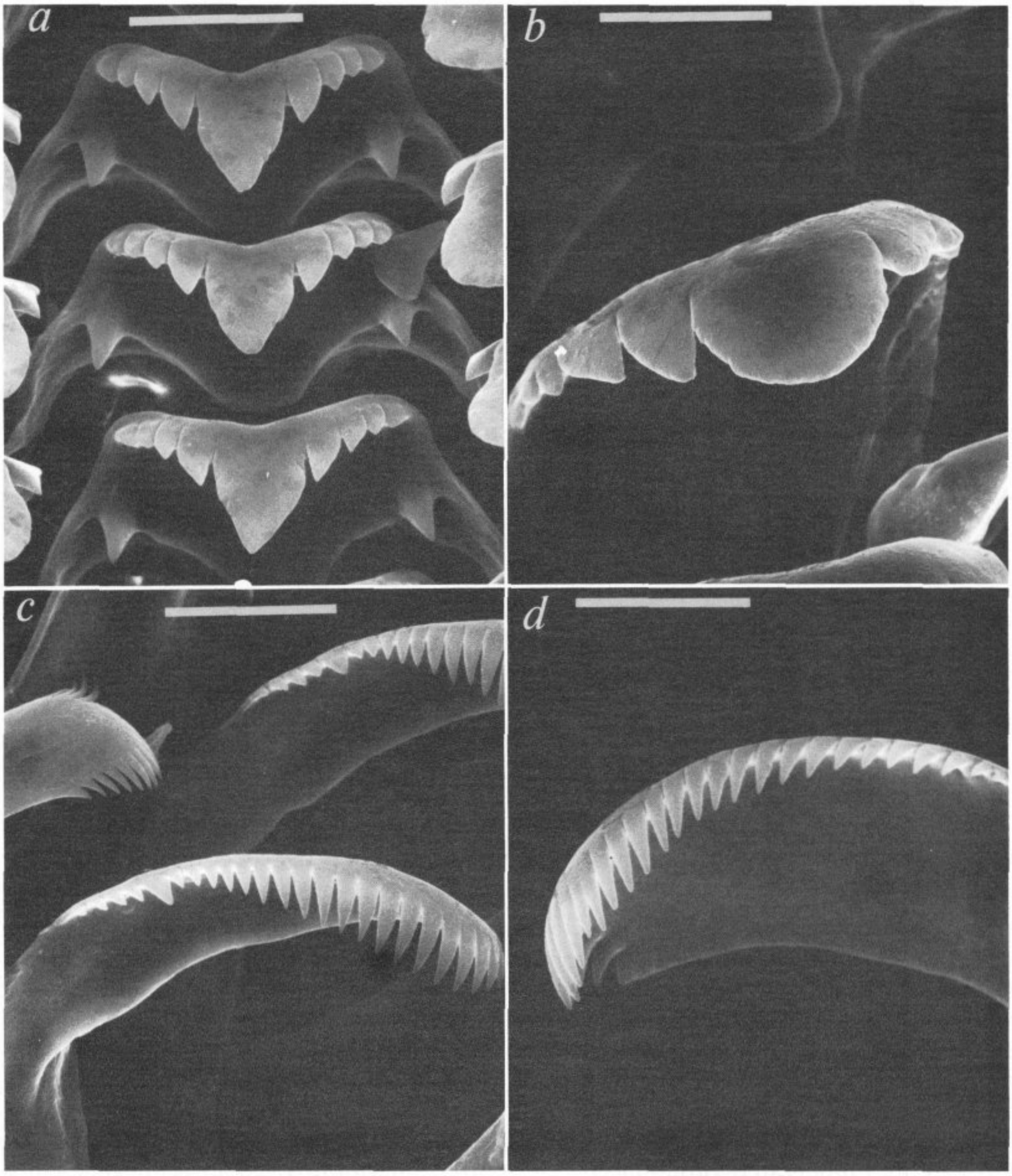


Fig. 37. Radula of *P. isolatus,* USNM 850366, spring S of Clay Pits. a, Centrals (bar = 15 μm); b, Lateral (bar = 10 μm); c, Inner marginals (bar = 10.7 μm); d, Outer marginal (bar = 5 μm).

oviduct complex (Fig. 43) as for genus. Capsule gland with small anterior sphincter (Cg2, Fig. 43a) and small (4–8) number of shelled embryos. Bursa copulatrix (Bu) ovate, partly covered by pallial oviduct; seminal receptacle (Sr) minute, positioned ventral to anterior portion of bursa. Oviduct (Ov) with small distal loop; oviduct and albumen gland (Ag) joining ventral to bursa, posterior to rear wall of pallial cavity (Emc). Just anterior to this point, oviduct joins duct of seminal receptacle (Fig. 43b), which then loops several times before joining narrow duct of bursa at or just posterior to end of pallial

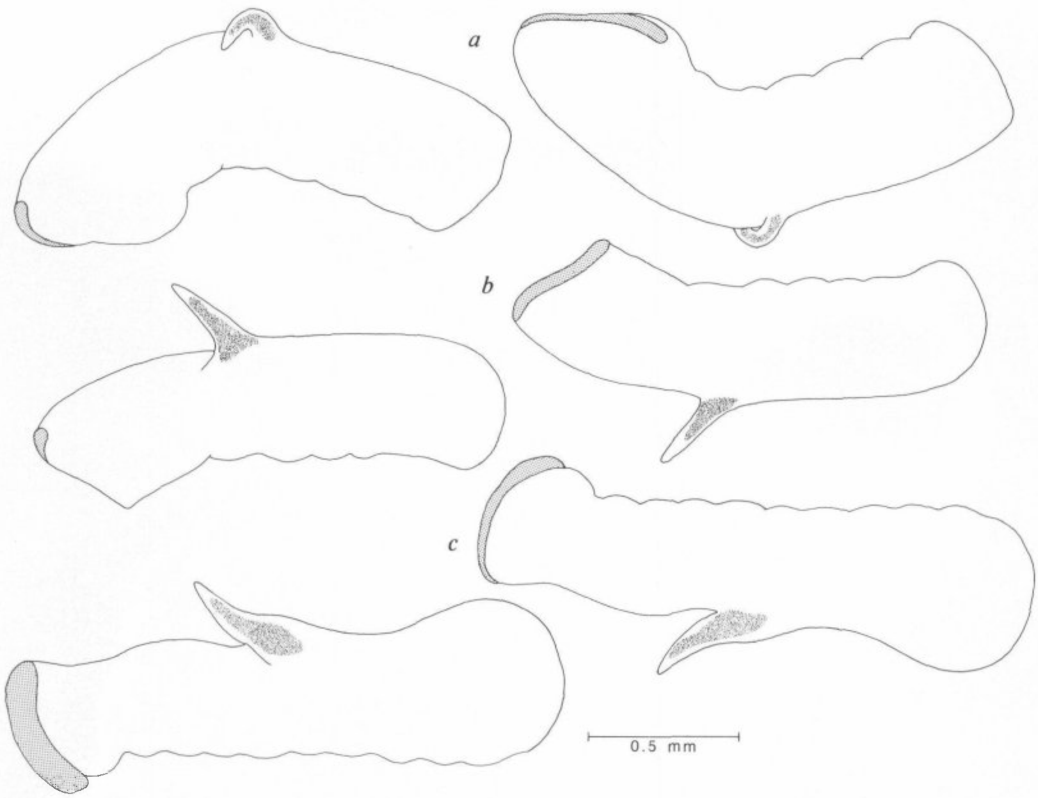


Fig. 38. Penes of *P. isolatus*, USNM 850366, spring S of Clay Pits.

cavity. Spermathecal duct (Sd) pressed against capsule gland, opening at about one-third of pallial cavity length from posterior wall.

Type locality.—Fairbanks Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to three large limnocrenes in Ash Meadows at ca. 671 m elevation (Fig. 44). Common at all three sites.

Etymology.—From Latin *angulus,* corner or bend, referring to characteristic angulate shell whorls.

Comparisons.—Shell form of *T. angulata* reminiscent of that of *T. clathrata* Stimpson from southeastern Nevada but separated from latter by smaller size, absence of teleoconch sculpture, and pattern of penial lobation. United with other Ash Meadows *Tryonia* by possession of three papillae on inner curvature (two distal); pattern differing from those seen in *T. clathrata* (>four papillae on inner curvature; Hershler and Thompson 1987) and taxa from Arizona (two papillae; Hershler and Landye 1988) and New Mexico (single papilla; Taylor 1983).

Distinguished from other Ash Meadows *Tryonia* by combination of large size and elongate-conic shell shape; angulate whorl profile; and strongly sinuate outer apertural lip. Most closely resembles *T. variegata,* n. sp. (described below), as both are relatively large-sized and occasionally have a papilla on outer penial curvature.

Tryonia variegata, new species
Amargosa Tryonia
Figs. 39e–g, 42b, e, g, h, 44–52

Tryonia.—Minckley and Deacon, 1975:108.
Small solid Tryonia.—Sada and Mozejko, 1984: fig. 5.

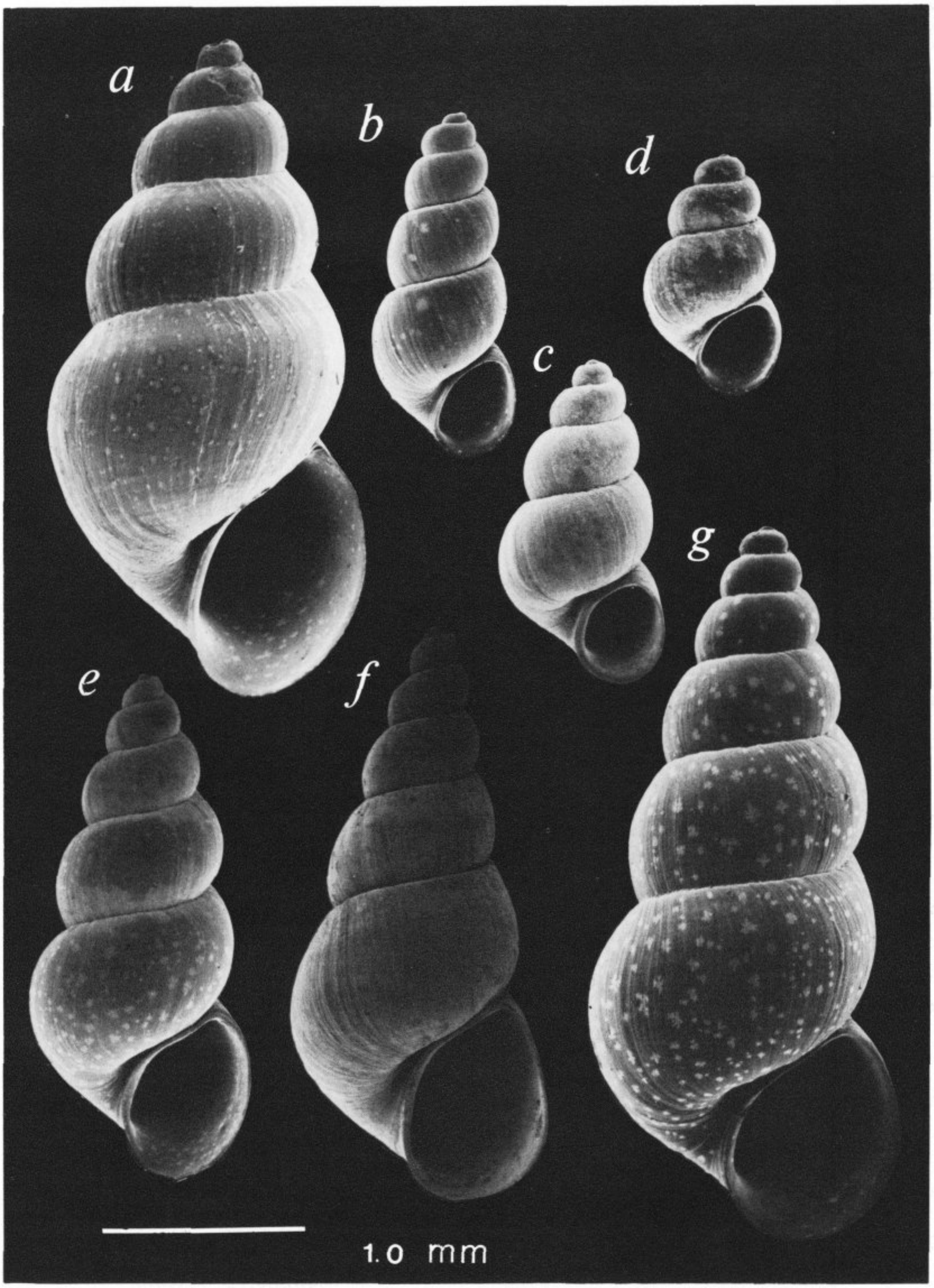


Fig. 39. SEM micrographs of shells of *Tryonia* spp.: a, *T. angulata,* holotype, USNM 859151, Fairbanks Spring; b, *T. elata,* holotype, USNM 859159, Point of Rocks Springs (Locality 35); c, d, *T. ericae* (c, holotype, USNM 859162, North Scruggs Spring; d, USNM 859165, spring (northern) N of Collins Ranch Spring); e–g, *T. variegata* (e, USNM 859157, Collins Ranch Spring; f, USNM 859155, Devils Hole; g, holotype, USNM 859166, Five Springs). Spots on shells are artifacts of SEM preparation.

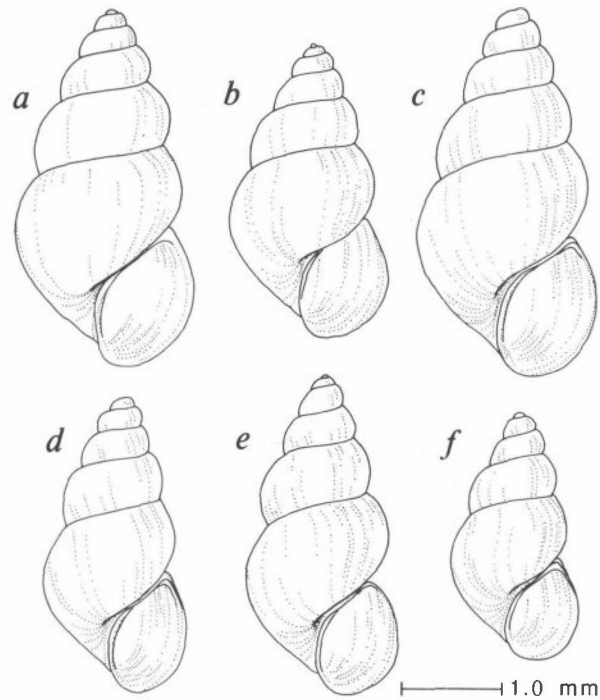


Fig. 40. Shells of *T. angulata*: a, b, Paratypes, USNM 859152, Fairbanks Spring; c, d, USNM 859153, Crystal Pool; e, f, USNM 859212, Big Spring.

Point of Rocks Tryonia.—Sada and Mozejko, 1984: fig. 5.

Devils Hole Amargosa Tryonia.—Sada and Mozejko, 1984: fig. 5.

Amargosa Tryonia snail.—USDI, 1984: 21673.

Point of Rocks Tryonia snail.—USDI, 1984:21673.

Amargosa tryonia.—Taylor in Williams et al., 1985:43.

Point-of-Rocks tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Five Springs, 859166 (holotype), 859167 (paratypes), UF 93961 (paratypes), 850314, 7 Nov 1985.—Chalk Spring, 850315, 859168, 10 Nov 1985.—Mary Scott Spring, 850316, 859169, 9 Nov 1985; 850317, 8 Jul 1986.—North Scruggs Spring, 850327, 859175, 9 Nov 1985; 850326, 8 Jul 1986.—South Scruggs Spring, 850318, 859170, 9 Nov 1985.—Marsh Spring, 850319, 859171, 10 Nov 1985; 850320, 8 Jul 1986.—North Indian Spring, 850321, 859172, 10 Nov 1985.—South Indian Spring, 850322, 10 Nov 1985.—School Spring, 850323, 859173, 10 Nov 1985; Observation pond below School Spring, 850324, 10 Nov 1985.—Devils Hole, 859155, 850304, 8 Nov 1985; 850303, 8 Jul 1986.—Spring (southern) N of Collins Ranch Spring, 850307, 859158, 9 Nov 1985; 850308, 8 Jul 1986.—Collins Ranch Spring, 859156, 859157, 850305, 9 Nov 1985; 850306, 8 Jul 1986.—Spring S of Clay Pits, 850331, 10 Jul 1986.—Spring (western) near Crystal Reservoir, 850325, 859174, 10 Nov 1985.—Spring (eastern) near Crystal Reservoir, 850328, 859176, 9 Nov 1985.—Point of Rocks Springs (Locality 38), 850329, 859177, 8 Nov 1985.—Point of Rocks Springs (Locality 39), 850330, 859178, 9 Nov 1985. CALIFORNIA, INYO

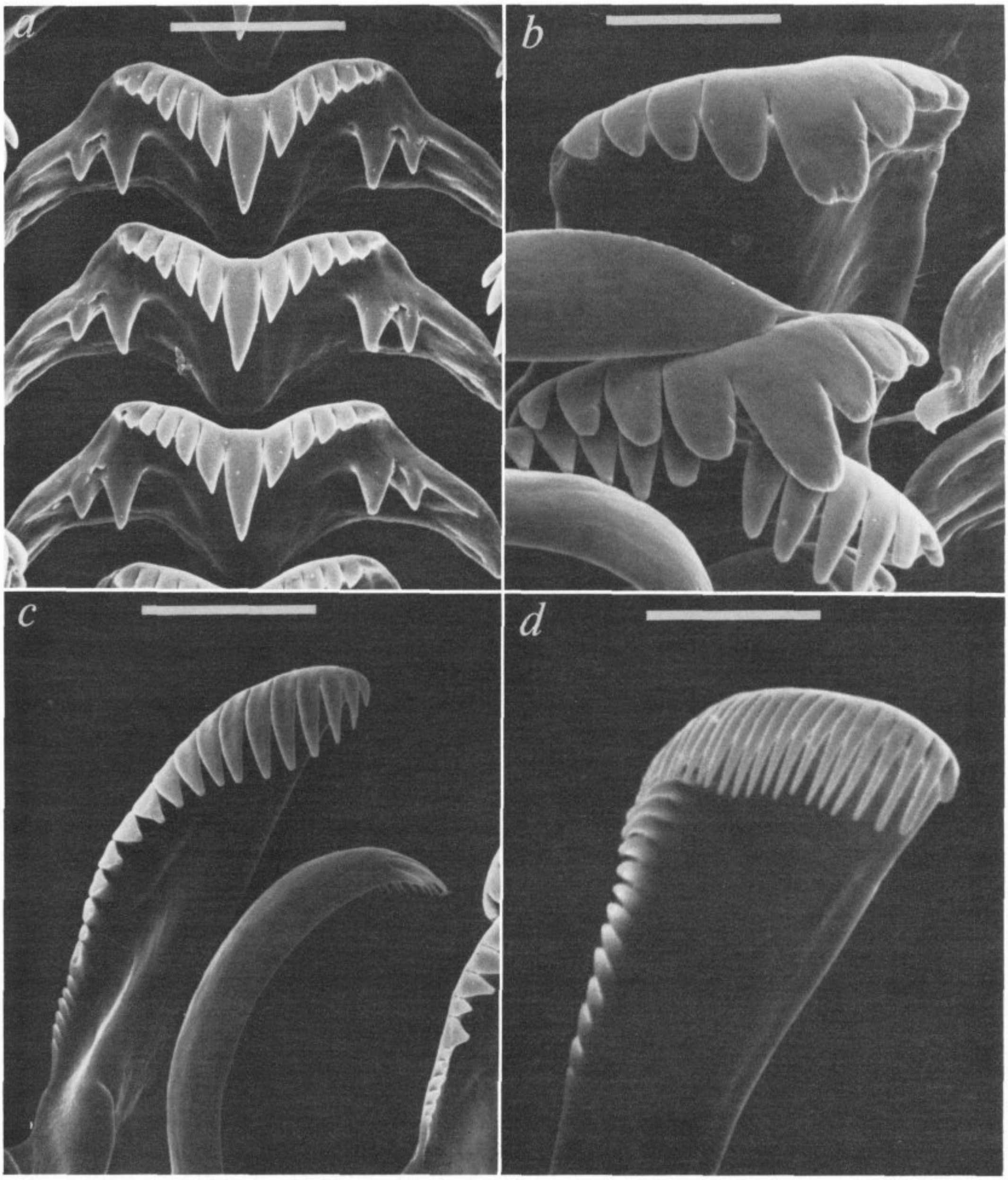


Fig. 41. Radula of *T. angulata,* USNM 850299, Fairbanks Spring. a, Centrals (bar = 8.6 μm); b, Laterals (bar = 6 μm); c, Inner marginals (bar = 7.5 μm); d, Outer marginal (bar = 3.8 μm).

→

Fig. 43. Female reproductive anatomy of *T. angulata,* USNM 850299, Fairbanks Spring: a, Pallial oviduct and associated structures, viewed from right side; b, Bursa copulatrix complex, viewed from right side. Position of bursa and anterior portion of duct in b indicated by dashed lines. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior section of capsule gland; Cg2 = anterior section of capsule gland; Dsr = duct of seminal receptacle; Emc = posterior end of pallial cavity; Oov = opening of oviduct into albumen gland; Osd = opening of spermathecal duct; Ov = oviduct; Sd = spermathecal duct; Sr = seminal receptacle.

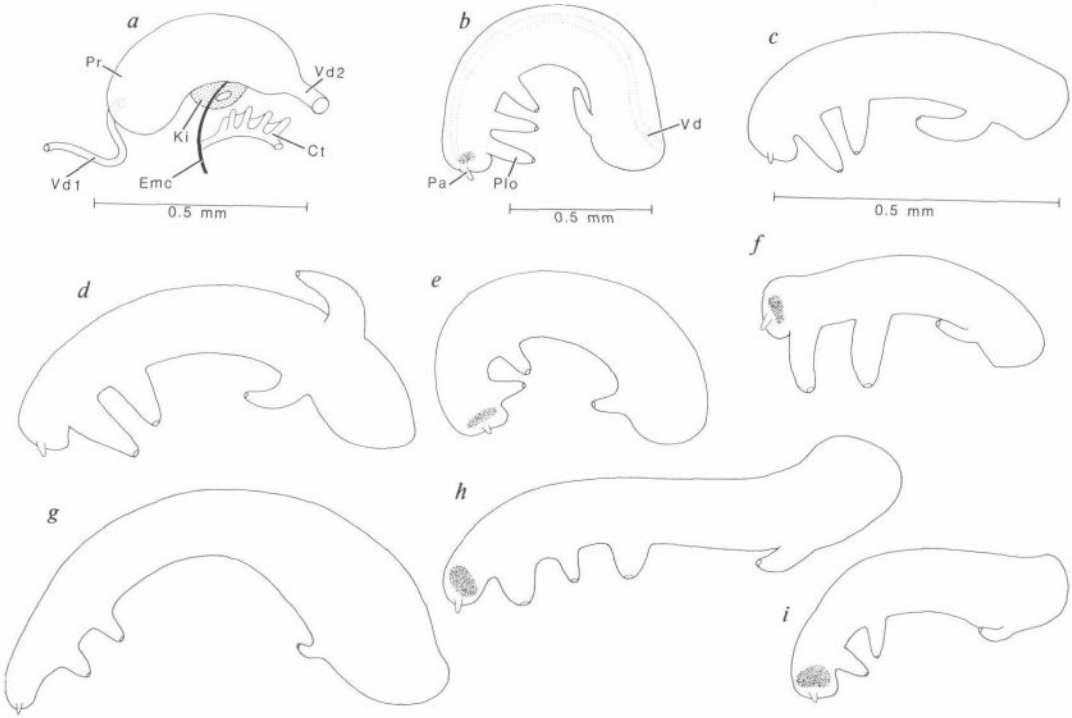
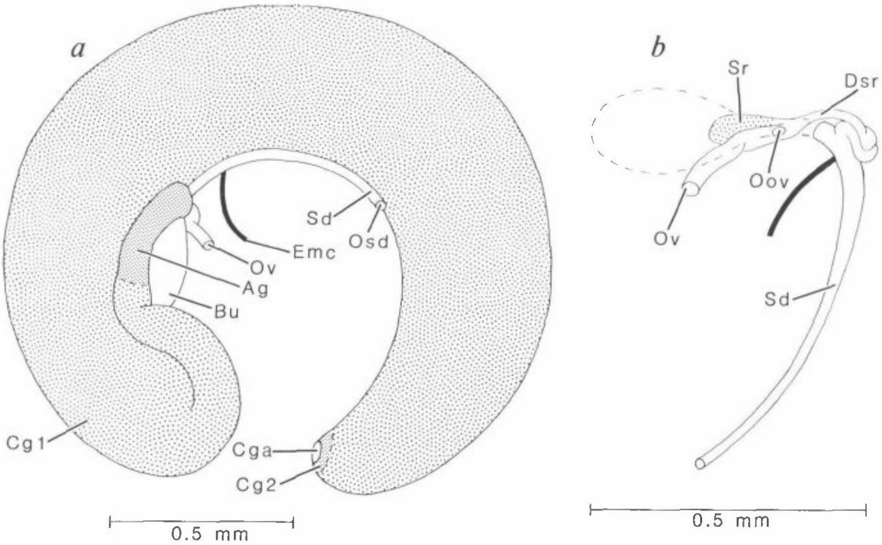


Fig. 42. Male reproductive anatomy of *Tryonia* spp.: a, d, *T. angulata,* USNM 850299, Fairbanks Spring (a, prostate gland and associated structures and organs, viewed from right side; d, penis); b, e, g, h, Penes of *T. variegata* (b, USNM 850329, Point of Rocks Springs [Locality 38]; e, USNM 850314, Five Springs; g, USNM 850303, Devils Hole; h, USNM 850305, Collins Ranch Spring); c, Penis of *T. elata,* USNM 850309, Point of Rocks Springs [Locality 35]; f, i, Penes of *T. ericae* (f, USNM 850312, North Scruggs Spring; i, USNM 850313, spring (northern) N of Collins Ranch Spring). "a," d, b, e, g, h; and c, f, i drawn to same scales, respectively. Ct = ctenidium; Emc = posterior end of pallial cavity; Ki = kidney; Pa = terminal papilla; Plo = penial lobe; Pr = prostate gland; Vd1 = posterior vas deferens; Vd2 = anterior vas deferens.



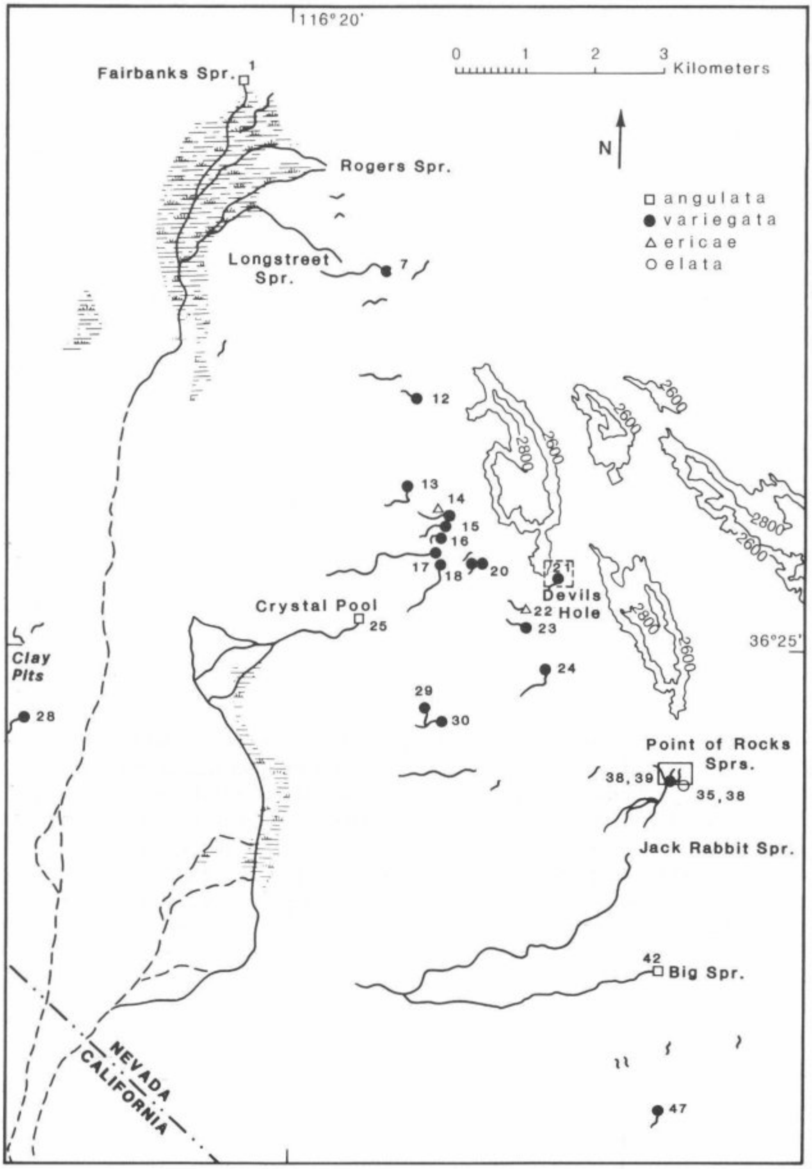


Fig. 44. Map showing distribution of *Tryonia* spp. in Ash Meadows.

COUNTY: Shoshone Spring (Shoshone), T22N, R7E, NW corner sec. 30, 12 Mar 1985.—Spring by Grimshaw Lake (Tecopa), T21N, R7E, NE corner sec. 9, 13 Mar 1985.

Diagnosis.—A variably-sized species (medium to large), with high-spired, turriform-aciculate shell. Aperture moderately sinuate. Central radular teeth with 2 pairs of basal cusps. Penis with 3 or 4 papillae on inner curvature (all but 1 distal); outer curvature occasionally with basal papilla.

Description.—Shell (Figs. 39e–g, 45–48) 2.8–7.5 mm high, more than twice as tall as wide. Whorls, 5.25–9.75, slightly to moderately convex, with slightly impressed su-

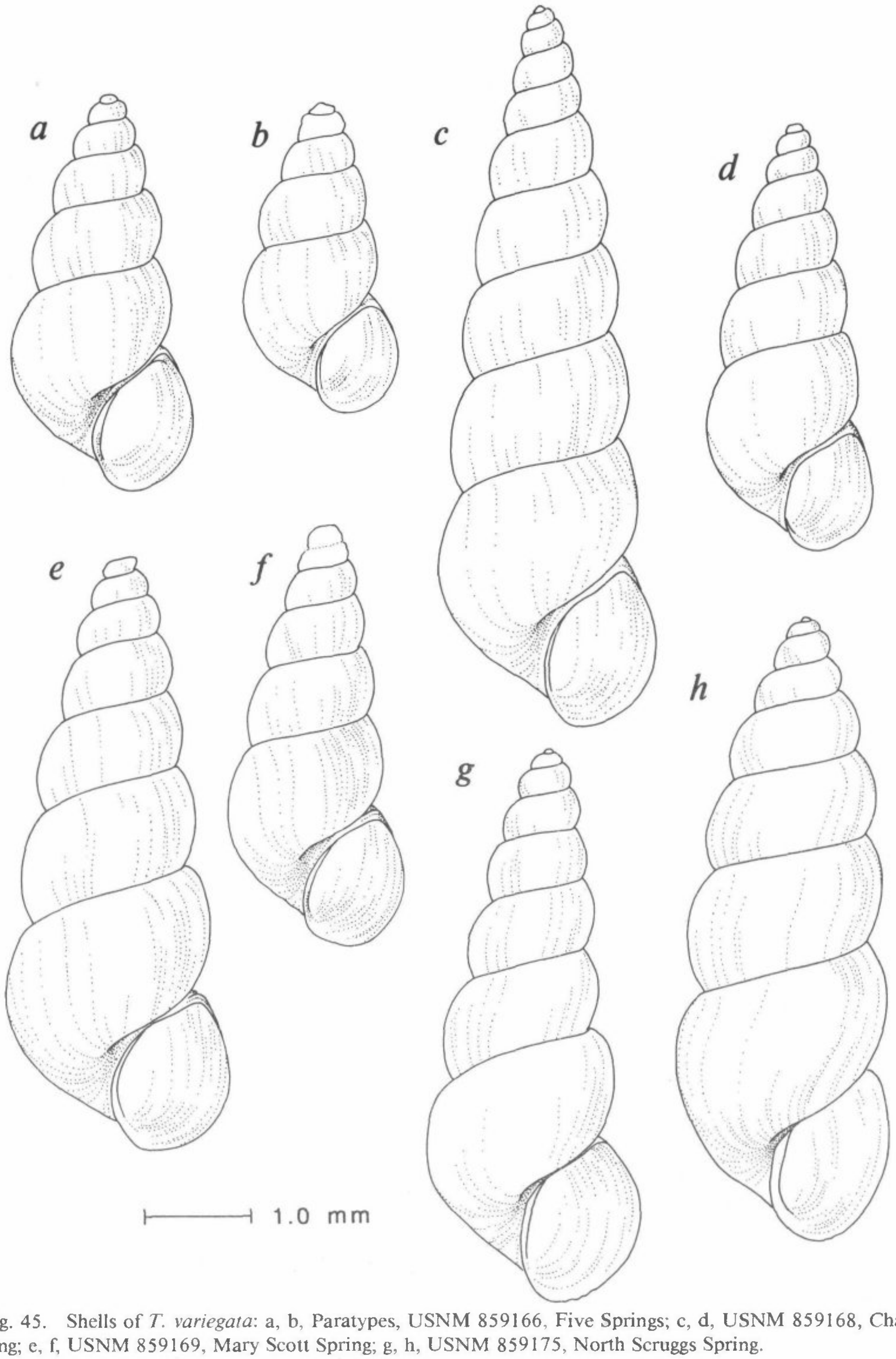


Fig. 45. Shells of *T. variegata*: a, b, Paratypes, USNM 859166, Five Springs; c, d, USNM 859168, Chalk Spring; e, f, USNM 859169, Mary Scott Spring; g, h, USNM 859175, North Scruggs Spring.

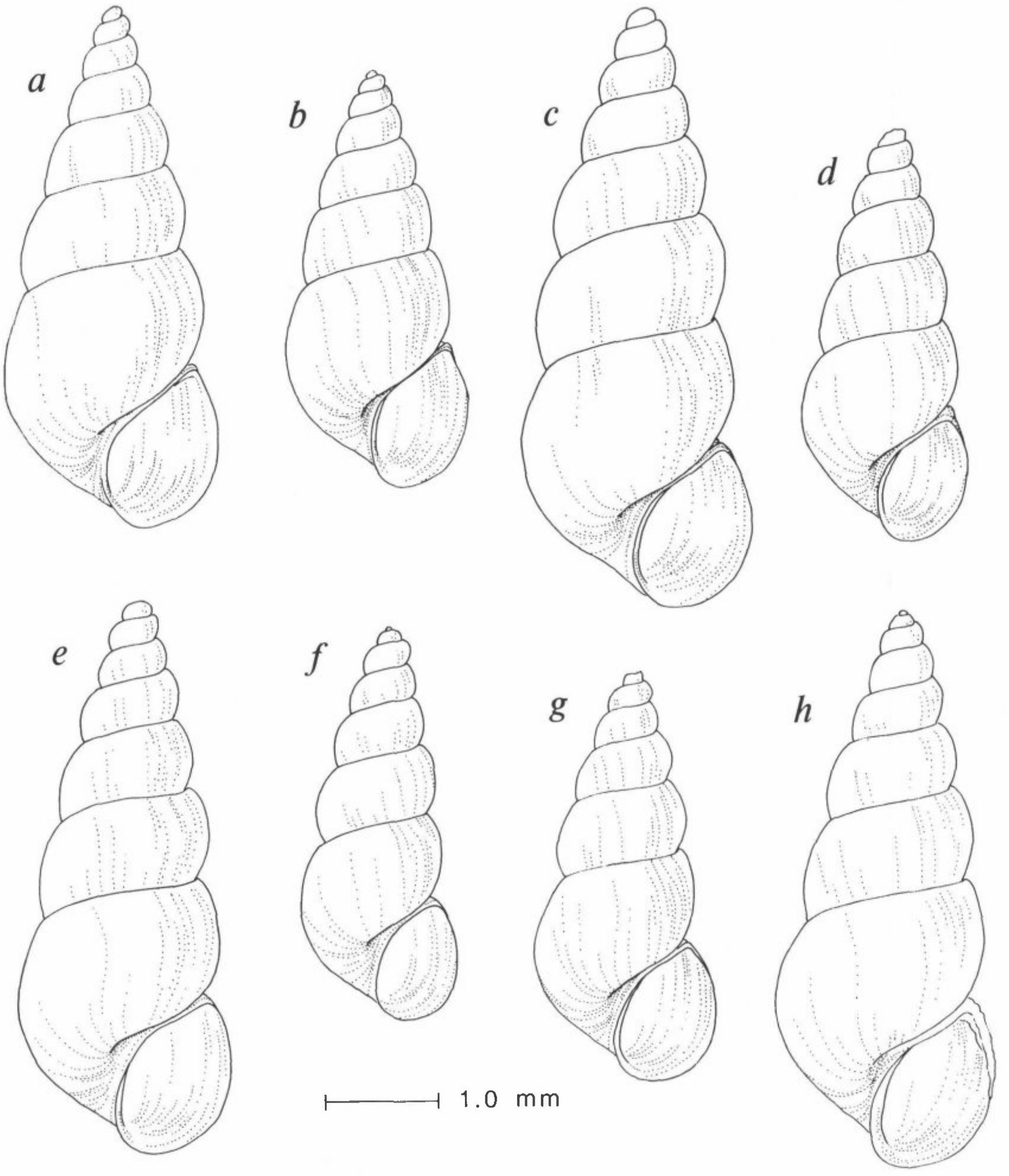


Fig. 46. Shells of *T. variegata*: a, b, USNM 859170, South Scruggs Spring; c, d, USNM 859171, Marsh Spring; e, f, USNM 859172, North Indian Spring; g, h, USNM 859173, School Spring.

tures. Elongation of shell reflected in high values of T varying from 5.3–21.7 (averaging 9.7). Whorls sometimes slightly shouldered; whorl outline unusually asymmetrical in one population (Figs. 39f, 48a, b), with abaxial point well below (rather than at) mid-point of whorl. Spire convex, with middle portion sometimes near-straight due

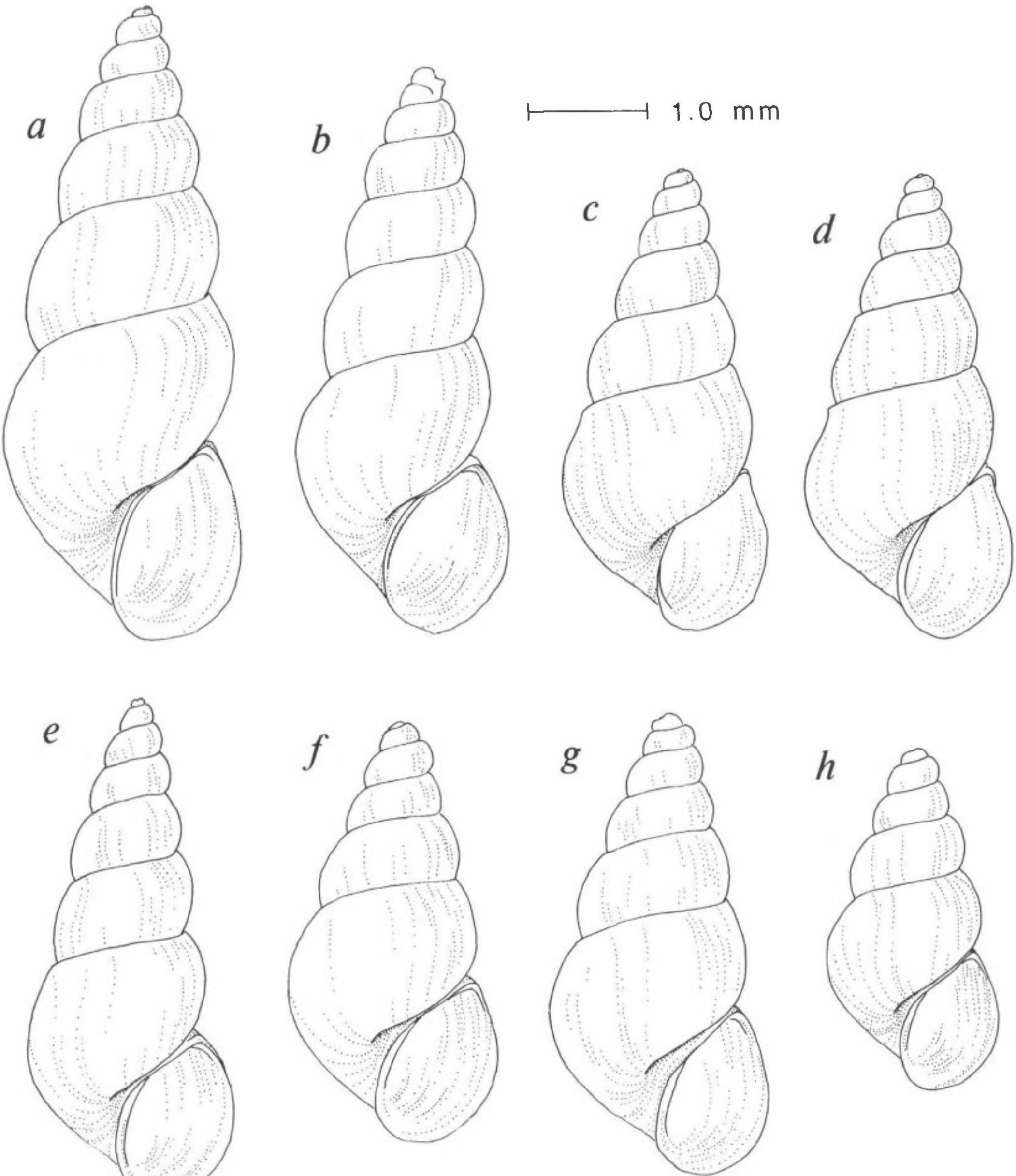


Fig. 47. Shells of *T. variegata*: a, b, USNM 859174, spring (western) near Crystal Reservoir; c, d, USNM 859176, spring (eastern) near Crystal Reservoir; e, f, USNM 859177, Point of Rocks Springs (Locality 38); g, h, USNM 859178, Point of Rocks Springs (Locality 39).

to little whorl expansion; apex often eroded. Body whorl ca. 50% of shell height. Shell colorless, transparent; periostracum thin, light brown. Aperture narrowly ovate, slightly angled above, often slightly loosened from body whorl (or with short adnate section). Inner lip slightly thickened, reflected below; outer lip thin. Umbilicus chink-

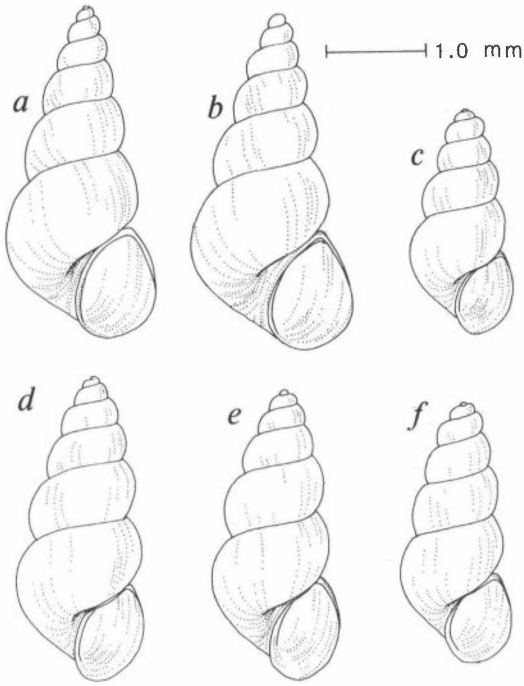


Fig. 48. Shells of *T. variegata*: a, b, USNM 859155, Devils Hole; c, d, USNM 859157, Collins Ranch Spring; e, f, USNM 859158, spring (southern) N of Collins Ranch Spring.

like to open. Growth lines pronounced; weak collabral threads or costae sometimes present.

Visceral coil darkly pigmented with melanin, especially on digestive gland and stomach. Snout and sides of head/foot usually darkly pigmented. Operculigerous lobe darkly pigmented internally. Penis frequently with small, distal pigment patch (Fig. 42b, e, h).

Radular (Figs. 49–52) formula: (4-7)-1-(4-7)/2-2, (3)4-1-5, 17–29, 22–30; width of central tooth, 0.023 mm. Penis (Fig. 42b, e, g, h) large: third distal papilla occasionally present on inner penial curvature. Median distal papilla often small, and likely representing an addition to common pattern of 2 distal lobes.

Type locality.—Five Springs, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Occurs in at least 19 small springs in Ash Meadows, Nye County, Nevada (Fig. 44), and in a few similar springs at Shoshone and Tecopa, Inyo County, California. Common at virtually all sites. Found on macrophytes, in detritus-covered areas, or on travertine blocks in springpools; and on travertine and in soft sediment along sides of upper portions of stream outflows.

Syntopic with *T. ericae*, n. sp. (described below) in North Scruggs Spring, and with *T. elata*, n. sp. (described below) in small spring at Point of Rocks.

Etymology.—From Latin *variegatus*, of different sorts, referring to variable shell of this species.

Comparisons.—Shell similar in general aspect to *T. protea* (Gould), but never exhibiting sculptural features characteristic of that species. Among Ash Meadows congeners, most similar to *T. angulata* (see above).

Remarks.—Species may be polytypic, as distinctive forms are found in Devils Hole (see above, Fig. 48a, b), in springs near Crystal Reservoir (shells highly aciculate, with collabral sculpture, Fig. 47a–d) and in a spring N of Collins Ranch Spring (unusually small-sized shells, Fig. 47c–f).

Tryonia ericae, new species
Minute Tryonia
Figs. 39c, d, 42f, i, 44, 53a–d, 54, 55

Minute slender Tryonia.—Sada and Mozejko, 1984: fig. 5.

Minute slender tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: North Scruggs Spring, 859162 (holotype), 859163 (paratypes), UF 93962 (paratypes), 850312, 9 Nov 1985.—Spring (northern) N of Collins Ranch Spring, 859165, 850313, 9 Nov 1985.

Diagnosis.—A very small-sized species with elongate-conic to turriform shell. Central teeth with 1 or 2 pair(s) of basal cusps.

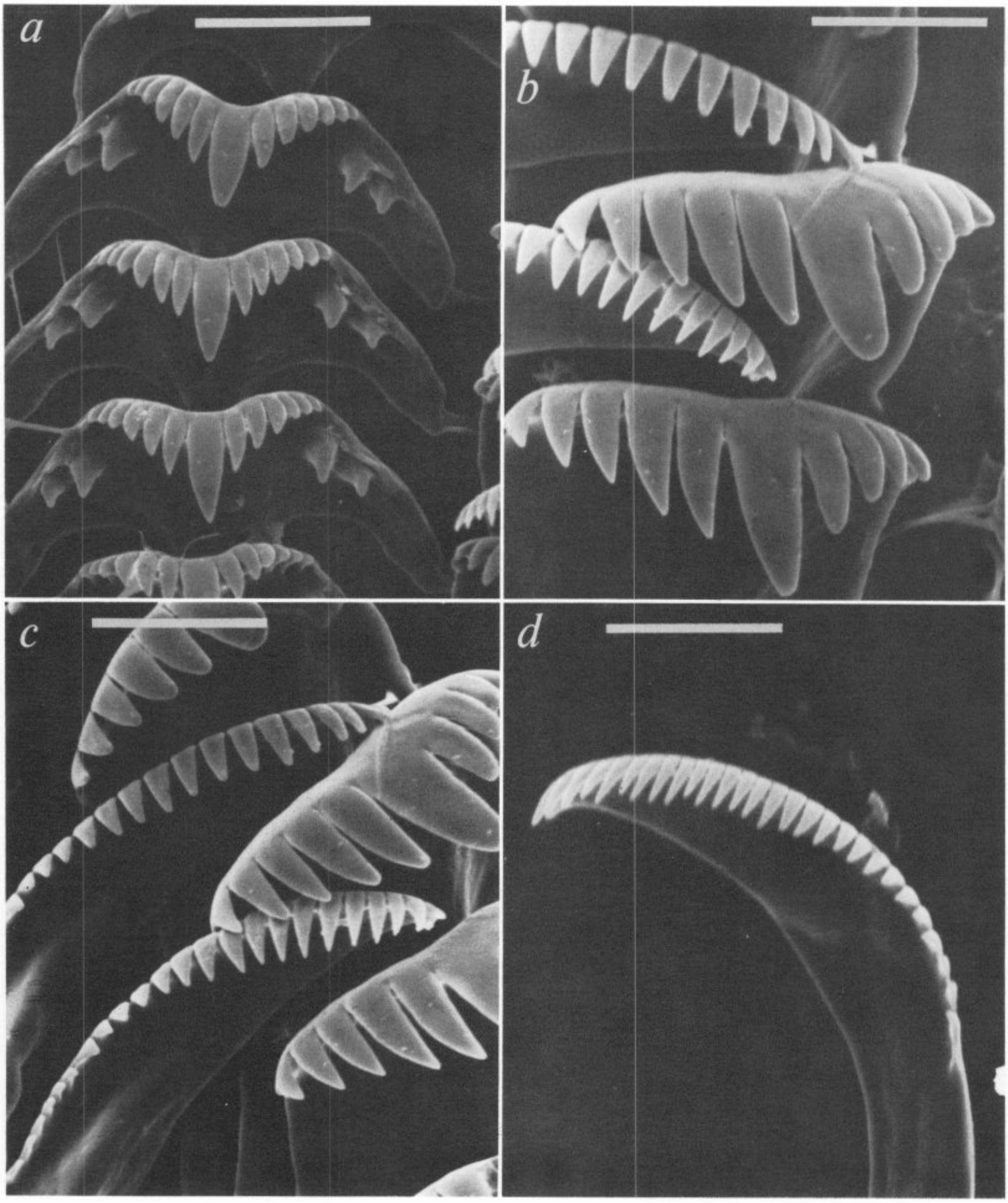


Fig. 49. Radula of *T. variegata*, USNM 850314, Five Springs: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginals (bar = 5.0 μm); c, Laterals and inner marginals (bar = 6.0 μm); d, Outer marginal (bar = 4.3 μm).

Penis small, with 3 papillae (2 distal) on inner curvature.

Description.—Shell (Figs. 39c, d, 53a–d) 1.2–1.9 mm high, slightly less than twice as tall as wide. Whorls, 3.75–6.0 well-rounded, with deeply impressed sutures. Whorls sometimes shouldered below sutures. Translation rate moderate, ca. 5.8. Spire

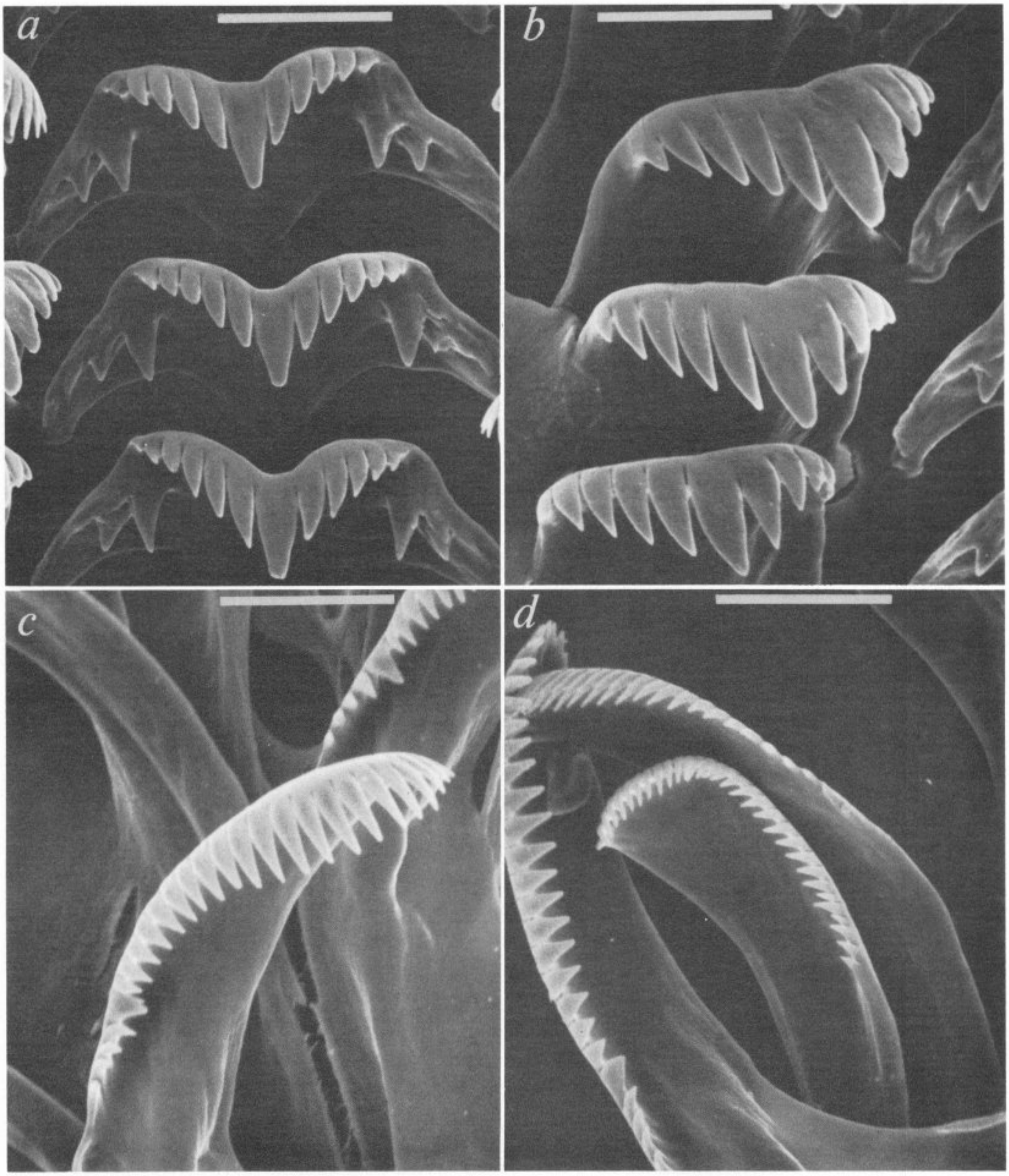


Fig. 50. Radula of *T. variegata,* USNM 850325, spring (western) near Crystal Reservoir: a, Centrals (bar = 8.6 μm); b, Laterals (bar = 7.5 μm); c, Inner marginal (bar = 6.0 μm); d, Inner and outer marginals (bar = 6.0 μm).

slightly convex. Body whorl ca. 65% of shell height. Shell colorless, transparent; periostracum very faint, light brown. Aperture ovate, slightly angled above, usually slightly separated from body whorl. Inner lip thickened, slightly reflected; outer lip thin, straight or very slightly convex. Umbilicus chink-like. Growth lines moderately pronounced.

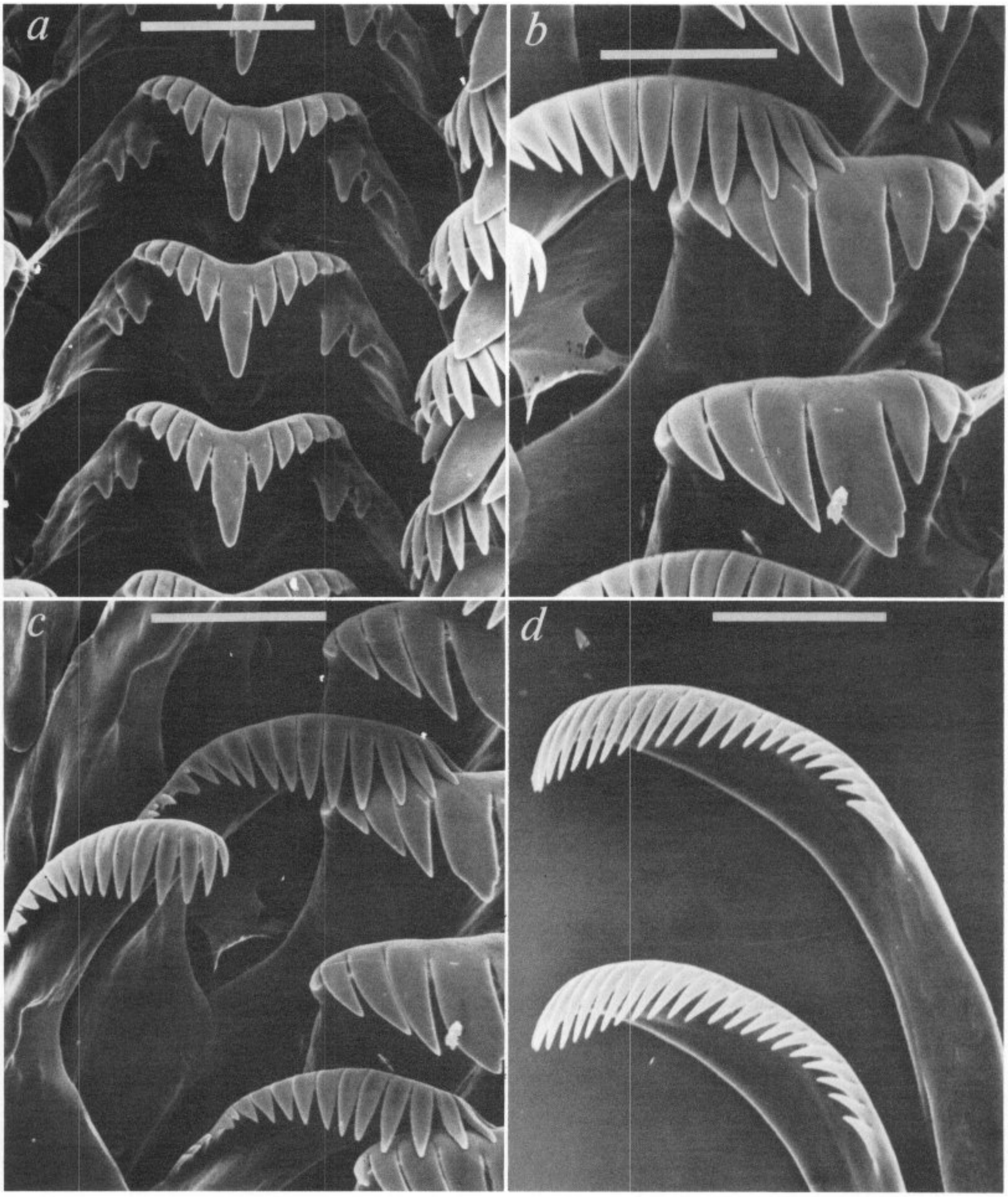


Fig. 51. Radula of *T. variegata,* USNM 850303, Devils Hole: a, Centrals (bar = 10 μm); b, Laterals and inner marginal (bar = 7.5 μm); c, Laterals and inner marginals (bar = 10 μm); d, Outer marginals (bar = 6 μm).

Visceral coil darkly pigmented. Head/foot usually lightly pigmented with grey-black melanin. Operculigerous lobe dark. Distal tip of penis with pigment patch.

Radular (Figs. 54, 55) formula: 6-1-6/(1)2-(1)2, 4-1-4(5), 20–25, 20–22; width of central tooth, 0.015 mm. Outer marginals with relatively few cusps (Figs. 54d, 55d). Distal penial papillae sometimes enlarged (Fig. 42f) relative to proximal papilla.

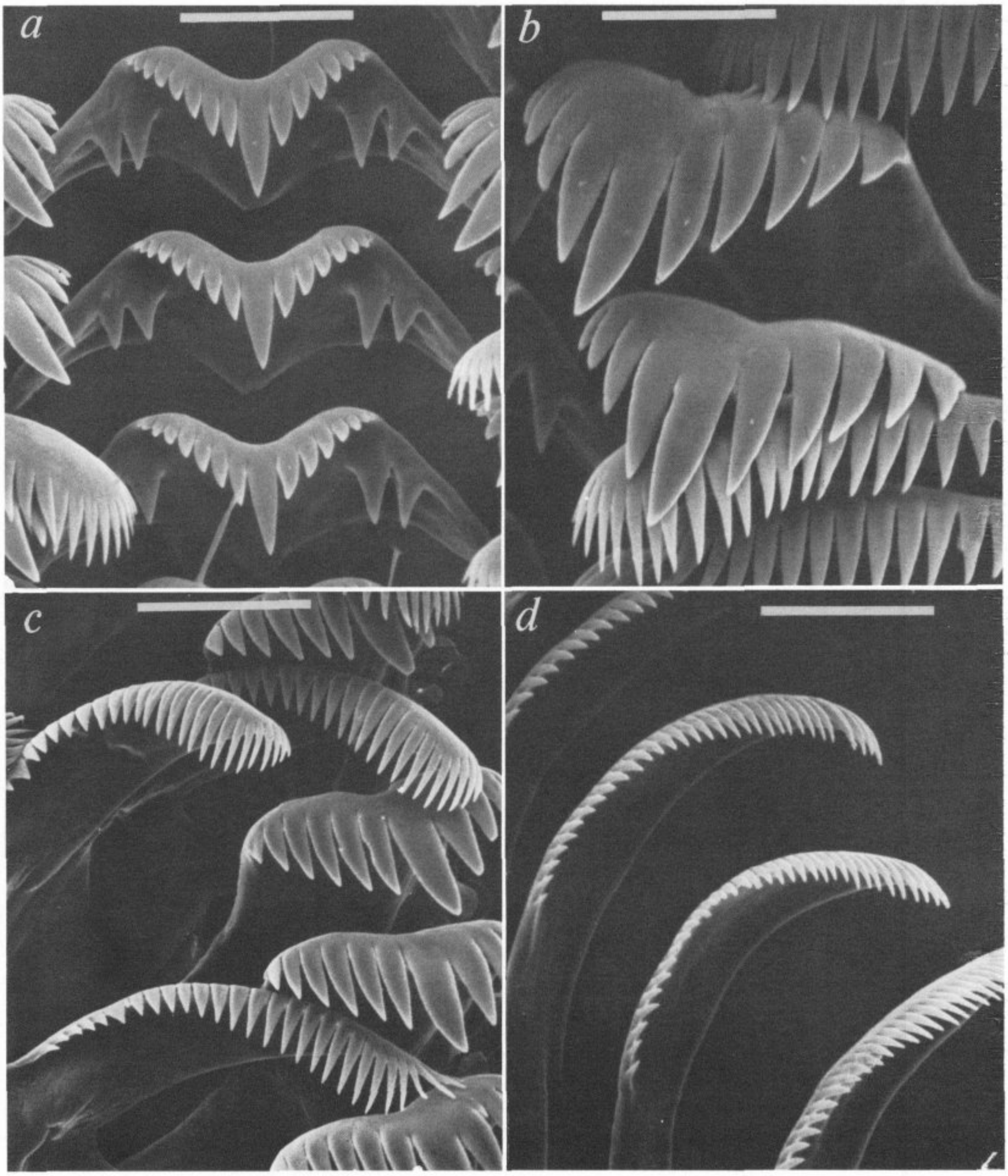


Fig. 52. Radula of *T. variegata*, USNM 850305, Collins Ranch Spring: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginals (bar = 5 μm); c, Laterals and inner marginals (bar = 7.5 μm); d, Outer marginals (bar = 5 μm).

Type locality.—North Scruggs Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to two small springs, North Scruggs Spring and spring (northern) N of Collins Ranch Spring, within four km of one another at ca. 708 m elevation in Ash Meadows (Fig. 44). Common in small springpool of former, on various macrophytes, and in stream outflow of latter, on loose travertine bits and algal mats.

Etymology.—Named after spouse of senior author.

Comparisons.—Distinguished from *T. angulata* and *T. variegata* by much smaller size. Overlaps in adult size with *T. elata,* n. sp. (described below) and shares with this probable sister species unusual character-states of small penis (relative to body size), and (occasional in former) single pair of basal cusps on central radular teeth. Separable from *T. elata* by typically smaller size, less elongate shell, and more rounded whorls.

Tryonia elata, new species
Point of Rocks Tryonia
Figs. 39b, 42c, 44, 53e–h, 56

Material examined.—NEVADA, NYE COUNTY: Point of Rocks Springs (Locality 35), 859159 (holotype), 859160 (paratypes), UF 93963 (paratypes), 850309, 8 Nov 1985.—Point of Rocks Springs (locality 38), 850310, 859161, 8 Nov 1985.

Diagnosis.—A small-sized species, with narrow, turriform shell. Central teeth with single pair of basal cusps. Penis with 3 papillae (2 distal) on inner curvature.

Description.—Shell (Figs. 39b, 53e–h) 1.8–2.9 mm high, slightly more than twice as tall as wide. Whorls, 5.25–6.75, moderately rounded with impressed sutures and prominent shoulders below sutures. Translation rate high, averaging 8.9. Spire slightly convex, with middle whorls often exhibiting little expansion; apex often eroded. Body whorl about half shell height. Shell colorless, transparent; periostracum very faint, light brown. Aperture ovate, slightly angled above. Inner lip slightly thickened, reflected, either broadly adnate (above) to or slightly separated from body whorl; outer lip straight or very slightly sinuate. Umbilicus chink-like to open. Faint spiral lines often on second whorl. Growth lines well-developed, with periodic elevated lines common.

Visceral coil darkly pigmented. Head/foot variably dusted with epithelial melanin. Operculigerous lobe lightly pigmented internally. Distal penis with pigment patch.

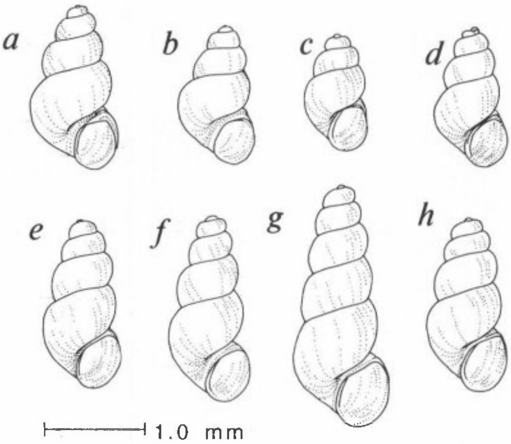


Fig. 53. Shells of *Tryonia* spp.: a–d, *T. ericae* (a, b, paratypes, USNM 859163, North Scruggs Spring; c, d, USNM 859165, spring (northern) N of Collins Ranch Spring); e–h, *T. elata* (e, f, paratypes, USNM 859160, Point of Rocks Springs [Locality 35]; g, h, USNM 859161, Point of Rocks Springs [Locality 38]).

Radular (Fig. 56) formula: 6-1-6/1-1, 4-1-4, 19, 23; width of central tooth, 0.015 mm. Penial lobation undistinctive (Fig. 42c).

Type locality.—Point of Rocks Springs (Locality 35), Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to two small springs on travertine mound at Point of Rocks, Ash Meadows (Fig. 44). Common in stream outflows in silted areas.

Etymology.—From Latin *elatus,* exalted or high, referring to endemism of species on elevated mound at Point of Rocks.

Comparisons.—Most similar to *T. ericae* (see above).

Morphometrics

Significant heterogeneity among species occurred in all three groups for each standard shell measurement used (ANOVA, $P < 0.05$). However, for two of three groups several Raupian parameters did not vary significantly among species (Group II; T, AS, W, $P > 0.08$; Group III, D, W, $P > 0.27$).

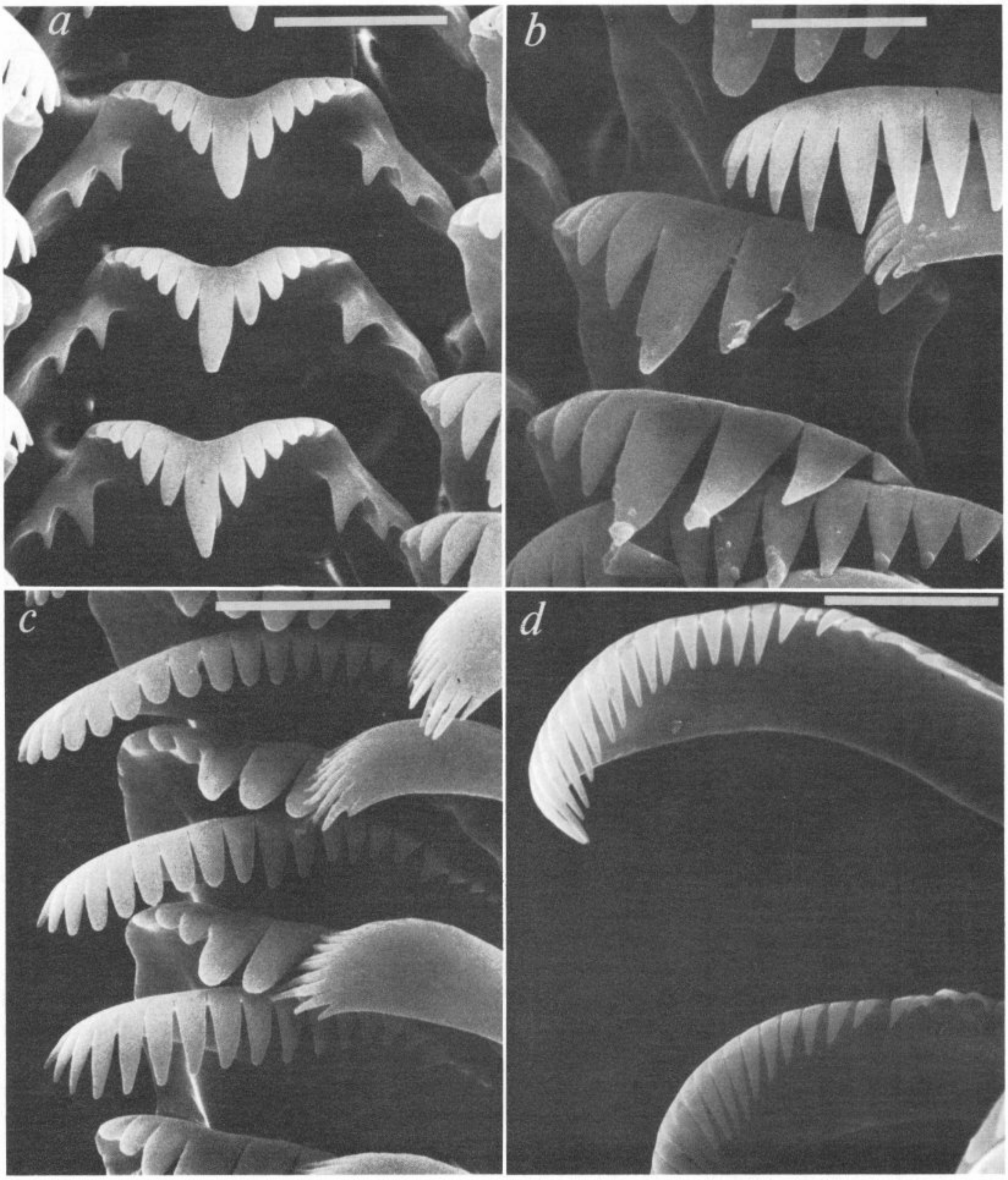


Fig. 54. Radula of *T. ericae,* USNM 850312, North Scruggs Spring: a, Centrals (bar = 6 μm); b, Laterals (bar = 4.3 μm); c, Laterals, inner and outer marginals (bar = 5 μm); d, Outer marginals (bar = 3 μm).

Results of discriminant analyses are in Tables 4–6. Overall classification was 86–93% in analyses using standard shell measurements. In analyses using Raupian parameters, classification was 71% for Groups I and II, but only 48% for Group II. If classification of individual species is considered, classification based on standard measurements was higher (often by >20%) in every case, with values exceeding 80% for every species except *P. crystalis,* in which one of three shells measured was misclassified (67%

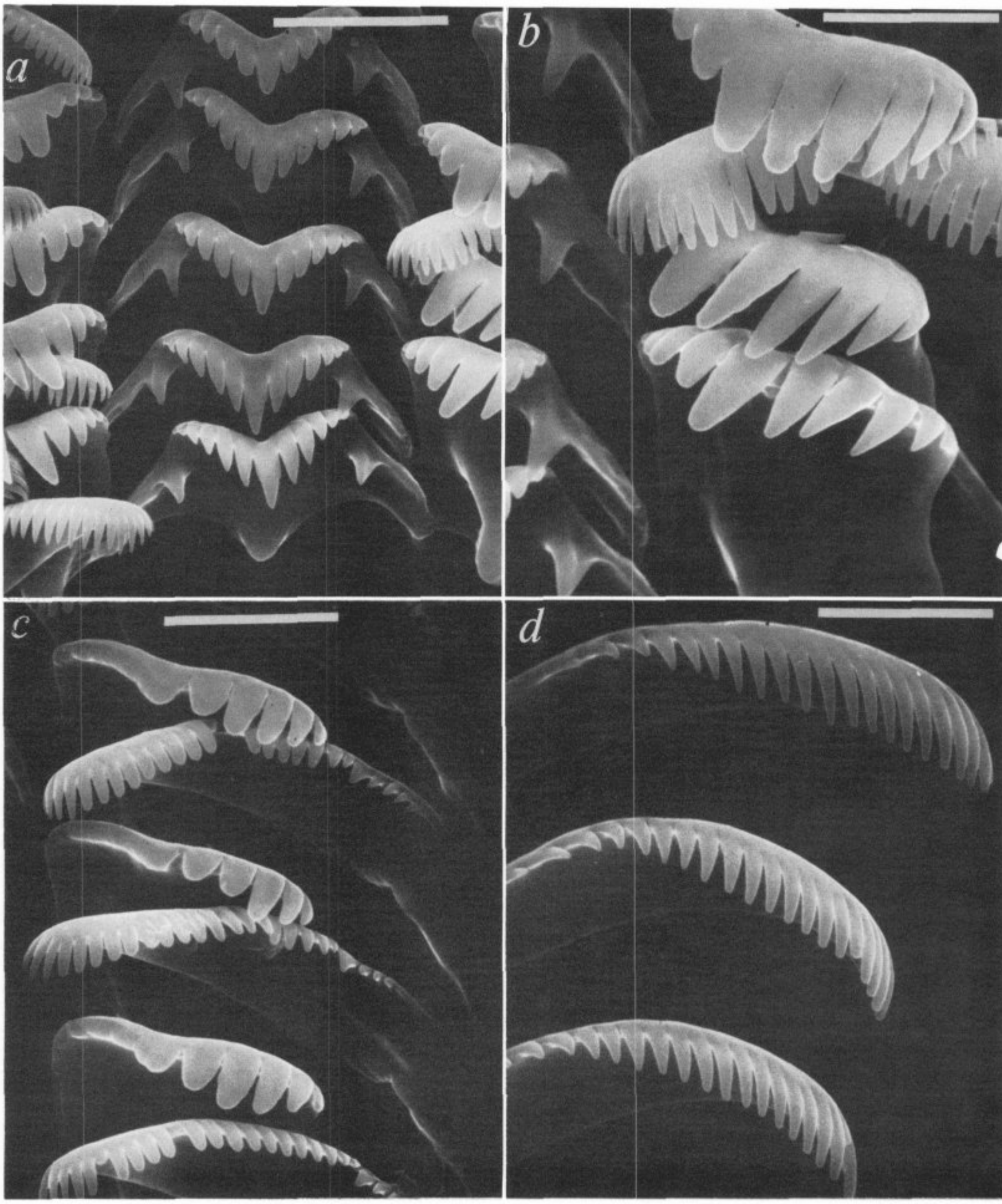


Fig. 55. Radula of *T. ericae*, USNM 850313, spring (northern) N of Collins Ranch Spring: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginal (bar = 4.3 μm); c, Laterals (worn) and inner marginals (bar = 5 μm); d, Outer marginals (bar = 3 μm).

classification). Significant ($P < 0.05$) separation of closest groups was achieved in all three analyses using standard measurements, but only in one of three (for *Tryonia* spp.) using Raupian parameters.

For this local example, standard shell measurements were obviously superior to Raupian parameters in discriminating among the taxa concerned. Poor performance by the latter suggests that size or size-

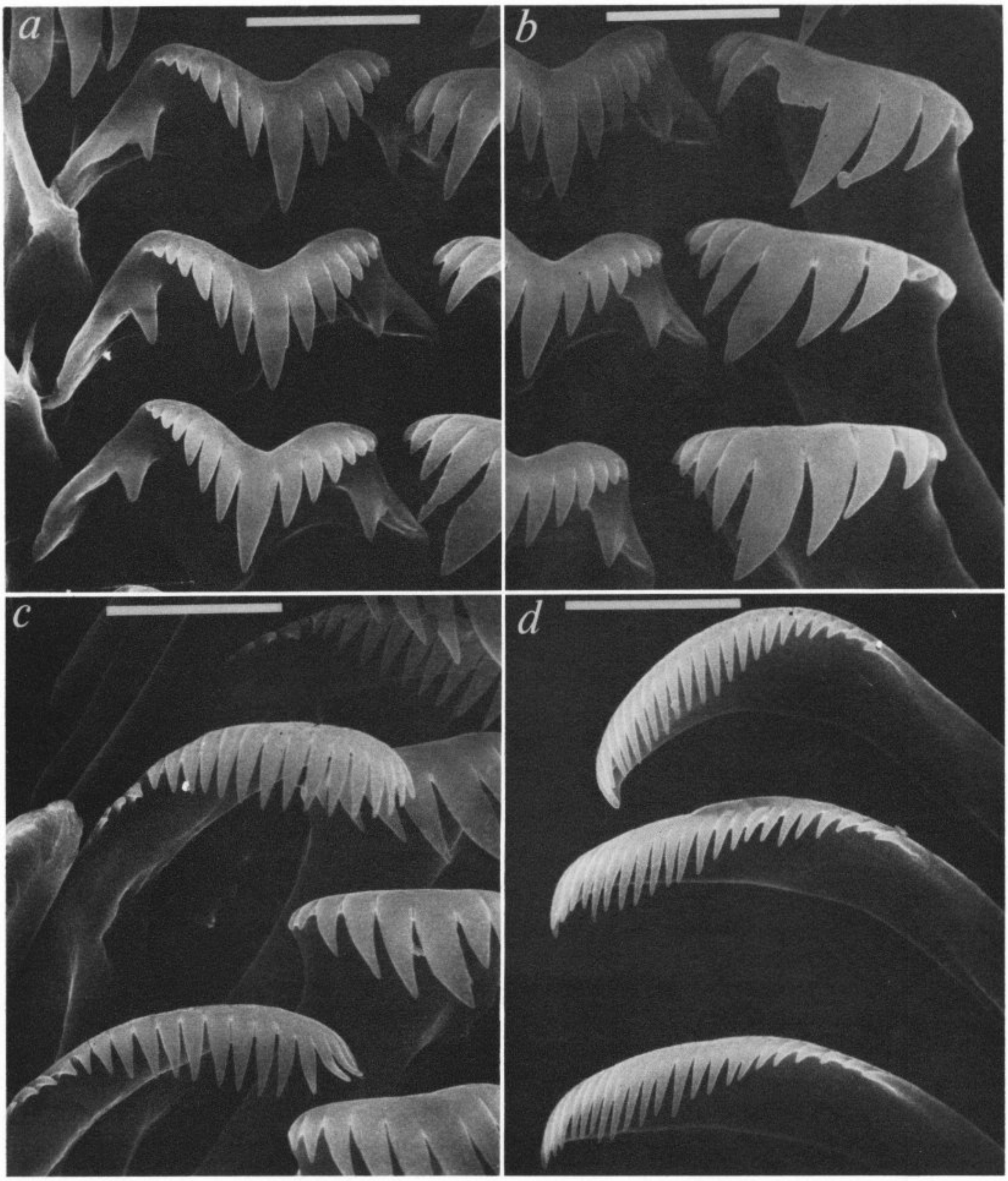


Fig. 56. Radula of *T. elata,* USNM 850309, Point of Rocks Springs (Locality 35): a, Centrals (bar = 6.7 μm); b, Centrals and laterals (bar = 6.7 μm); c, Laterals and inner marginals (bar = 7.5 μm); d, Outer marginals (bar = 4 μm).

correlated features (as quantified by standard measurements) vary more among species involved than shape (alone) as quantified by Raupian parameters. Translation (T) and whorl expansion (W) rates, responsible for much shape variation among gastropods (Raup 1966), were not even selected in two of three stepwise discriminant analyses. In the analysis of *Tryonia* spp., T was incorporated into the discriminant equation

Table 3.—List of species groups with number of specimens and populations used in discriminant analyses. Mean shell height (mm) is given for each species.

Group and species	$\overline{SH}$	Number of specimens	Number of populations
I—*Pyrgulopsis fairbanksensis*	2.84	14	1
P. crystalis	2.04	3	1
P. erythropoma	2.09	68	5
II—*P. nanus*	1.82	43	3
P. pisteri	2.41	31	2
P. isolatus	2.94	13	1
III—*Tryonia variegata*	4.53	180	14
T. angulata	3.29	39	3
T. elata	2.10	30	2
T. ericae	1.47	19	2

and used to separate species differing in shell elongation. We feel that our determination of Raupian parameters was accurate enough to have discerned variation among species except in the possible case of W, although the simplified estimate used was able to detect differences between the two genera involved (see Tables 1 and 2).

Discussion

The uniformly high percentage of correct classification of species using standard shell measurements lends support to our species level decisions. *Pyrgulopsis* species are also distinguished by anatomical features (mostly penial morphology), with *Tryonia* species exhibiting lesser variation. Significant differentiation within the three groups can also be demonstrated by comparing shell variation among species with variation within *P. micrococcus*, a widespread species in Ash Meadows (not used in discriminant analyses). This was done by generating F values for each character, using variance among species as numerator and variance within *P. micrococcus* as denominator (data from ANOVA). For each group, significant heterogeneity of all variables occurred (F test, $P < 0.01$).

Clear morphological separation of species is also indicated in two cases of syntopy involving *T. variegata* and either of two congeners, *T. ericae* (North Scruggs Spring) and *T. elata* (spring at Point of Rocks). In each case, syntopic species differ significantly in size (shell height) and number of whorls (t test, $P < 0.05$), and there was no misclassification of specimens of either in discriminant analyses.

Origins of Ash Meadows springsnails are largely conjectural at this time not only because the regional fauna remains unstudied,

Table 4.—Results of discriminant function analyses on Group I (*Pyrgulopsis fairbanksensis, P. crystalis, P. erthropoma*) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
			Standard (86)			
SW	−0.01	0.26	−0.62	3.34	0.88	0.46
LBW	0.01	−0.10	0.81	−1.46	0.96	0.16
AW	0.11	−0.22	0.82	−1.64	0.95	0.20
(Constant)	−7.48	−3.14				
C. correlation	0.70	0.36				
			Raupian (71)			
D	−14.60	14.81	−0.71	0.72	−0.58	0.82
AS	12.06	8.55	0.82	0.58	0.71	0.70
(Constant)	−15.36	−9.24				
C. correlation	0.44	0.26				

Table 5.—Results of discriminant function analyses on Group II (*Pyrgulopsis nanus, P. pisteri, P. isolatus*) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
			Standard (93)			
LBW	0.01	−0.18	0.56	−1.35	0.94	−0.14
AW	0.01	0.36	0.02	1.61	0.83	0.51
AL	0.10	−0.01	0.50	−0.06	0.93	0.14
(Constant)	−13.44	−2.41				
C. correlation	0.92	0.44				
			Raupian (48)			
D	−11.39	13.94	−0.63	0.78	−0.59	0.81
AS	11.36	8.28	0.81	0.59	0.77	0.63
(Constant)	−13.40	−8.73				
C. correlation	0.30	0.14				

but also because phyletic relationships among taxa involved are not easily elucidated solely on the basis of morphological data provided by such phenotypically conservative snails. The highly endemic Ash Meadows fauna is probably an old one, with progenitors entering the area along with fishes during late Pliocene–early Pleistocene (Hubbs and Miller 1948, Smith 1978, Minckley et al. 1986). Faunal antiquity coupled with occurrence in a region having complex drainage history further clouds zoogeographic inquiry. Minckley et al. (1986:565) commented in this regard (while discussing fishes of the region), "It is important to understand that available time has provided ample opportunity for aquatic connections through most unlikely areas and that bits of evidence for such events may not be contemporaneous."

We recognize at least three lineages in the fauna, which includes apparent species flocks

Table 6.—Results of discriminant function analyses on Group III (*Tyronia* spp.) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
			Standard (86)			
SH	−0.01	−0.06	−1.35	2.43	0.55	0.74
WBW	−0.01	−0.11	0.97	−1.10	0.83	0.43
LBW	0.01	−0.10	0.93	−1.45	0.79	0.51
AL	0.01	0.10	0.23	0.86	0.85	0.48
(Constant)	−9.71	1.79				
C. correlation	0.89	0.62				
			Raupian (71)			
AS	4.95	−7.61	0.56	−0.86	0.65	−0.74
T	0.36	0.31	0.87	0.75	0.76	0.50
D	6.85	2.40	0.46	0.16	−0.07	−0.06
(Constant)	−10.14	8.76				
C. correlation	0.63	0.36				

(sensu Greenwood 1984:18) of *Pyrgulopsis* and *Tryonia* that may have arisen from local evolution. Local *Pyrgulopsis* is separable into (at least) two lineages, corresponding to endemic and non-endemic components. *Pyrgulopsis micrococcus,* restricted to Amargosa basin, has affinities with similar-shelled, undescribed forms occurring in Death Valley and other basins to the west. All other Ash Meadows *Pyrgulopsis* belong to an informal *Fluminicola*-like group. No known members of this group occur west of Amargosa basin and affinities of Ash Meadows forms apparently lie with fauna of either Amargosa or Colorado River drainage. Monophyly of this endemic component may be indicated by shared absence of fleshy penial crests (contrasting with taxa from southwestern Nevada). However, conflicting groupings based on shell form and habitat type versus soft-part and radular morphology suggest a more complex situation.

Ash Meadows *Tryonia,* including three endemic species plus *T. variegata* (which also occurs elsewhere in Amargosa drainage), are separable from other nominal congeners by penial lobation pattern, but quite similar to undescribed taxa from Death Valley. Given their morphological uniformity, local endemics are probably monophyletic and possibly derived from *T. variegata.*

Ash Meadows springsnails thus parallel local fish fauna in having affinities with taxa from both Death Valley System and Colorado River drainage: *Empetrichthys,* now extinct in Ash Meadows, also occurred in nearby Pahrump Valley, and is related to *Crenichthys* from southeastern Nevada; Ash Meadows pupfish (*Cyprinodon*) are related to forms occurring in lower Amargosa drainage and in Death Valley; local speckled dace (*Rhinichthys*) are members of a widespread species occurring in Amargosa and Owens Valleys (Soltz and Naiman 1978, Miller 1981, Minckley et al. 1986).

Springsnail distribution in Ash Meadows reflects divergent habitat utilization as well as possible local allopatric speciation. Most taxa occur in small springs and outflows although several *Fluminicola*-like *Pyrgulopsis* and *Tryonia angulata* are restricted to large spring pools. The former are obviously specialized for clinging to hard substrate in strong current (present at spring orifices).

The two nonendemic species are widespread in Ash Meadows, while endemics are more narrowly distributed (Figs. 25, 44). Distribution of closely related endemics suggests that local differentiation of taxa has occurred largely among disjunct habitats having a narrow range of altitude (note *Pyrgulopsis* of large springs [Fig. 25] and small-sized *Tryonia* spp. [Fig. 44]). Such a pattern is in contrast to that seen for local pupfishes, in which species are zoned by elevation. The Devils Hole pupfish, *Cyprinodon diabolis,* is endemic to the highest spring in Ash Meadows (741 m); Warm Springs pupfish, *C. nevadensis pectoralis,* occur in springs isolated at a lower elevation of 715 m; and Ash Meadows Amargosa pupfish, *C. n. mionectes,* occur in springs at elevations of 683–695 m elevation. Miller (1948) suggested that this pattern reflects local differentiation that occurred as springs at these elevations became progressively isolated as pluvial wetland receded, with the highly divergent Devils Hole pupfish having been isolated for the longest time period. Among springs, only the presumed sister species pair of *P. isolatus* and *P. nanus* (Fig. 25) provide a possible example of such differentiation along an altitudinal gradient. Distribution of springsnails in Ash Meadows must be interpreted with caution, however, given probable alteration of historical patterns due to extensive modification of aquatic habitats in the area.

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Appendix 1

Collection localities, numbered as in Figs. 5 and 6. Data (in parentheses, with subsets lacking for some sites) include location (from Ash Meadows Quadrangle, Nevada-California [1952], USGS 15 minute series [topographic]), water temperature, conductivity, dissolved oxygen, discharge, and elevation of site. Discharge estimated or from Dudley and Larson (1976) or Garside and Schilling (1979). Capsule habitat descriptions are provided, with notes on condition of site, springsnail deployment, and presence of native fishes and introduced biota.

1. Fairbanks Spring (NE ¼ Sec. 9, T17S, R50E; 27°C, 700 micromhos/cm, 3.5 mg/liter, 6500 liters/min, 695 m). Large limnocrene tributary to outflows from Rogers, Soda, Longstreet, and Five Springs in Carson Slough. Spring enlarged by heavy equipment; springpool now circular, approximately 15 m in diameter and four meters deep. Bordering vegetation a mixture of mesquite and salt grass. Submergent vegetation absent in springpool; cattails bordering much of pool perimeter and common in outflow. *Pyrgulopsis fairbanksensis* common, clinging to travertine at spring orifice; *T. angulata* common in soft substrate of outflow. Ash Meadows Amargosa pupfish present; speckled dace and poolfish extinct. Mosquito fish, red-rim melania, and crayfish abundant.

2. Soda Spring (NW ¼ Sec. 10, T17S, R50E, 22°C, 290 liters/min, 695 m). Moderate-sized, disturbed spring consisting of seemingly stagnant pool heavily

overgrown by salt cedar, willow, and mesquite. Seasonally tributary to outflow from Fairbanks Spring. Springsnails absent. Mosquito fish and red-rim melania abundant.

3. Rogers Spring (NE ¼ Sec. 15, T17S, R50E; 28°C, 700 micromhos/cm, 2.0 mg/liter, 2700 liters/min, 695 m). Deep limnocrene seasonally tributary to outflows from Soda, Longstreet, Fairbanks, and Five Springs in Carson Slough. Spring pool and outflow altered by heavy equipment; outflow contained in man-made channels. Springpool without submerged vegetation, but cattails and rushes dense along pool perimeter and in outflow. Springsnails absent. Ash Meadows Amargosa pupfish present in springpool, less common in outflows. Ash Meadows speckled dace and Ash Meadows poolfish extinct. Mosquito fish, crayfish, and red-rim melania present.

4. Spring 0.2 km S of Rogers Spring (SE ¼ Sec. 15, T17S, R50E; 12°C, 560, 4.3 mg/liter, <10 liters/min, 695 m). Northern-most of many small seeps (two containing springsnails) located along north-south bluff extending almost to Longstreet Spring. Spring isolated. Flow not evident, but small stringer maintained for approximately 75 m. Heavily overgrown by rushes. *Pyrgulopsis micrococcus* rare in soft mud at springsource.

5. Spring 0.3 km S of Rogers Spring (SE ¼ Sec. 15, T17S, R50E; 17°C, 780 micromhos/cm, 7.3 mg/liter, <10 liters/min, 695 m). Small, isolated seep similar to above, located along same bluff. Flow not evident, but discharge maintaining moist area of about 30 × 50 m. Heavily overgrown by rushes and saw grass. *Pyrgulopsis micrococcus* restricted to source area, moderately common.

6. Longstreet Spring (NE ¼ Sec. 22, T17S, R50E; 27°C, 700 micromhos/cm, 4.3 mg/liter, 4700 liters/min, 701 m). Large limnocrene impounded by meter high dike diverting outflow in two directions; both outflow channels man-made. Submergent vegetation absent in impoundment and outflows, but latter with dense cattails. Impoundment periphery dominated by salt grass, salt ceder, and cattail, with occasional mesquite. Springsnails absent. Ash Meadows Amargosa pupfish common; speckled dace extinct. Bullfrogs, mosquito fish, crayfish, and red-rim melania common.

7. Five Springs (NW ¼ Sec. 23, T17S, R50E; 32°C, 820 micromhos/cm, 3.1 mg/liter, 546 liters/min, 716 m). Complex of at least eight small springs; discharges combining to form outflow extending three kilometers to west. All springs channelized and diverted into carthen canals by heavy equipment. *Chara* sp. primary submergent vegetation; cattail dominant emergent. Salt grass and rushes border springs and outflows. *Pyrgulopsis nanus* and *T. variegata* common on all substrates in restricted small area of stream isolated from lower segment (having red-rim melania) by 0.75 m vertical drop probably created by equipment during spring development. Ash Meadows Amargosa pupfish and mosquito fish present.

8. Purgatory Spring (SW ¼ Sec. 14, T17S, R50E; 32°C, 820 micromhos/cm, 7.0 mg/liter, 87 liters/min [from well casing], 722 m). Small, isolated seep badly disturbed by wild horse activity. Discharge contained in narrow, shallow channel for about 10 m before spreading over area of about 75 × 75 m. Emergent vegetation, salt grass and rushes. *Pyrgulopsis micrococcus* restricted to and rare in submergent *Chara* sp. lining a small gauging box having cool (25°C) water.

9. Spring 1.0 km S of Five Springs (SW ¼ Sec. 23, T17S, R50E; 29°C, 740 micromhos/cm, 3.3 mg/liter, <10 liters/min, 716 m). Isolated seep with broad, shallow outflow extending about a kilometer. Disturbance minimal, although source likely deepened. Densely covered by rushes; bordered by salt grass. *Pyrgulopsis micrococcus* moderately common upstream, in soft substrate within dense rushes.

10. Cold Spring (SE ¼ Sec. 21, T17S, R50E; 284 liters/min, 683 m). Small spring on eastern border of and tributary to Carson Slough. Springsnails absent. Crayfish abundant.

11. Shaft Spring (NW ¼ Sec. 26, T17S, R50E; 26°C, 650 micromhos/cm, 3.2 mg/liter, 600 liters/min [est.], 719 m). Isolated spring with broad outflow densely covered by rushes and cattail. Flows for about 1.5 km to west. Appearance pristine although small abandoned mine near source. *Pyrgulopsis micrococcus* common on all substrates.

12. Chalk Spring (NW ¼ Sec. 26, T17S, R50E; 18.5°C, 700 micromhos/cm, 3.9 mg/liter, <10 liters/min, 719 m). Small isolated spring, located about 200 m S of Shaft Spring. Outflow less than 100 m long, spreading to cover area of about 25 × 75 m. Disturbed but restabilized: now covered by dense rushes and wild grape. *Tryonia variegata* and *P. micrococcus* common in soft substrate at source.

13. Mary Scott Spring (NW ¼ Sec. 35, T17S, R50E; 27°C, 750 micromhos/cm, 4.5 mg/liter, 600 liters/min [est.], 704 m). Isolated spring discharging from deep pool about 0.75 m in diameter and 1.0 m across. Spring diverted in past. Outflow channel well defined, extending 1.5 km; densely covered by shrub and mesquite. Rushes cover open areas. *Tryonia variegata* common in soft substrates in backwaters upflow; *P. nanus* common on travertine bits.

14. North Scruggs Spring (NE ¼ Sec. 35, T17S, R50E; 32°C, 810 micromhos/cm, 2.8 mg/liter, 227 liters/min, 710 m). Moderate-size spring located about 30 m from South Scruggs Spring: springs connected by man-made channels. Springpool and upper 50 m of deeply incised outflow overgrown by salt grass; lower areas modified and impounded. A two meter wide outflow channel extends 3 km to west. Channel densely covered by rushes and bordered by mesquite, ash trees, and shrub. *Pyrgulopsis pisteri* and *T. variegata* abundant near

source in vegetated areas. Warm Springs pupfish present.

15. South Scruggs Spring (NE ¼ Sec. 35, T17S, R50E; 32°C, 800 micromhos/cm, 2.8 mg/liter, 230 liters/min [est.], 710 m). Moderate-size spring with broad (1.5 m), shallow outflow densely vegetated by rushes. Spring manipulated and badly trampled by wild horses. Outflow extending three kilometers to west. Spring source with sparsely scattered rushes, bordered by salt grass. *Tryonia variegata* common in soft substrate and on submerged *Chara* sp. Warm Springs pupfish and mosquito fish present.

16. Marsh Spring (SE ¼ Sec. 35, T17S, R50E; 30°C, 700 micromhos/cm, 2.7 mg/liter, 600 liters/min [est.], 710 m). Isolated spring. Sourcepool 4.0 m across and 2.0 m deep. Source and upper 30 m of outflow undisturbed; below a small dike impounds flow, producing wet area about 50 × 30 m. Bordering vegetation primarily salt grass with some saw grass. Rushes sparse in stream; impoundment densely covered by cattails. *Tryonia variegata* abundant in soft substrate and *P. pisteri* common on travertine in areas with current. Warm Springs pupfish and bullfrogs present.

17. North Indian Spring (SE ¼ Sec. 35, T17S, R50E; 27°C, 780 micromhos/cm, 3.3 mg/liter, 400 liters/min [est.], 710 m). Moderate size spring: sourcepool 0.8 m wide and 0.3 m deep. Old diversion structures indicate past manipulation. Spring now restabilized and flowing in isolated, well-defined channel for about 3.0 km. Dense ash tree/mesquite thicket covers much of outflow; rushes thick in exposed areas of stream. *Tryonia variegata* common in soft substrate of uppermost 60 m of outflow. Warm Springs pupfish present. Mosquito fish restricted to lower reaches of stream.

18. South Indian Spring (SE ¼ Sec. 35, T17S, R50E; 28°C, 790 micromhos/cm, 3.8 mg/liter, 200 liters/min [est.], 710 m). Small spring with narrow outflow channel. Located 150 m south of North Indian Spring; springs isolated from one another. Disturbance not apparent, but proximity to above suggests probable past alteration. Outflow densely covered by rushes, with scattered ash trees, mesquite, and shrub. Seepage from Indian Springs maintaining one of few remaining ash tree/mesquite bosques in Ash Meadows. *Tryonia variegata* common in soft substrates of outflow channel. Warm Springs pupfish and mosquito fish present.

19. Mexican Spring (SE ¼ Sec. 35, T17S, R50E). Formerly a small pool that largely dried in 1973 (Soltz and Naiman 1978). Heavily overgrown by rushes; open water absent. Springsnails absent; Warm Springs pupfish extinct.

20. School Spring (SE ¼ Sec. 35, T17S, R50E; 32.5°C, 710 micromhos/cm, 3.2 mg/liter, 75 liters/min [est.], 715 m). Moderate size spring: sourcepool 1.0 m across and 3 cm deep. Current strong in narrow outflow. Spring altered in 1970's to increase pool habitat for Warm Springs pupfish. Additional pools constructed in 1981. Mesquite and shrub now reestablished at site. Rushes, cattail, and *Chara* sp. dense in springpool and outflow. *Tryonia variegata* common in soft sediments at spring source. Above common and *P. pisteri* rare in soft substrate of large (7.0 m across), cool (22°C) observation pond below spring. Warm Springs pupfish present.

21. Devil's Hole (SE ¼ Sec. 35, T17N, R50E; 32°C, 820 micromhos/cm, 3.2 mg/liter, no discharge, elevation, 741 m). A 4 × 17 m pool, deep to one side, without outflow. Lies 15 m below surrounding terrain in limestone cavern. Surrounding and emergent vegetation absent. Submergent vegetation on shallow shelf includes several species of filamentous algae. Water level temporarily lowered during period of local groundwater mining during 1970's. *Tryonia variegata* moderately common on large travertine blocks in shelf. Devils Hole pupfish and Devils Hole Warm Spring riffle beetle endemic to site.

22. Spring N of Collins Ranch Spring (NE ¼ Sec. 1, T18S, R50E; 31°C, 800 micromhos/cm, 3.1 mg/liter, 100 liters/min [est.], 710 m). Small spring with shallow outflow extending westward from north-south bluff originating near Collins Ranch Spring. Isolated from nearby Locality 23. Nearby rusted pipes suggest past alteration. Outflow a well defined channel bordered by shrub and ash trees, extending ca. 1.0 km. Rushes dense in sun-exposed areas. *Tryonia ericae* common in soft sediments and on algal mats.

23. Spring N of Collins Ranch, about 150 m S of Locality 22 (SE ¼ Sec. 1, T18S, R50E; 27°C, 650 micromhos/cm, 5.4 mg/liter, 75 liters/min [est.], 710 m). Small spring with shallow outflow extending 1.0 km to west. Spring and outflow densely covered by rushes, shrub, and wild grape; ash trees scattered along length. Scattered debris suggest past disturbance. *Tryonia variegata* and *P. micrococcus* common in soft mud beneath dense rushes, *P. nanus* rare.

24. Collins Ranch Spring (SW ¼ Sec. 1, T18S, R50E; 25.5°C, 700 micromhos/cm, 4.3 mg/liter, 40 liters/min, 707 m). Several small springs on ranch, but only eastern-most seep occupied by springsnails. Diversion structures and nearby building foundations indicate past modifications. Broad, shallow outflow densely covered by rushes, flowing 75 m. Scattered ash trees, shrub, and mesquite provide little shade. *Pyrgulopsis nanus* and *T. variegata* common in mud and on travertine bits along outflow margins.

25. Crystal Pool (NE ¼ Sec. 3, T18S, R50E; 27°C, 870 micromhos/cm, 3.9 mg/liter, 11,000 liters/min, 668 m). Large limnocrene about 5.0 m deep and 15 m across. Although pumped during 1970's for irrigation, springpool appears undisturbed. Outflow channelized and impounded. Historically tributary to Carson Slough and therefore seasonally connected to outflows from Fairbanks, Rogers, Longstreet, Five, Big, and Jack Rabbit Springs. Springpool bordered by rushes, sedges (primarily *Scirpus robustus*), and salt grass. Outflow

heavily overgrown with cattails. Submergent vegetation, filamentous algae. *Pyrgulopsis crystalis* extremely rare, located on less than 1 m^2 of travertine in strongly voided water at orifice. *Tryonia angulata* abundant in soft substrate throughout springpool. Ash Meadows Amargosa pupfish present, Ash Meadows speckled dace and Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, crayfish, and red-rim melania abundant in spring and outflow.

26. Spring N of Clay Pits (SE ¼ Sec. 6, T18S, R50E; 10°C, 580 micromhos/cm, < 10 liters/min [est.], 652 m). Isolated small seep in west side of Carson Slough, flowing to east for about 50 m. Some evidence of past alteration by heavy equipment to enhance discharge. Densely covered by rushes. Several mesquite shrubs scattered along outflow. *Pyrgulopsis micrococcus* common in mud.

27. Spring at Clay Pits (SW ¼ Sec. 6, T18S, R50E; 13°C, 500 micromhos/cm, 50 liters/min [est.], 658 m). Isolated spring lying in 70 × 150 m pit created for clay mining. Wetland vegetation supported by spring and outflow includes salt grass, cattail, and rushes. Outflow extending 1.0 km to north. *Pyrgulopsis micrococcus* common on *Chara* sp. in outflow channel.

28. Spring S of Clay Pits (NE ¼ Sec. 7, T18S, R50E; 7°C, 430 micromhos/cm, 400 liters/min [est.], 658 m). Isolated spring W of Carson Slough. Discharge from large, 50 × 50 m area enclosed in (artificial?) pit surrounded by 2.0 m high travertine walls. Character of site seemingly natural, although slightly impacted by grazing horses. Outflow extends to south for 100 m before spreading to form a 0.5 ha wetland. Spring source bordered by salt grass and rushes; *Chara* sp. abundant. Emergent cattails in outflow; wetland vegetated by bunch grass. *Pyrgulopsis isolatus* moderately common along pool perimeters in spring area, extremely common on rocks in outflow, absent from wetland; *P. micrococcus* rare.

29. Spring near Crystal Reservoir (NW ¼ Sec. 11, T18S, R50E; 16°C, 700 micromhos/cm, 3.0 mg/liter, 200 liters/min [est.], 665 m). Marshy area watered by discharge from well casing atop a spring-mound densely covered by rushes. Scattered debris indicates past disturbance. Outflow tributary to that of Locality 30, and extending 1.0 km to south and then west toward Crystal Reservoir. *Tryonia variegata* common and *Pyrgulopsis micrococcus* very rare in soft substrate.

30. Spring 200 m east of Locality 30 (NW ¼ Sec. 11, T18S, R50E; 19°C, 730 micromhos/cm, 4.4 mg/liter, 400 liters/min [est.], 665 m). Habitat similar to above; outflows combine to create 2.0 ha wetland dominated by rushes and sedges. Spring source altered by heavy equipment during agricultural development. Outflow channel 2.0 m wide and shallow. *Pyrgulopsis micrococcus* common on watercress; *T. variegata* common in soft sediments.

31. Bradford Springs (SE ¼ Sec. 11, T18S, R50E; 21.5°C, 850 micromhos/cm, 3.2 mg/liter, 1700 liters/min [est.], 684 m). Site includes three adjacent springs formerly flowing westward. Springs now altered and connected by earthen canal capturing flow from Point of Rocks Springs (Localities 34–40) and extending southward to spread over land cleared and leveled for agriculture. Site remains badly degraded. Spring sources populated by cattails; canal with filamentous algae. Springsnails absent from single (middle) spring examined. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace present in springs and canal. Bullfrogs, mosquito fish, sailfin mollies, red-rim melania, and crayfish abundant.

32. Tubbs Spring (SW ¼ Sec. 12, T18S, R50E; 600 liters/min [est.], 684 m). Small springpool lying 2.0 m below surrounding terrain; outflow tributary to Bradford Springs through small pipe. Spring altered during clearing of land for agriculture: surrounding vegetation now consisting of weeds. Cattails surrounding springpool. Although not sampled, site's degraded condition suggests absence of springsnails.

33. Forest Spring (SW ¼ Sec. 7, T18S, R51E; 22°C, 660 micromhos/cm, 6.8 mg/liter, 0.0 liters/min, 698 m). Spring greatly altered during agricultural development, now surrounded by salt cedar. Springsnails absent. Ash Meadows Amargosa pupfish, Ash Meadows speckled dace, and Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, red-rim melania, and crayfish present.

Point of Rocks Springs (Localities 34–40; SE ¼ Sec. 7, T18S, R51E). Site altered a number of times during agricultural and municipal development. Many small springs now inundated by series of four ponds constructed in 1982, with Localities 35–40 representing springs remaining above impoundments. Discharge from Point of Rocks Springs historically flowed for 3.0 km in braided channels to southwest through a mesquite bosque, without surface connection to other springs. Outflows from Localities 34–37 now combined in ponds, which feed King's Pool and then connect with Bradford Springs via artificial channel.

34. King's Pool (30°C, 810 micromhos/cm, 3.1 mg/liter, 4500 liters/min, 701 m). Largest and westernmost of Point of Rocks Springs with single discrete orifice at SE corner of pool. Size, depth, and configuration of pool changed several times during agricultural and municipal development. Surrounding vegetation primarily salt cedar and cattails; mesquite and yerba mansa (*Anemopsis californica*) also present. Submergent vegetation, filamentous green algae. *Pyrgulopsis erythropoma* restricted to small area at orifice, abundant on travertine. Ash Meadows Amargosa pupfish present; Ash Meadows speckled dace and Ash Meadows poolfish extinct. Bullfrogs, sailfin mollies, mosquito fish, red-rim melania, and crayfish present.

35. Spring about 150 m east of King's Pool (32°C, 810 micromhos/cm, 5.0 mg/liter, 450 liters/min [est.], 705 m). Small rheocrene emerging from crevice and flowing southward through limestone trough before

cascading down 15 m embankment and entering artificial pond. Habitat appears pristine. Outflow 0.5 m wide, several centimeters deep; bordered by salt grass and rushes. *Pyrgulopsis erythropoma* common on travertine; *T. elata* common in soft sediments in limestone trough.

36. Spring about 60 m east of Locality 35 (29°C, 790 micromhos/cm, 6.0 mg/liter, 450 liters/min [est.], 705 m). Similar, pristine-appearing rheocrene also cascading southward down narrow channel into artificial pond. Channel 0.2 m wide, 15 m long, several centimeters deep; bordered by saw grass, salt grass, and rushes. *Pyrgulopsis erythropoma* abundant on stones.

37. Spring 30 m east of Locality 36 (30°C, 680 micromhos/cm, 6.6 mg/liter, 450 liters/min [est.], 705 m). Very swiftly flowing rheocrene. Outflow 15 m long and 0.2 m wide, cascading southward into artificial pond. Outflow disturbed during pond construction in 1982, but habitat regained natural character. Bordering vegetation similar to that found at Localities 35 and 36, with addition of scattered mesquite. *Pyrgulopsis erythropoma* abundant on travertine.

38. Seep 100 m N of Locality 35 (28°C, 700 micromhos/cm, 7.1 mg/liter, <10 liters/min [est.], 707 m). Seep watering area of 2 × 10 m. Site modified by backhoe in past; currently impacted by wild horse activity. Rushes and *Chara* sp. dominate as emergent and submergent vegetation, respectively. Salt grass, scattered mesquite, and wild grape enclose downflow portions of site (and those of Localities 39 and 40). *Tryonia elata* and *T. variegata* common in mud; *P. erythropoma* rare.

39. Spring 4.0 m N of Locality 38 (30°C, 780 micromhos/cm, 6.5 mg/liter, 75 liters/min [est.], 707 m). Seep with small outflow extending 5.0 m to west; densely covered by rushes. Site regained stability following past backhoe disturbance. *Tryonia variegata* common in mud; *P. erythropoma* rare on travertine.

40. Spring 7.0 m N of Locality 39 (32°C, 810 micromhos/cm, 6.1 mg/liter, 45 liters/min [est.], 707 m). Swiftly flowing rheocrene; outflow a well defined channel extending 5.0 m. Site in good condition despite past alteration by heavy equipment. Bordering vegetation matches that for Localities 37–39. *Pyrgulopsis erythropoma* abundant on travertine.

41. Jack Rabbit Spring (NW ¼ Sec. 18, T18S, R51E; 27°C, 870 micromhos/cm, 3.9 mg/liter, 2500 liters/min, 692 m). Large limnocrene temporarily dried by pumping during early 1970's. Outflow extending about 5.0 km in well defined channel before converging with that from Big Spring. Will seasonally connect with waters from Fairbanks, Rogers, Longstreet, Soda, Five Springs, and Crystal Pool in Carson Slough. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace now reestablished. Bullfrogs, red-rim melania, and crayfish present (Williams and Sada 1985).

42. Big Spring (NE ¼ Sec. 19, T18S, R51E; 26°C, 850 micromhos/cm, 3940 liters/min, 683 m). Large limnocrene about 20 m across and 7.0 m deep. Outflow channelized and used for irrigation, but spring otherwise undisturbed. Bordering vegetation includes salt grass, saw grass, and bunch grass. Mesquite and salt cedar scattered along outflow. Filamentous green algae moderately common in springpool and outflow; cattails also in latter. *Tryonia angulata* scarce in springpool and outflow. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace present; Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, and crayfish present (Williams and Sada 1985).

43. Brahma Spring (NW ¼ Sec. 29, T18S, R51E; 50 liters/min [est.], elevation, 693 m). Isolated site badly degraded by horse grazing to point of no longer resembling natural spring. Springsnails absent.

44. Bole Spring (NE ¼ Sec. 30, T18S, R51E; 45 liters/min [est.], 686 m). Spring in same condition as above. Springsnails absent; crayfish present.

45, 46. Frenchy Springs (NW ¼ Sec. 30, T18S, R51E; 16°C, 410 micromhos/cm, < 10 liters/min [est.], 686 m). Six isolated seeps occupying area in which small ponds (about 1.5 m deep and 2.5 m^2 area) created by heavy equipment. Site trampled by wild horses. Mesquite, salt grass, and rushes border seeps; ponds covered by duck weed (*Lemmna* sp.). *Pyrgulopsis micrococcus* present and moderately common in two seeps, in mud of shallows well vegetated by rushes.

47. Last Chance Spring (Center Sec. 30, T18S, R51E; 16°C, 520 micromhos/cm, 3.9 mg/liter, <10 liters/min, 684 m). Seep flowing about 5.0 m before entering dense wild grape/mesquite thicket. Site badly trampled by wild horses. *Pyrgulopsis micrococcus* and *T. variegata* common in mud and on emergent vegetation.