

Arizona Hydrobiidae  
(Prosobranchia: Rissoacea)

ROBERT HERSHLER  
and  
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## ABSTRACT

Hershler, Robert, and J. Jerry Landye. Arizona Hydrobiidae (Prosobranchia: Rissoacea). *Smithsonian Contributions to Zoology*, number 459, 63 pages, 49 figures, 6 tables, 1988.—A diverse fauna of Arizona Hydrobiidae is documented as a result of recent collecting from numerous springs in the state. The fauna is composed of 14 species in two genera, *Pyrgulopsis* Call and Pilsbry and *Tryonia* Stimpson. Thirteen species are described as new herein and the fourteenth represents a new state record. All have relatively restricted distributions, and two are single-spring endemics. All congeners are allopatric to one another.

Stepwise canonical discriminant function analyses using sets of shell and anatomical data confirmed the distinctiveness of the 12 species of Arizona *Pyrgulopsis*, as classification of (grouped) topotypes was 89%–93% using shell data, and 100% using anatomical data. Discriminant analyses also confirmed that differentiation among congeners largely involves male anatomy (especially penial features), as this data set yielded the best separation of species in plots of discriminant function scores.

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# Arizona Hydrobiidae (Prosobranchia: Rissoacea)

Robert Hershler  
and J. Jerry Landye

## Introduction

Prosobranch snails of the family Hydrobiidae comprise a diverse component of the inland aquatic fauna of the American Southwest, with numerous locally endemic taxa found in isolated springs, spring complexes, or drainage systems (Taylor, 1966; Landye, 1973). In part due to difficulties of collecting and studying these minute snails, they remain poorly known. There are no published, modern, comprehensive, systematic treatments of these faunas (but see Taylor, 1983), and what little work has been done largely consists of isolated, single-species descriptions based on studies of empty shell.

There is a clear and urgent need to address the systematics of these faunas given the fact that many species are threatened or endangered as a result of deterioration or disappearance of natural aquatic habitats (Taylor, 1970a). As an illustration, 12 of 21 southwestern hydrobiid species currently being considered for federal listing as threatened or endangered (USDI, 1984) are undescribed.

To further this end, we present a systematic description of Arizona Hydrobiidae. To date, not a single hydrobiid species has been described from the state. Prior to 1969, the sole published record of live collected hydrobiids in Arizona was by Pilsbry and Ferriss (1909), who obtained *Paludestrina stearnsiana*(?) from a single spring in the Huachuca Mountains. In their monograph on Arizona mollusks, Bequaert and Miller (1973) listed six additional such records for the family, representing several possible species. Additional published records of collections of Recent or subfossil shell are listed by Taylor (1970b, 1975).

In the past 18 years the junior author has intensively surveyed permanent Arizona waters and found a large hydrobiid fauna, with estimated specific diversity ranging

upwards to 18 species (see Landye, 1973, 1981; Williams et al., 1985). The bulk of this collection, large alcohol holdings from 38 localities in the state and peripheral areas (Figure 1), was made available to the senior author, whose taxonomic work is presented herein. Fourteen species are recognized, representing two genera, *Tryonia* Stimpson, 1865, and *Pyrgulopsis* Call and Pilsbry, 1886. Thirteen of the species are new, and the fourteenth, *Pyrgulopsis deserta* (Pilsbry), represents a new state record. Stepwise discriminant function analyses using separate shell and anatomical data sets were performed in order to examine patterns of variation and test whether the 12 new, allopatric *Pyrgulopsis* species are distinct from one another.

Only brief habitat description is provided, as a separate paper treating ecological (and biogeographical) aspects of the fauna will be published elsewhere. Hydrobiid localities in the state are spring fed, and include spring pools, stream outflows, and marshy wetlands known as cienegas (Hendrickson and Minckley, 1985). Springs range from small seeps to Montezuma Well, a limnocrene with maximum length of 112 m and depth of 17 m (Cole and Barry, 1973). Snails are usually restricted to headsprings and upper sections of outflows. *Pyrgulopsis* typically occurs on rock or aquatic macrophytes in moderate current, whereas *Tryonia* is usually restricted to soft sediment in still water.

## LIST OF RECOGNIZED SPECIES

*Pyrgulopsis glandulosus* Hershler, new species  
*Pyrgulopsis deserta* (Pilsbry)  
*Pyrgulopsis bacchus* Hershler, new species  
*Pyrgulopsis conicus* Hershler, new species  
*Pyrgulopsis morrisoni* Hershler, new species  
*Pyrgulopsis montezumensis* Hershler, new species  
*Pyrgulopsis solus* Hershler, new species  
*Pyrgulopsis simplex* Hershler, new species  
*Pyrgulopsis sancarlosensis* Hershler, new species  
*Pyrgulopsis confluentis* Hershler, new species

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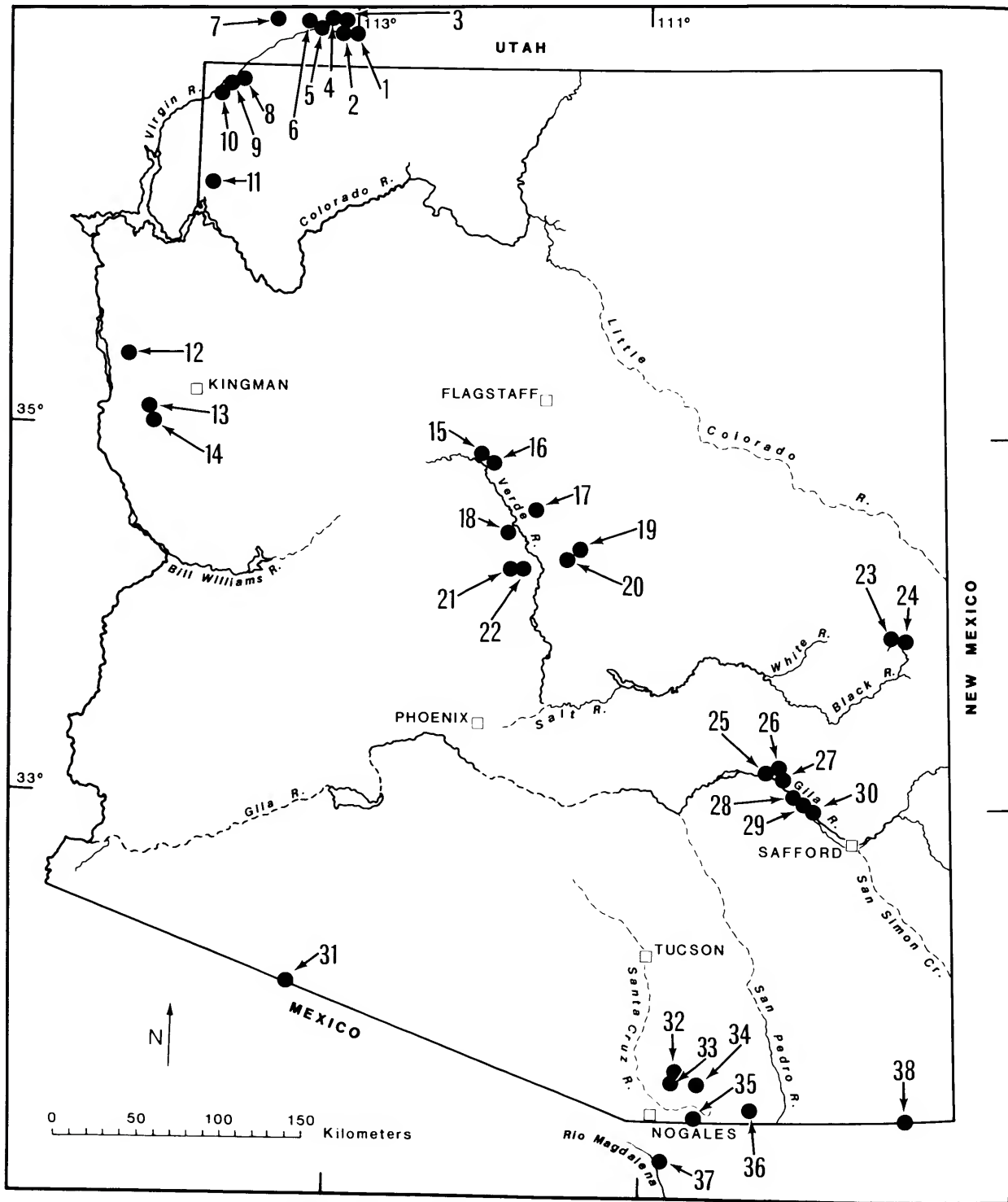


FIGURE 1.—Map of Arizona drainages, showing the 38 collecting sites numbered as in detailed list of collection localities on facing page.



## Collection Localities

Locality data includes appropriate information from USGS topographic quadrangle sheets (7.5/15 minute series). Numbers in parentheses refer to localities in Figure 1; name of quadrangle map follows each reference number.

## United States

UTAH.—*Washington County*: Spring on Old Bastion Ranch (1), Hurricane quadrangle, 0.0 km S, 0.05 km E from NE corner Sec. 13, T. 42S, R. 15W; Sam Adair Spring (2), St. George quadrangle, 0.8 km S, 0.6 km E from NW corner Sec. 14, T. 42S, R. 15W; small spring, 70 m N of Interstate 15 (3), St. George quadrangle, 0.1 km N, 0.1 km E from SW corner Sec. 15, T. 42S, R. 15W; Green Spring (4), St. George quadrangle, 0.6 km N, 0.7 km W from SE corner Sec. 15, T. 42S, R. 15W; spring in Middleton (5), St. George quadrangle, 0.2 km W from NE corner Sec. 21, T. 42S, R. 15W; spring on west side of Middleton (6), St. George quadrangle, 0.1 km S, 0.5 km E from NW corner Sec. 21, T. 42S, R. 15W; spring on Red Hill (7), St. George quadrangle, 0.7 km N, 0.6 km E from SW corner Sec. 19, T. 42S, R. 15W.

ARIZONA.—*Mohave County*: Spring about 7.0 km E of Littlefield (8), Littlefield quadrangle, 0.05 km N, 0.3 km W from SE corner Sec. 25, T. 42N, R. 15W; spring upstream on Virgin River from Littlefield (9), Littlefield quadrangle, 0.5 km S, 0.2 km E from NW corner Sec. 3, T. 40N, R. 15W; spring NE of Littlefield (10), Littlefield quadrangle, 0.8 km S, 0.5 km W from NE corner Sec. 4, T. 40N, R. 15E; Grapevine Spring (11), Gypsum Hills quadrangle, 0.0 km S, 0.4 km W from NE corner Sec. 26, T. 34N, R. 16W; Burns Spring (12), Burns Spring quadrangle, 0.1 km S, 0.2 km W from NE corner Sec. 9, T. 22N, R. 20W; Dripping Springs (13), Mount Nutt quadrangle, 0.6 km S, 0.7 km W from NE corner Sec. 4, T. 19N, R. 19W; Cool Spring (14), Mount Nutt quadrangle, 0.5 km N, 0.5 km W from SE corner Sec. 20, T. 19N, R. 19W.

*Yavapai County*: Tavasci Springs (15), Clarkdale quadrangle, 0.4 km N, 0.4 km E from SW corner Sec. 15, T. 16N, R. 3E; Page Springs (16), Page Springs quadrangle, 0.1 km N, 0.3 km W from SE corner Sec. 23, T. 16N, R. 4E; Montezuma Well (17), Lake Montezuma quadrangle, 0.9 km S, 1.1 km E from NW corner Sec. 31, T. 15N, R. 6E; Brown Spring (18), Horner Mountain quadrangle, 0.3 km N, 0.4 km W from SE corner Sec. 23, T. 12N, R. 9E; Fossil Springs (19), Strawberry quadrangle, 0.4 km N, 0.2 km W from SE corner Sec. 14, T. 12N, R. 7E; Nelson Place Spring (21), Tule Mesa quadrangle, 6.0 km S, 4.3 km E from NW corner of quadrangle, Sec. 16, T. 11N, R. 5E; spring 150 m E of Nelson Place Spring (22), Tule Mesa quadrangle, 6.1 km

S, 4.8 km E from NW corner of quadrangle, Sec. 15, T. 11N, R. 5E.

*Gila County*: Spring near Strawberry (20), Strawberry quadrangle, 0.3 km N, 0.3 km E from SW corner Sec. 22, T. 12N, R. 7E.

*Apache County*: Spring on N side of Blanket Creek at Three Forks (23), Big Lake quadrangle, 0.5 km N, 0.2 km W from SE corner Sec. 6, T. 5N, R. 29E; spring at Three Forks (24), Big Lake quadrangle, 0.2 km N, 0.0 km W from SE corner Sec. 6, T. 5N, R. 29E.

*Graham County*: Small spring near Bylas (25), Bylas quadrangle, 0.2 km N, 0.3 km E from SW corner Sec. 17, T. 3S, R. 22E; spring near Gila River bridge NW of Bylas (26), Bylas quadrangle, 0.1 km N, 0.3 km E from SW corner Sec. 17, T. 3S, R. 22E; large spring N of Bylas (27), Bylas quadrangle, 0.1 km N, 0.3 km E from SW corner Sec. 28, T. 3S, R. 22E; springs W of Tom Niece Springs (28), Fort Thomas quadrangle, 0.8 km S, 0.0 km W from NE corner Sec. 21, T. 4S, R. 23E; seeps W of Tom Niece Springs (29), Fort Thomas quadrangle, 0.6 km S, 0.4 km W from SE corner Sec. 21, T. 4S, R. 23E; Cold Springs (30), Fort Thomas quadrangle, 0.1 km N, 0.5 km W from SE corner Sec. 8, T. 5S, R. 24E.

*Pima County*: Quitobaquito Springs (31), Quitobaquito Springs quadrangle, 6.8 km S, 1.8 km W from NE corner of quadrangle, T. 17S, R. 7W.

*Santa Cruz County*: Cottonwood Springs (32), Sonoita quadrangle, 0.6 km S, 0.1 km W from NE corner Sec. 33, T. 20S, R. 16E; Monkey Springs (33), Sonoita quadrangle, 0.5 km N, 0.4 km E from SW corner Sec. 3, T. 21S, R. 16E; Canelo Hills Cienega (34), O'Donnell Canyon quadrangle, 0.6 km N, 0.1 km W from SE corner Sec. 32, T. 21S, R. 18E; Sheehy Spring (35), Lochiel quadrangle, NW corner Sec. 12, T. 24S, R. 17E; Peterson Ranch Springs (36), Huachuca Peak quadrangle, 0.5 km N, 0.6 km W from SE corner Sec. 3, T. 23S, R. 19E.

*Cochise County*: Springs at San Bernardino Ranch (38), College Peaks quadrangle, 0.3 km N, 0.8 km E from SE corner Sec. 15, T. 34S, R. 30E.

## Mexico

SONORA. Ojo Caliente, 44 km S of Nogales (37).

*Pyrgulopsis cochisi* Hershler, new species  
*Pyrgulopsis thompsoni* Hershler, new species  
*Tryonia gilae* Hershler, new species  
*Tryonia quitobaquiae* Hershler, new species

## MATERIALS AND METHODS

MATERIAL EXAMINED.—Material from 38 localities (Figure 1), totalling 48 lots, was collected by fine-meshed hand sieve, relaxed with menthol crystals, fixed in dilute (4%), buffered formalin and preserved in 70% ethanol. Most of these lots comprise more than 100 specimens. All this material is housed in the United States National Museum collection in the National Museum of Natural History, Smithsonian Institution (USNM catalog numbers are referred to below), and other relevant material from that collection and that of the Academy of Natural Sciences of Philadelphia (ANSP) also was examined.

MORPHOLOGIC STUDY.—Shells and animals were studied and measured at  $\times 50$  using WILD M-5 and M-7 dissecting microscopes equipped with ocular micrometers. Shells, operculae, and radulae were photographed using a Hitachi S-570 scanning electron microscope (SEM). To obtain intact bodies for dissection, shells were decalcified by soaking in concentrated Bouin's Solution, and the remaining pellicle was removed. Animals were dissected in dilute Bouin's Solution. To examine penial morphology and ciliation patterns on the penis and cephalic tentacles, animals were dried using a Denton DCP-1 Critical Point Drier and then photographed by SEM.

Continuous and (to a lesser extent) meristic data were obtained from shell and anatomy of selected series of sexed specimens of *Pyrgulopsis* (Table 1) for use in discriminant function analyses. Separate series were used for shell (n = seven to eleven) and anatomical (n = five) study.

Shells were cleaned with Clorox to remove surface deposits

and oriented in the standard apertural aspect after counting of whorls. Necessary points or aspects of shell outline were pinpointed or traced onto paper using a camera lucida. Distances between points were then determined using a fine-scaled millimeter ruler. The following characters were measured (Figure 2a) or counted:

number of whorls (NW)  
 shell height (SH)  
 shell width (SW)  
 aperture height (AH)  
 aperture width (AW)  
 height of body whorl (LBW)  
 width of body whorl (WBW)  
 length of line connecting sutures at posterior ends of body and penultimate whorls (AB)  
 length of perpendicular bisector of line segment AB, extended to edge of penultimate whorl (CD)

The following ratios were formed using the above data:

shell height/shell width (SH/SW)  
 aperture height/shell height (AH/SH)  
 body whorl length/shell height (LBW/SH)  
 whorl convexity (CD/AB), following Kohn and Riggs (1975:352)

Body and gonad lengths were measured with the animal pinned in an apical aspect, with the former representing length from mantle collar to posterior tip of digestive gland. The penis was cut from the neck and measured in dorsal aspect. The pallial roof and visceral coil were removed from the head/foot and separated from one another along the end of the pallial cavity. Pallial structures were measured with the pallial roof flattened and pinned. Penial measurements are shown in Figure 2b as an example of continuous anatomical data. The following counts and measurements were made:

#### Both Sexes

body length (BL)  
 osphradium length (OSL)  
 osphradium width (OSW)  
 distance from posterior end of osphradium to posterior tip of ctenidium (OCT)  
 ctenidium length (CTL)  
 ctenidium width (CTW)  
 number of ctenidial filaments (FI)

#### Females

ovary length (OL)  
 capsule gland length (CGL)  
 capsule gland width (CGW)  
 albumen gland length (AGL)  
 albumen gland width (AGW)  
 diameter (anterior-posterior) of anterior coil of oviduct (COL)  
 distance from anterior end of oviduct coil to posterior end of capsule gland (COP)  
 maximum diameter of anterior portion of oviduct (COD)  
 bursa copulatrix length (BUL)  
 bursa copulatrix width (BUW)  
 width of bursa copulatrix duct (BDW)  
 distance from posterior end of albumen gland to posterior tip of bursa (BAG)

TABLE 1.—List of *Pyrgulopsis* populations receiving morphometric study of shell and anatomy. USNM collection numbers are followed by locality numbers (see Figure 1). Specimens from type-localities are indicated with asterisks. (Plus = data taken, dash = no data taken.)

Species and locality	Shell	Anatomy
<i>P. deserta</i>		
*847202 (9)	+	+
847206 (8)	+	—
<i>P. bacchus</i>		
*847203 (1)	+	+
<i>P. conicus</i>		
*847237 (13)	+	+
847201 (14)	+	—
<i>P. morrisoni</i>		
*847231 (16)	+	+
847220 (15)	+	—
<i>P. montezumensis</i>		
*847233 (17, swallet)	+	+
847230 (17, outflow)	+	—
<i>P. solus</i>		
*850290 (18)	+	+
<i>P. glandulosus</i>		
*847205 (21)	+	+
<i>P. simplex</i>		
*847236 (20)	+	+
847222 (19)	+	—
<i>P. confluentis</i>		
*847234 (23)	+	+
847229 (24)	+	—
<i>P. sancarlosensis</i>		
*847226 (28)	+	+
847217 (25)	+	+
847224 (27)	+	—
<i>P. thompsoni</i>		
*847238 (36)	+	+
847221 (32)	+	+
847227 (34)	+	+
847228 (34)	+	+
<i>P. cochisi</i>		
*847218 (38)	+	+

seminal receptacle (body plus duct) length (SRL)  
 seminal receptacle width (SRW)

#### Males

testis length (TS)  
 prostate gland length (LPR)  
 prostate gland width (WPR)  
 length of penis from base to tip of penial lobe (L2)  
 penis width (at base) (PW)  
 distance from base of penis to base of penial filament (L3)  
 penial filament length (LFI)  
 penial filament width (WFI)  
 number of glandular ridges on penis (GLR)

The following ratios were formed using these anatomical data:

#### Both Sexes

osphradium length/ctenidium length (OSL/CTL)

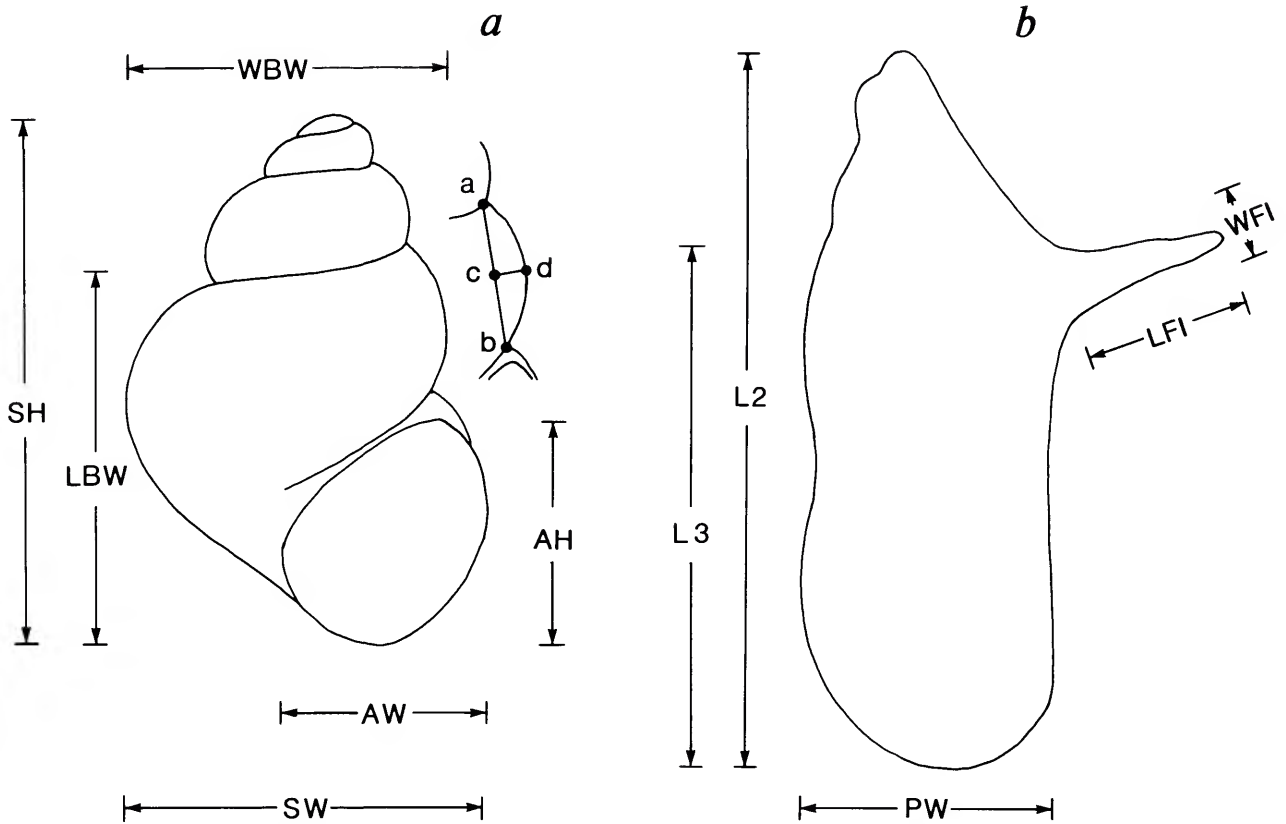


FIGURE 2.—Shell (a) and penial (b) measurements. Points: a, suture at posterior end of penultimate whorl; b, suture at posterior end of body whorl; c, mid-point of line segment ab; d, intersection of perpendicular bisector of ab and edge of whorl (Abbreviations: AH = aperture height; AW = aperture width; LBW = height of body whorl; LFI = length of penial filament; L2 = penis length; L3 = length from proximal end of penis to distal edge of filament base; PW = penis width; SH = shell height; SW = shell width; WFI = width of penial filament; WBW = width of body whorl.)

distance from posterior tip of osphradium to ctenidium tip/ctenidium length (OCT/CTL)  
 ctenidium length/body length (CTL/BL)

**Females**

ovary length/body length (OV/BL)  
 capsule gland length/albumen gland length (CGL/AGL)  
 oviduct coil diameter/albumen gland length (COL/AGL)  
 bursa length/albumen gland length (BUL/AGL)  
 distance from albumen gland tip to bursa tip/bursa length (BAG/BU1.)  
 seminal receptacle length/bursa length (SRL/BUL)

**Males**

testis length/body length (TS/BL)  
 prostatic length/body length (LPR/BL)  
 distance from base of penis to base of penial filament/penis length (L3/L2)  
 length of filament/penis length (LFI/L2)

filament length/width (WFI/LFI)

The total character breakdown is as follows: male and female shell, nine raw characters, four ratios (totaling 13 characters); male anatomy, 16 and eight (24); female anatomy, 21 and nine (30).

DATA ANALYSIS.—As discussed by Mayr (1963) and Wiley (1981), assessment of systematic status of differentiated allopatric populations without genetic or experimental data involves gauging population divergence using morphological criteria. Multivariate analysis of morphological data can contribute to the decision-making process in such situations (Wiley, 1981:65–67, 355–365) and was therefore used to examine patterns of variation among the 12 allopatric *Pyrgulopsis* species described below.

We employed canonical discriminant function analysis, also known as canonical variates analysis when applied (as in this

case) to more than two groups, as this technique is particularly suitable when one seeks to evaluate distinctiveness of a priori designated taxa. Unlike principal component analysis, discriminant analysis provides statistical evaluation of specimen classification. We stress that these analyses were for the purposes of description and exploration of the data set and are not intended as inferential.

MAHAL stepwise procedure was used in discriminant analyses, in which variables are selected on the basis of providing the largest Mahalanobis distance between the closest pair of groups. Stepwise procedure was used, as it allows recognition of the most effectively discriminating variables. Topotypes of each species were considered as 12 separate groups, with other populations input as ungrouped to prevent biases resulting from having data available for varying numbers (one to four) of populations for the various species. All populations used are listed in Table 1. Separate analyses (including raw plus ratio data) were performed not only for male and female anatomical data sets, but also for male and female shell data, as sexual dimorphism in size is evident in at least one population for 10 of 12 species and in 11 of 23 total populations studied (Appendix 1). The pooled within-groups covariance matrix was used to compute probabilities of group membership.

Means for all raw counts, measurements, and ratios except one (OSW, females) were heterogeneous among the 12 sets of topotypes. Ratios were used in the analyses as a way of dealing with shape. Initial discriminant analyses using all variables indicated that significant separation (partial F-test,  $p < 0.05$ ) of closest groups (consisting of topotypes of given species) occurred after stepwise selection of subsets of male and female anatomical variables. Selection of additional variables no further separated groups, and eventually (after 16 to 20 variables added) resulted in decreased separation. To avoid possible confusion of patterns generated by addition of later variables, discriminant analyses were rerun using subsets, with each consisting of all variables selected (in initial analyses) to the point at which consistent significant separation occurred between closest groups. The reduced variable sets thus selected were as follows: male anatomy (11 variables), CTW, TS/BL, L2, BL, L3/L2, GLR, LFI, WFI, CTL, LPR/BL, L3; female anatomy (13), CTL, BAG, BUW, COP, CGW, FI, AGL, OV, SRL/BUL, OSL, BDW, OCT, OSL/CTL. For shell data (consisting of relatively few variables), decreased separation of closest groups occurred after every step in initial analyses, and therefore runs utilizing all variables were used.

Descriptive statistics were generated, and analyses of variance (ANOVA), t-tests, and stepwise discriminant function analyses were performed using the SPSS-X program, subprograms BREAKDOWN, T-TEST, and DISCRIMINANT.

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#### Systematics

Accounts for each species consist of provision of common name, synonymy, material examined, diagnosis, description, remarks (where applicable), type-locality, distribution, and etymology (where applicable). Designation of common names largely follows that of Landye (1981) and Williams et al. (1985). Most species were recognized in unpublished reports by Landye (1973, 1981). Our synonymies include references to these works only when identities of his taxa are unclear. Congeners are not greatly divergent in morphology and expanded descriptions are provided for only one species per genus, with other descriptions emphasizing distinctive features. Such features involve (in order of importance) penial morphology, shell, head-foot and penial pigmentation, and morphology of the pallial oviduct and bursa copulatrix complex. Radular data are in Table 2. Shell and anatomical data for *Pyrgulopsis* species are in Appendices 1-3.

#### Key to Arizona Hydrobiidae

1. Shell elongate-conic to turreted; penis with glandular, papillae-like lobes (*Tryonia*).  
 . . . . . 2
- Shell globose to elongate-conic; penis bilobed, with glandular ridges (*Pyrgulopsis*).  
 . . . . . 3

- 2. Adult shell height 1.9–3.3 mm; penis with two lobes on inner curvature near distal tip and single, enlarged lobe on outer curvature at base . . . . . *Tryonia gilae*, new species  
 Adult shell height, 1.4–1.8 mm; penis with single lobe on inner curvature near distal tip and enlarged lobe on inner curvature at base . . . . . *Tryonia quitobaquiae*, new species
- 3. Penial filament narrow, short (less than 30% of penis length); dorsal penial surface with two or more glandular ridges . . . . . 4  
 Penial filament wide, long (greater than 40% of penis length); dorsal penial surface with one or no glandular ridges . . . . . 6
- 4. Ventral penial surface without accessory crests . . . . . *Pyrgulopsis montezumensis*, new species  
 Ventral penial surface with accessory crest(s) . . . . . 5
- 5. Dorsal penial surface with at least two elongate ridges; ventral surface with two accessory crests . . . . . *Pyrgulopsis glandulosus*, new species  
 Glandular ridges on dorsal penial surface circular; ventral surface with single accessory crest . . . . . *Pyrgulopsis confluentis*, new species
- 6. Penial lobe reduced or absent . . . . . 7  
 Penial lobe prominent . . . . . 8
- 7. Adult shell height, 1.3–1.7 mm; penial lobe absent; dorsal and ventral penial surfaces each with single glandular ridge . . . . . *Pyrgulopsis cochisi*, new species  
 Adult shell height, 1.7–3.2 mm; penial lobe reduced; ventral penial surface with single glandular ridge . . . . . *Pyrgulopsis thompsoni*, new species
- 8. Dorsal penial surface with glandular ridge(s) . . . . . 9  
 Dorsal penial surface without glandular ridges . . . . . 11
- 9. Dorsal surface of penial filament with elongate glandular ridge . . . . . *Pyrgulopsis deserta* (Pilsbry)  
 Dorsal surface of penial filament without elongate glandular ridge . . . . . 10
- 10. Penis short (about 13%) relative to body length; penial filament 40%–50% of penis length . . . . . *Pyrgulopsis solus*, new species  
 Penis long (about 33%) relative to body length; penial filament greater than 67% of penis length . . . . . *Pyrgulopsis sancarlosensis*, new species
- 11. Penial lobe bi- or trifurcate; ventral penial surface with single elongate or several circular glandular ridges . . . . . *Pyrgulopsis bacchus*, new species  
 Penial lobe simple; ventral penial surface with single, circular glandular ridge . . 12
- 12. Penial filament length greater than 50% of penis length, typically extending beyond distal tip of penial lobe . . . . . *Pyrgulopsis simplex*, new species  
 Penial filament length 50% or less than penis length, rarely extending beyond distal tip of penial lobe . . . . . 13
- 13. Penis length about 15% of body length; penial filament length less than three times filament width . . . . . *Pyrgulopsis conicus*, new species  
 Penis length 24%–30% of body length; penial filament length about three and a half times filament width . . . . . *Pyrgulopsis morrisoni*, new species

**Family HYDROBIDAE**

**Genus *Pyrgulopsis* Call and Pilsbry, 1886**

DIAGNOSIS.—Shell globose to ovate-conic, 1.2 to 8.0 mm high. Aperture simple, umbilicus absent to open. Teleoconch smooth or unicarinate on periphery. Penis with one to fifteen glandular ridges. Penial lobe small relative to size of penis, filament narrow.

REMARKS.—A detailed generic description (with synonymies) is provided by Hershler and Thompson (1987), in which *Marstonia* F.C. Baker, 1926, *Fontelicella* Gregg and Taylor, 1965, *Microannicola* Gregg and Taylor, 1965, *Natricola* Gregg and Taylor, 1965, and *Mexistiobia* Hershler, 1985 are considered synonymous with *Pyrgulopsis*. The genus occurs in much of eastern North America as well as in the Southwest and northern Mexico and comprises 35 (including the below) described species as well as an additional 20 to 25

TABLE 2.—Generalized cusp formulae for the four tooth types.

Species	Central	Lateral	Inner marginal	Outer marginal
<i>Pyrgulopsis glandulosus</i>	5-1-5 1-1	3-1-3(4)	23	31
<i>P. deserta</i>	4-1-4(5) 1-1	3(4)-1-3	17-19	19-21
<i>P. bacchus</i>	3(4,5)-1-3(4,5) 1-1	2(3)-1-2	18-19	30-31
<i>P. conicus</i>	4-1-4 1-1	3(4)-1-3	19	25-28
<i>P. morrisoni</i>	6(7)-1-6(5) 1-1	3-1-3(4)	22-26	27-29
<i>P. montezumensis</i>	8-1-8 1-1	3(4,5)-1-5(6)	27-31	28-30
<i>P. simplex</i>	5-1-5 1-1	3-1-5	23-24	28-30
<i>P. solus</i>	5(6)-1-5(6) 1-1	3(4,5)-1-4(5)	21	25-26
<i>P. confluentis</i>	4-1-5 1-1	3-1-4	24-32	23
<i>P. sancarlosensis</i>	3(5)-1-3(5) 1-1	2(3)-1-3	16-22	23-25
<i>P. cochisi</i>	4-1-4 1-1	3-1-3	22-23	22-23
<i>P. thompsoni</i>	4(5,6)-1-5(6) 1-1	3-1-3(4)	20-24	26-32
<i>Tryonia gilae</i>	5(6)-1-5(6) 2-2	4(5,6)-1-5(6)	24-30	28-31
<i>T. quitobaquiatae</i>	6-1-6 1-1	3-1-4	23	26

undescribed species from the Southwest. The closest relative of the genus appears to be *Cincinnatia* Pilsbry, 1891, which is restricted to eastern North America. *Cincinnatia* differs from *Pyrgulopsis* in having a larger and broader shell, and a penis with a much smaller penial filament (relative to size of penis) and more glandular ridges.

***Pyrgulopsis glandulosus* Hershler, new species**

Verde Rim springsnail

FIGURES 3a-c, 4-9, 10a,b

*Fontelicella* species.—Williams et al., 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Yavapai County*: Nelson Place Spring, USNM 859047 (holotype), USNM 859048 (5 paratypes), USNM 847205, J.J. Landye and G. Edwards, 28 Sep 1973; spring 150 m E of Nelson Place Spring, USNM 847232, J.J. Landye and G. Edwards, 28 Sep 1973.

DIAGNOSIS.—An ovate-shelled, large size (shell height, 2.0 to 2.8 mm) species. Penis elongate, massive (41% of body length), filament short relative to penis length. Dorsal penial surface with several glandular ridges, two or more of which are elongate; ventral surface with additional ridges borne on accessory crests. Holotype (Figure 3a) height, 2.80 mm; width,

1.92 mm; whorls 4.0.

DESCRIPTION.—Shell white-clear, transparent; periostracum light brown, thin, covering much of shell surface, or absent. Shell (Figure 3a-c) about a third taller than wide. Whorls, 3.5 to 4.0, convex and slightly shouldered, sutures slightly impressed. Spire outline convex, largely due to allometric translation of body whorl. Sexual dimorphism significant (Appendix 2) with females larger than males. Protoconch slightly protruding, with 1.25 partly pitted whorls. Body whorl relatively inflated and large (about 83% of shell height). Aperture ovate, moderate in size, occupying about half of shell height and 83% of body whorl height, somewhat angled above, rounded below, typically loosened from body whorl. Inner lip slightly thickened, moderately reflected, and near straight. Outer lip thin and broadly convex. Apertural plane nearly parallel to coiling axis with long axis tilted 20° to 30° relative to coiling axis. Umbilicus moderately to broadly open. Teleoconch sculpture consisting of strong growth lines. Amber, horny, paucispiral operculum about one and a half times as long as wide and with three whorls.

Snout (Figures 4f, 5c, 7a) longer than wide, fairly thickened, and terminating distally with fleshy lips. Cephalic tentacles (Tn) narrow, slightly less than twice as long as snout, somewhat expanded at tips. Tentacle surface with irregular

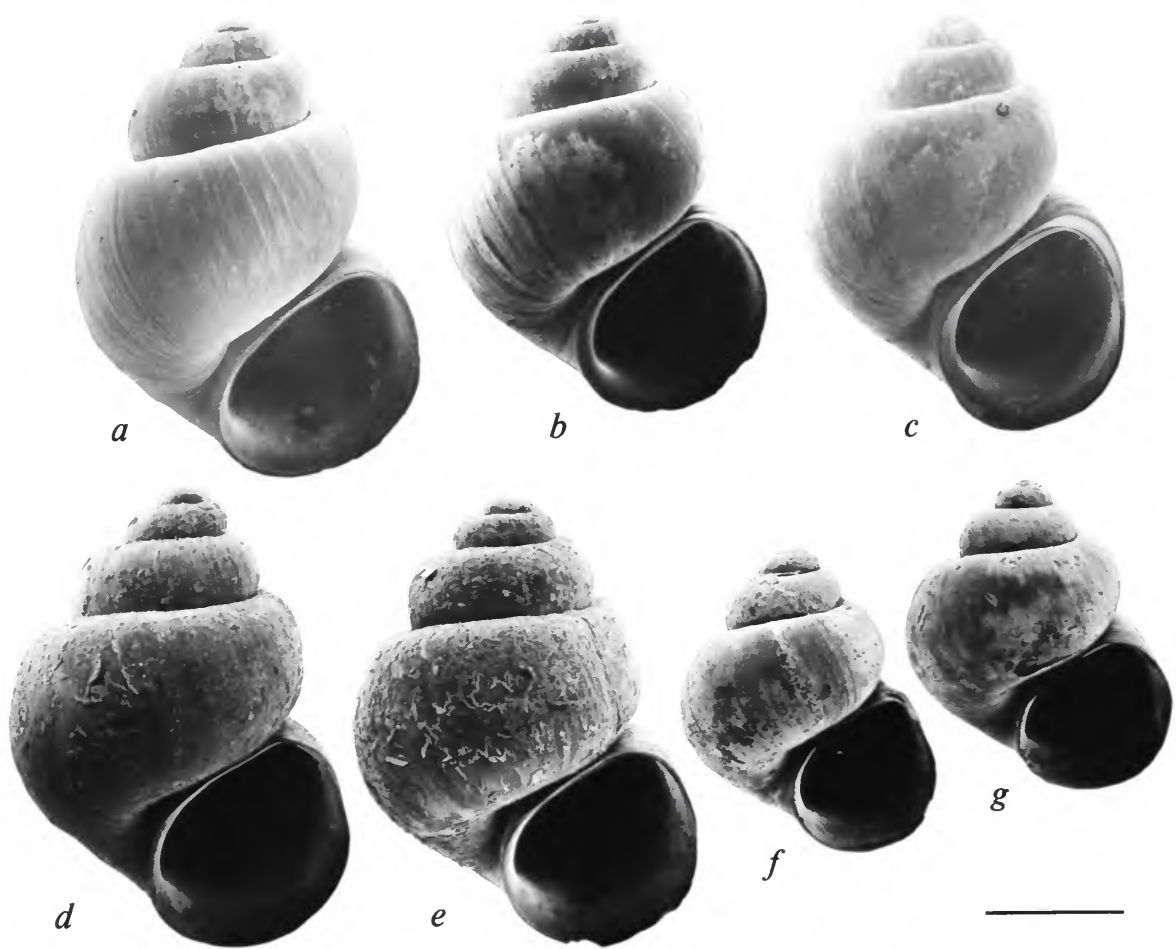


FIGURE 3.—*Pyrgulopsis glandulosus*, new species: *a*, holotype, USNM 859037, Nelson Place Spring, Yavapai County, Arizona; *b,c*, same locality, USNM 847205. *Pyrgulopsis confluentis*, new species: *d*, holotype, USNM 859053, spring on N side of Blanket Creek, Apache County, Arizona; *e*, same locality, USNM 847234; *f,g*, USNM 847229, spring at Three Forks, Apache County, Arizona. (Bar = 0.75 mm.)

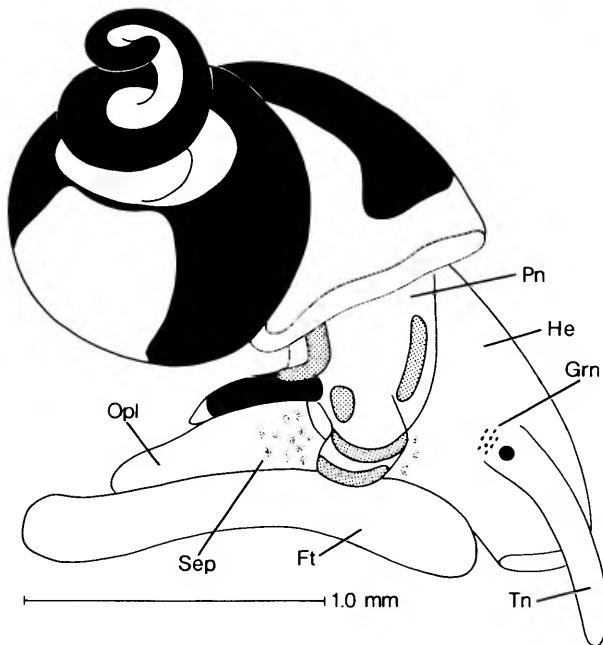


FIGURE 4.—Right lateral aspect of relaxed *P. glandulosus*, new species (without shell), USNM 847205, Nelson Place Spring, Yavapai County, Arizona: darkly pigmented epithelia appear black, and glandular ridges in penis screened. (Abbreviations: Ft = foot, Grn = white granules; He = head, Opl = operculigerous lobe, Pn = penis; Sep = subepithelial pigment; Tn = cephalic tentacle.)

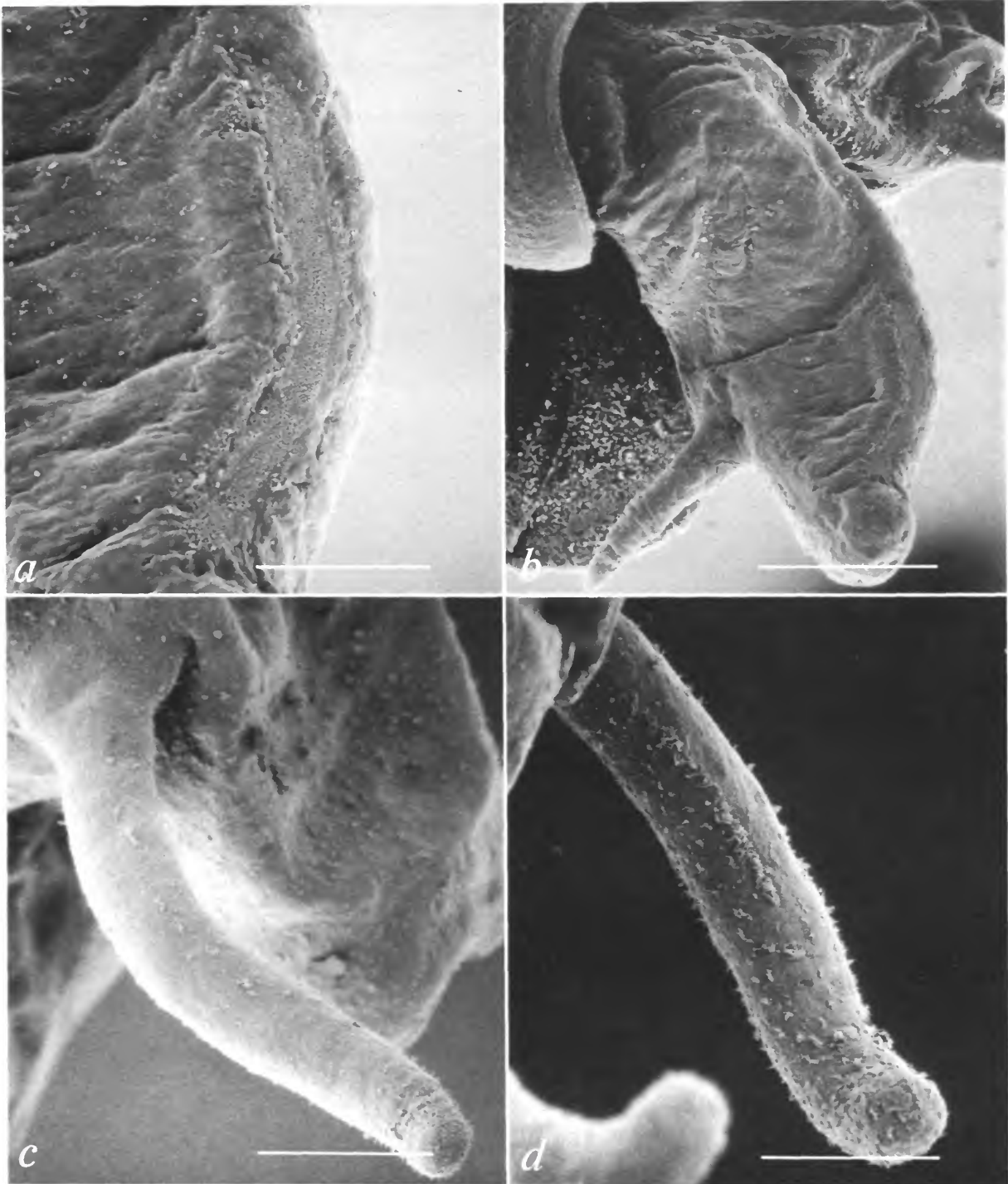


FIGURE 5.—SEM micrographs of penis and cephalic tentacles of *P. glandulosus*, new species, USNM 847205, Nelson Place Spring, Yavapai County, Arizona: *a*, close-up of glandular ridge, bar = 120  $\mu$ m; *b*, dorsal aspect of penis, bar = 0.33 mm; *c*, right tentacle, showing sparse ciliation, bar = 176  $\mu$ m; *d*, left tentacle, bar = 136  $\mu$ m.



tufts of cilia (Figure 5*b,c*), sometimes forming a short tract on dorsal surface of left tentacle. Slightly swollen outer edges of tentacle bases containing black eyes. Elongate foot thickened, posteriorly tapered. Fairly straight anterior edge of foot with central pore through which twelve to fifteen elongate pedal glands discharge.

Epithelial melanic pigment usually absent from head/foot although occasional snails may have light to fairly dark brown patches covering most of snout (posterior to distal lips). Dorsal surface of visceral coil covered with melanic pigment (Figure 4), although stomach region typically less pigmented or even lacking pigment. Light grey to black subepithelial pigment sometimes present as small patches just distal to bases of tentacles and on "neck" behind tentacles, as broad triangular patch on sides of head/foot (Figure 4, Sep), and as irregular patch on operculigerous lobe. Similar pigment present on right side of mantle collar. Opaque white granules densely clustered just behind eyes (Figure 4, Grn), with small clusters sometimes occurring along proximal half of tentacles as well. Dark, brown-black subepithelial pigment concentrated in proximal portion of penial filament, extending somewhat to rest of penis (Figure 4). Ventral pigmentation visible dorsally as in Figure 4.

Pallial cavity (Figure 6*a,b*) with large ctenidium (Ct) with 16 to 20 narrow filaments extending along most of pallial cavity (and 24% to 28% of body length), and extending anteriorly to mantle collar (Mc). Widest filaments centrally positioned and brushing against intestine (In). Osphradium (Os) fairly elongate, filling 22% to 33% of ctenidium length, positioned slightly posterior to middle of ctenidium. Kidney (Ki) with small opening (Oki) fringed by obvious lips.

Buccal mass short, filling only anterior half of snout. Paired, tubular, salivary glands dorsal to nerve ring. Oesophagus externally simple, and narrow. Pair of chitinous jaws positioned at anterior end of buccal cavity.

Radula (Figure 7) typically taenioglossate, with trapezoidal central teeth, each having single pair of basal cusps. Lateral angles of central tooth well developed, projecting about 45° from central axis of tooth. Basal process of central tooth well developed. Central and lateral teeth with enlarged central cusps. Outer and inner marginals similar in shape, with former having only few more cusps than latter (Table 2). Stomach (Figure 6*c*, Ast, Pst) and style sac (Sts) about equal in length, former with small caecal chamber (Cc) along its posterior edge. Posterior stomach chamber with single opening to digestive gland (Dgo) (posterior to oesophageal opening). Digestive gland covering posterior half of stomach, and extending (ventral to gonad) almost to posterior tip of visceral coil. Intestine (In) with slight bend in pallial cavity (Figure 6*b*).

Testis (Figure 6*d*, Ts) consisting of simple lobes, with anterior end lying against posterior edge of stomach, and filling about three-quarters of digestive gland length and 31% of body length. Seminal vesicle (Figure 6*d*, Sv) exiting near anterior end of testis and consisting of a few thickened coils ventral to

testis and partly covering dorsal stomach surface. Prostate gland (Figure 6*e*, Pr) simple, small (16%) relative to body length, largely posterior to pallial cavity. Anterior vas deferens (Figure 6*e*, Vd) exiting from mid-line of anterior end of prostate gland and extending along columellar (right) side of pallial cavity roof before entering "neck" posterior to penial attachment area (Figure 6*a*).

Penis (Figures 4, 5*a,b*, 6*a*, 8, 9) protruding well anterior to mantle collar (Figure 5*a*), flattened, broadly attached to neck well posterior to snout (Figure 6) and extending anteriorly from attachment area without coiling (Figure 6*a*, Pn). Penis much longer than wide, often expanding in width distal to base. Penial filament (Figure 8, Pf) one-quarter of penis length, positioned at about two-thirds of penis length, narrow (length/width, 25%), and rarely projecting distal to penial lobe (Figure 8, Plo), which tapers and sometimes has distinctive terminal process (Figure 8*b,d*). Vas deferens (Vd) extending as fairly straight tube along edge of penis (Figure 8*a*), and opening at tip of penial filament.

Penial surface with four to seven slightly elevated, glandular ridges, consisting of paired rows of small glands, each discharging through central slit (Hershler, 1985, fig. 8*b,c*). Dorsal penial surface with two elongate ridges, one positioned largely along edge containing penial filament, and other located along opposite edge, sometimes curving toward filament (Figures 8, 9). One to three additional and smaller ridges on same surface, typically positioned on tip of penial lobe (visible from ventral aspect also) and between two elongate ridges. Ventral penial surface with one to three ridges located on two accessory crests. Crest located closest to distal edge of penis somewhat swollen and bulging from penial surface, whereas other crests typically appearing as folds flattened against penis.

Ovary (not figured) simply lobular, abutting anteriorly against posterior edge of stomach, and filling 17% of body length. Oviduct passing over stomach surface before disappearing under (to left of) pallial oviduct. Left lateral aspect of pallial oviduct and bursa copulatrix complex shown in Figure 10*a,b*. Albumen gland (Ag) highly glandular and somewhat (104%) longer than capsule gland (Cg), which has posterior, yellow section and (smaller) anterior, clear section. Capsule gland opening (Cga) subterminal and fairly long and wide. Anterior to opening, presumed pathway of egg capsules fringed by thin, vestibule-like extension of glandular tissue from capsule gland (Figure 10*a*, Vsb), as typical of genus. Oviduct (Ov) with single loop proximal to point of merger with duct of seminal receptacle (Sr). Distal to this, oviduct merges with duct of bursa copulatrix to jointly enter albumen gland (Ag). Simple oviduct loop small, with diameter about 44% of albumen gland length. Body of small seminal receptacle, positioned on left surface of bursa, often narrow and indistinguishable from its duct; length of body plus duct almost equal (83%) to bursa length. Bursa (Figure 10*b*) moderately large (43% of albumen gland length), pear-shaped, and lying against left side (near ventral

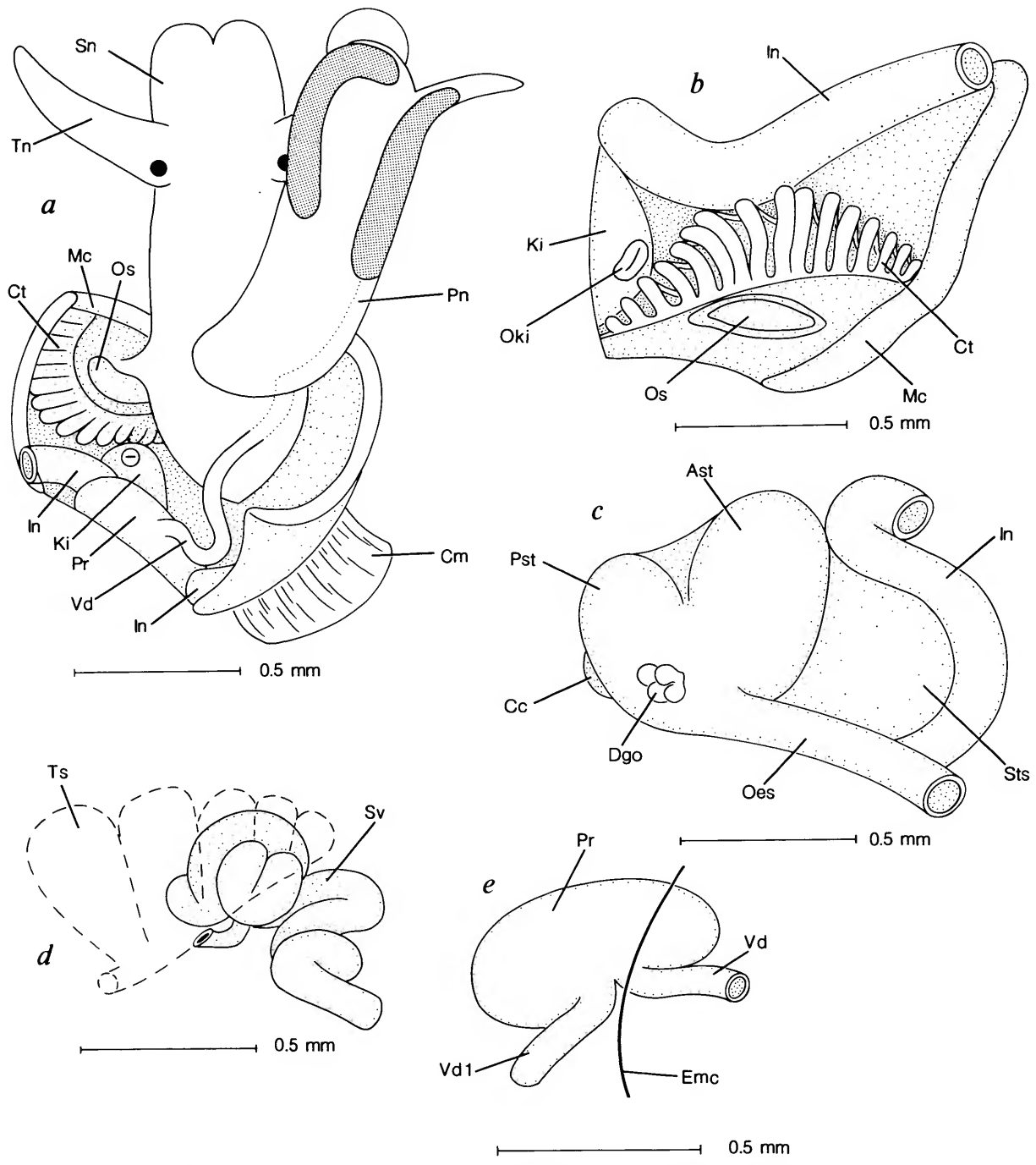


FIGURE 6.—Anatomy of *P. glandulosus*, new species, USNM 847205, Nelson Place Spring, Yavapai County, Arizona: *a*, head and contents of pallial cavity, which were exposed by slitting pallial roof mid-dorsally; *b*, ctenidium and adjacent structures; *c*, right lateral aspect of stomach; *d*, coiled seminal vesicle (testis removed); *e*, right lateral aspect of the prostate gland. (Abbreviations: Ast = anterior stomach chamber; Cc = caecal chamber; Cm = columellar muscle; Ct = ctenidium; Dgo = opening of the digestive gland into the stomach; Emc = posterior end of pallial cavity; In = intestine; Ki = kidney; Mc = mantle collar; Oes = oesophagus; Oki = kidney opening; Os = osphradium; Pn = penis; Pr = prostate; Pst = posterior stomach chamber; Sn = snout; Sts = style sac; Sv = seminal vesicle; Tn = cephalic tentacle; Ts = testis; Vd = anterior vas deferens; Vd1 = posterior vas deferens.)

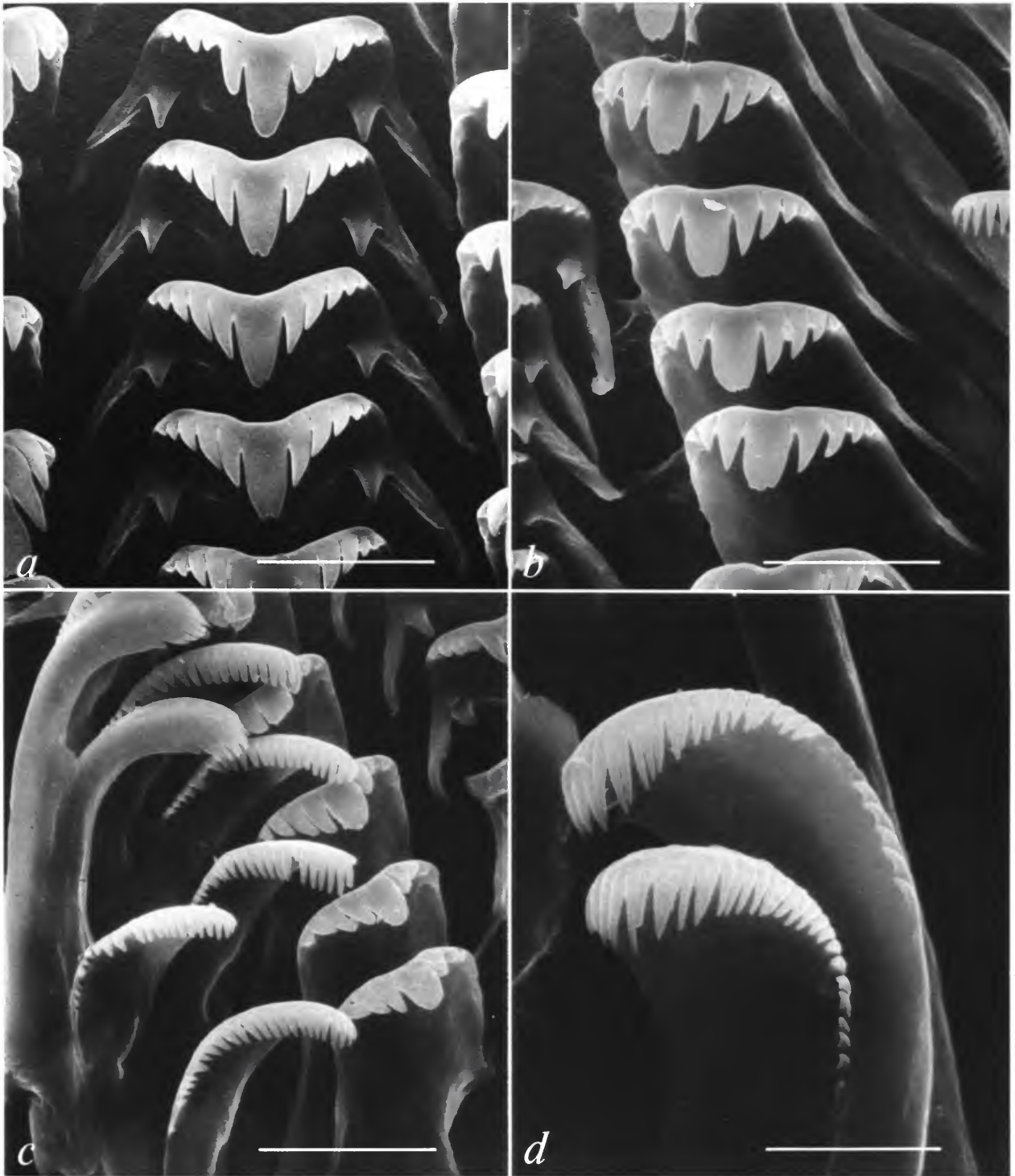


FIGURE 7.—Radula of *P. glandulosus*, new species, USNM 847205, Nelson Place Spring, Yavapai County, Arizona: *a*, centrals, bar = 13.6  $\mu\text{m}$ ; *b*, laterals, bar = 15.0  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 15.0  $\mu\text{m}$ ; *d*, outer marginals, bar = 5.0  $\mu\text{m}$ .

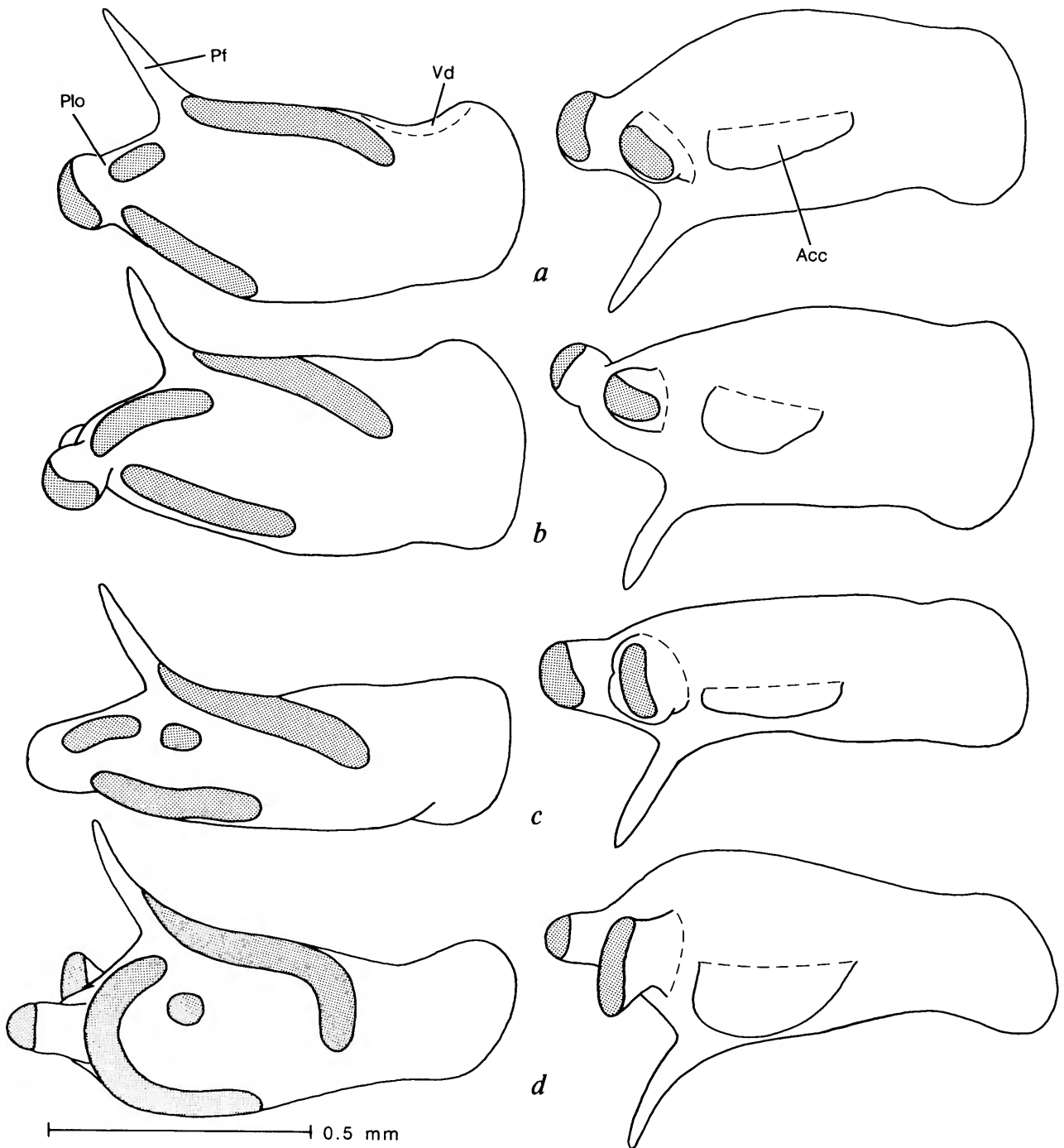


FIGURE 8.—Penial variation of *P. glandulosus*, new species, USNM 847205, Nelson Place Spring, Yavapai County, Arizona: Dorsal aspects to left, ventral aspects to right; screened areas indicate glandular ridges. (Abbreviations: Acc = accessory crest; Pf = penial filament; Plo = penial lobe; Vd = vas deferens.)



FIGURE 9.—Penial variation of *P. glandulosus*, new species: *a, b*, USNM 847205, Nelson Place Spring, Yavapai County, Arizona; *c*, USNM 847232, spring 150 m E of Nelson Place Spring, Yavapai County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

edge) of albumen gland. Two-thirds of bursa length posterior to gland. Thin, narrow duct of bursa tightly pressed to albumen gland.

REMARKS.—*Pyrgulopsis glandulosus* groups with a number of Arizona and New Mexico species (the latter undescribed,

see Taylor, 1983) having large, ovate shells and penes with small filament and relatively numerous glandular ridges. On the basis of penial morphology, the species is most similar to *P. montezumensis*, which also occurs in Verde River drainage, but differs in having a larger penis and accessory crests on

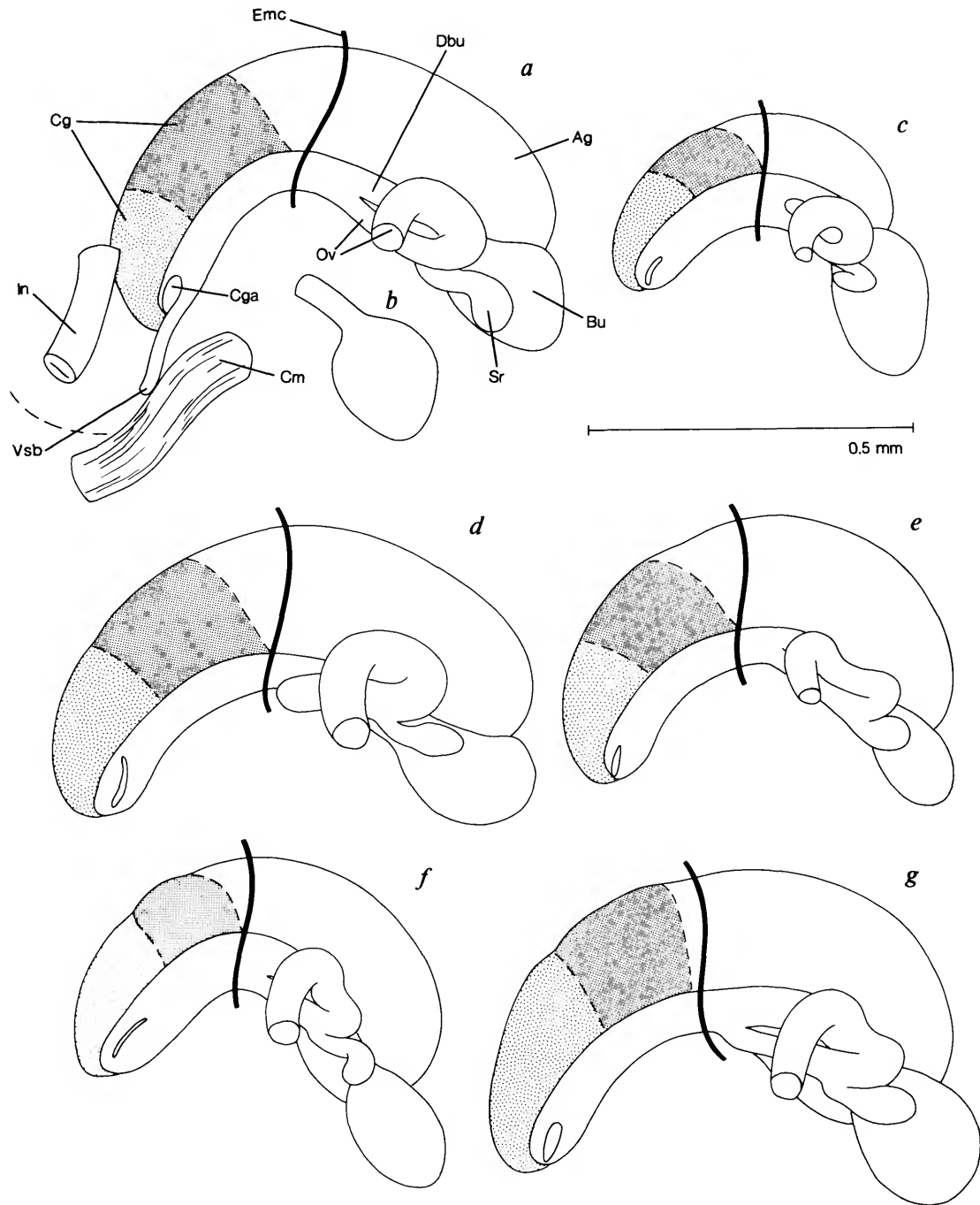


FIGURE 10.—Pallial oviducts of *Pyrgulopsis* species, viewed from the left side (two tissue sections indicated by screens): *a*, *P. glandulosus*, new species, USNM 847205, Nelson Place Spring, Yavapai County, Arizona (shows position of other structures at anterior end of pallial cavity, with mantle edge indicated by dashed line); *b*, bursa copulatrix from above; *c*, *P. deserta* (Pilsbry), USNM 847202, spring upstream on Virgin River from Littlefield, Mohave County, Arizona; *d*, *P. bacchus*, new species, USNM 847203, Grapevine Spring, Mohave County, Arizona; *e*, *P. conicus*, new species, USNM 847237, Dripping Springs, Mohave County, Arizona; *f*, *P. morrisoni*, new species, USNM 847231, Page Springs, Yavapai County, Arizona; *g*, *P. montezumensis*, new species, USNM 847233, Montezuma Well, Yavapai County, Arizona. (Abbreviations: Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cga = capsule gland opening; Cm = columnellar muscle; Dbu = duct of bursa; Emc = posterior end of pallial cavity; In = intestine; Vsb = capsule gland vestibule.)

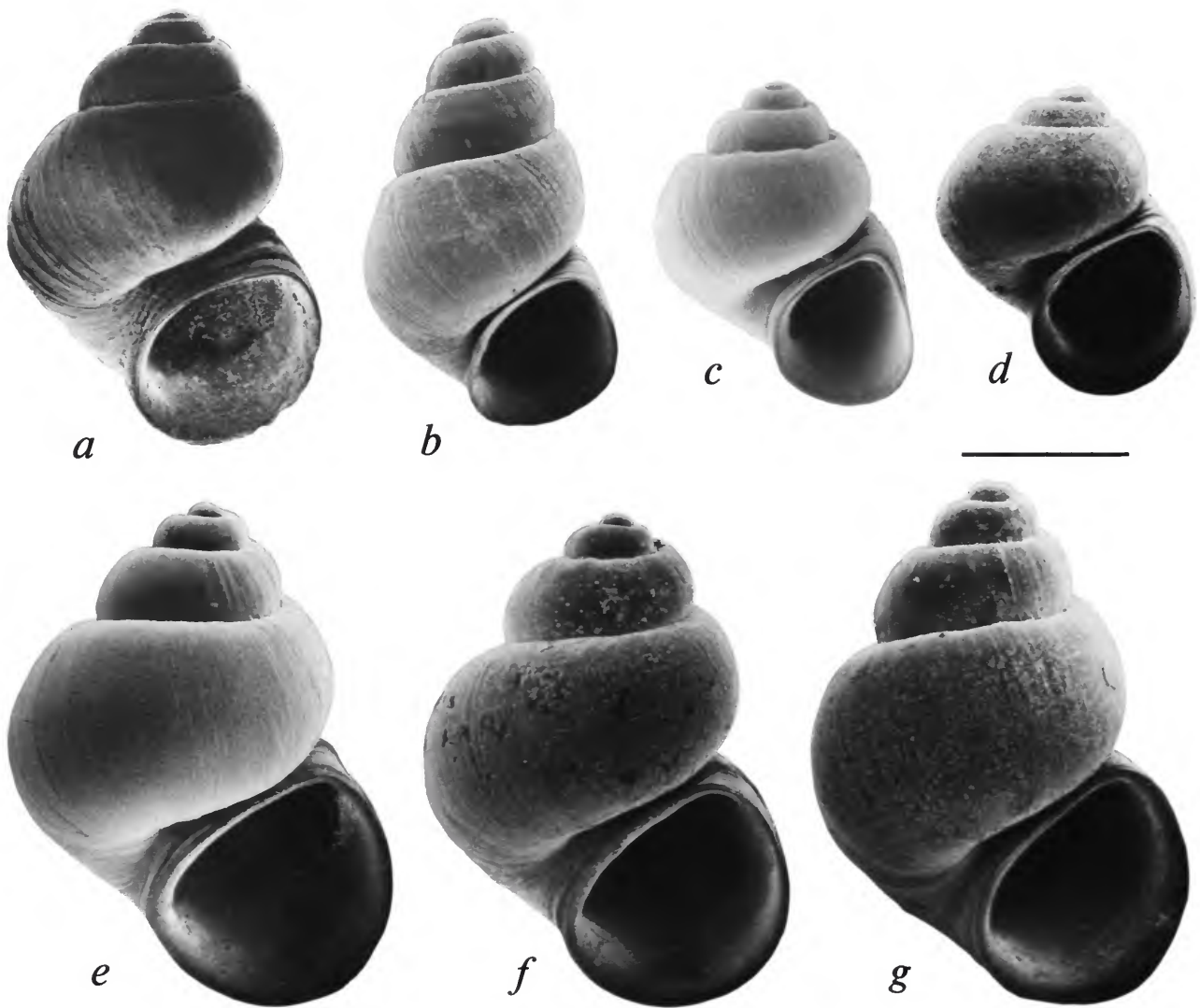


FIGURE 11.—*P. deserta* (Pilsbry): *a*, holotype, ANSP 12112, Washington County, Utah; *b*, USNM 847210, spring in Middleton, Washington County, Utah; *c*, USNM 847239, spring on Red Hill, Washington County, Utah; *d*, USNM 847202, spring upstream on Virgin River from Littlefield, Mohave County, Arizona. *P. bacchus*, new species: *e*, USNM 859037, holotype, Grapevine Spring, Mohave County, Arizona; *f, g*, USNM 847203, same locality. (Bar = 0.75 mm.)

ventral penial surface.

TYPE-LOCALITY.—Nelson Place Spring, Yavapai County, Arizona.

DISTRIBUTION.—Nelson Place Spring complex, consisting of two springs separated by 150 m that form the headwaters of Sycamore Creek.

ETYMOLOGY.—From Latin *glandis*, referring to the highly glandular nature of the penis in this species.

*Pyrgulopsis deserta* (Pilsbry)

Virgin springsnail

FIGURES 10c, 11a–d, 12a–c, 13

*Amnicola deserta* Pilsbry, 1916:111–112, figs. 8, 9.

New genus, new species.—Landye, 1973:48.

"*Amnicola*" *deserta*.—Landye, 1980:70.

Undescribed species.—Landye, 1980:70.

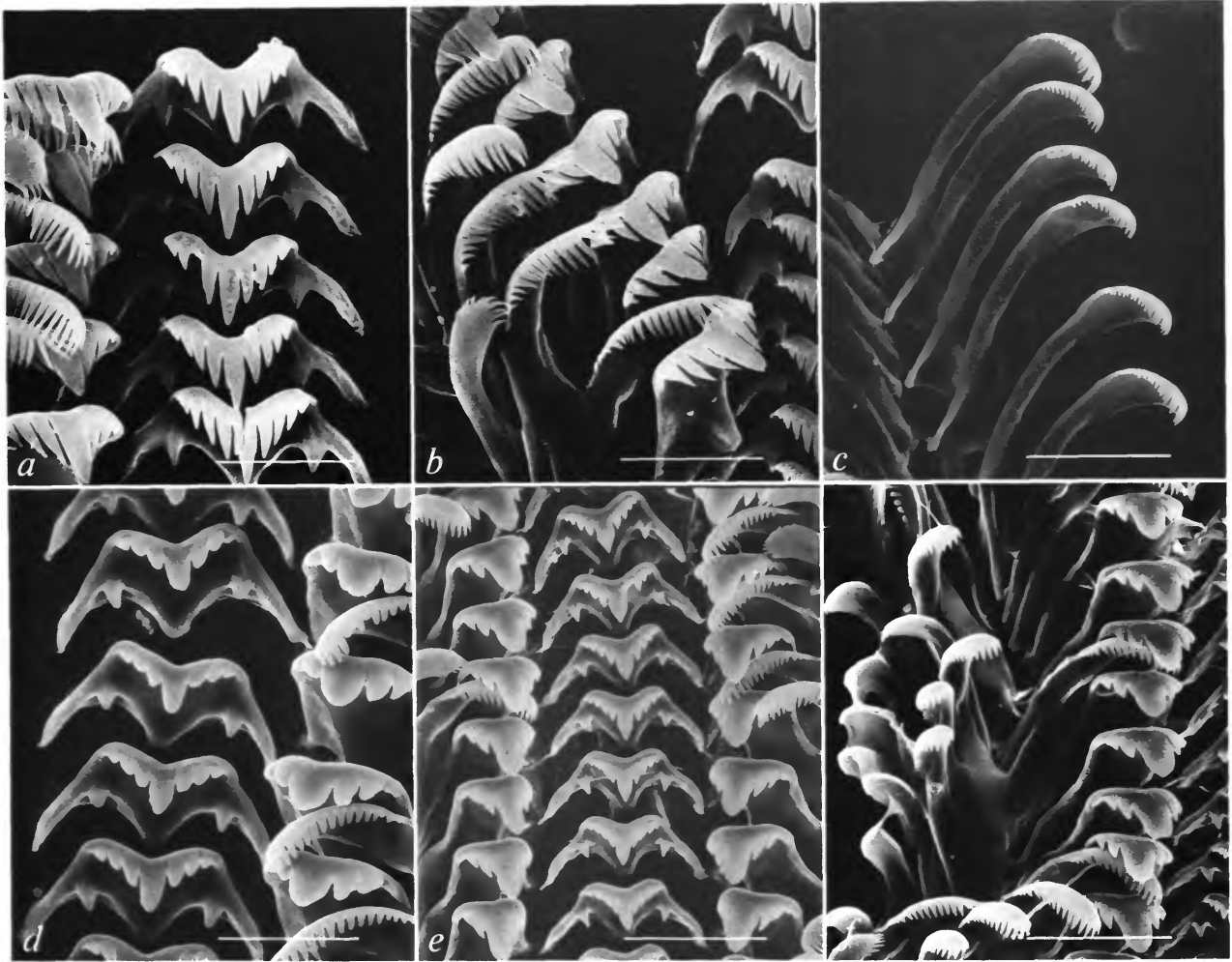


FIGURE 12.—Radula of *P. deserta* (Pilsbry), USNM 847202, spring upstream on Virgin River from Littlefield, Mohave County, Arizona: *a*, centrals, bar = 12.0  $\mu\text{m}$ ; *b*, laterals and inner marginals, bar = 15.0  $\mu\text{m}$ ; *c*, outer marginals, bar = 17.6  $\mu\text{m}$ . *P. bacchus*, new species, USNM 847203, Grapevine Spring, Mohave County, Arizona: *d*, centrals, bar = 20.0  $\mu\text{m}$ ; *e*, centrals, laterals, inner marginals, bar = 38  $\mu\text{m}$ ; *f*, laterals, inner and outer marginals, bar = 38  $\mu\text{m}$ .

**MATERIAL EXAMINED.**—UTAH. *Washington County*: spring on Old Bastion Ranch, USNM 847250, J.J. Landye, 21 Feb 1977; small spring, 70 m N of Interstate 15, USNM 847247, J.J. Landye, 21 Feb 1977; Green Spring, USNM 847242, J.J. Landye, 21 Feb 1977; spring in Middleton, USNM 847210, J.J. Landye, 21 Feb 1977; spring on Red Hill, USNM 847239, J.J. Landye, 30 Aug 1973; spring on west side of Middleton, USNM 847244, J.J. Landye, 20 Feb 1977; Sam Adair Spring, USNM 847245, J.J. Landye, 21 Feb 1977; ANSP 12112 (holotype). ARIZONA. *Mohave County*: spring just E of Littlefield, USNM 847206, J.J. Landye, 23 Feb 1977; spring upstream on Virgin River from Littlefield, USNM 847202, J.J.

Landye, 31 Aug 1973; spring NW of Littlefield, W. Rinne, 17 Dec 1970.

**DIAGNOSIS.**—A small species (shell height, 1.2 to 2.0 mm) with globose to ovate-conic shell. Penis moderate size, with enlarged filament bearing (on its dorsal surface) elongate glandular ridge; ventral penial surface with two to three additional ridges. Holotype (Figure 11*a*) height, 2.16 mm; width, 1.57 mm; whorls, 4.0.

**DESCRIPTION.**—Shell with 3.5 to 4.25 whorls, varying in shape from globose, with well-rounded, unshouldered whorls and relatively large (60% of shell height) aperture (Figure 11*c,d*) to ovate-conic, with fairly flattened whorls and smaller



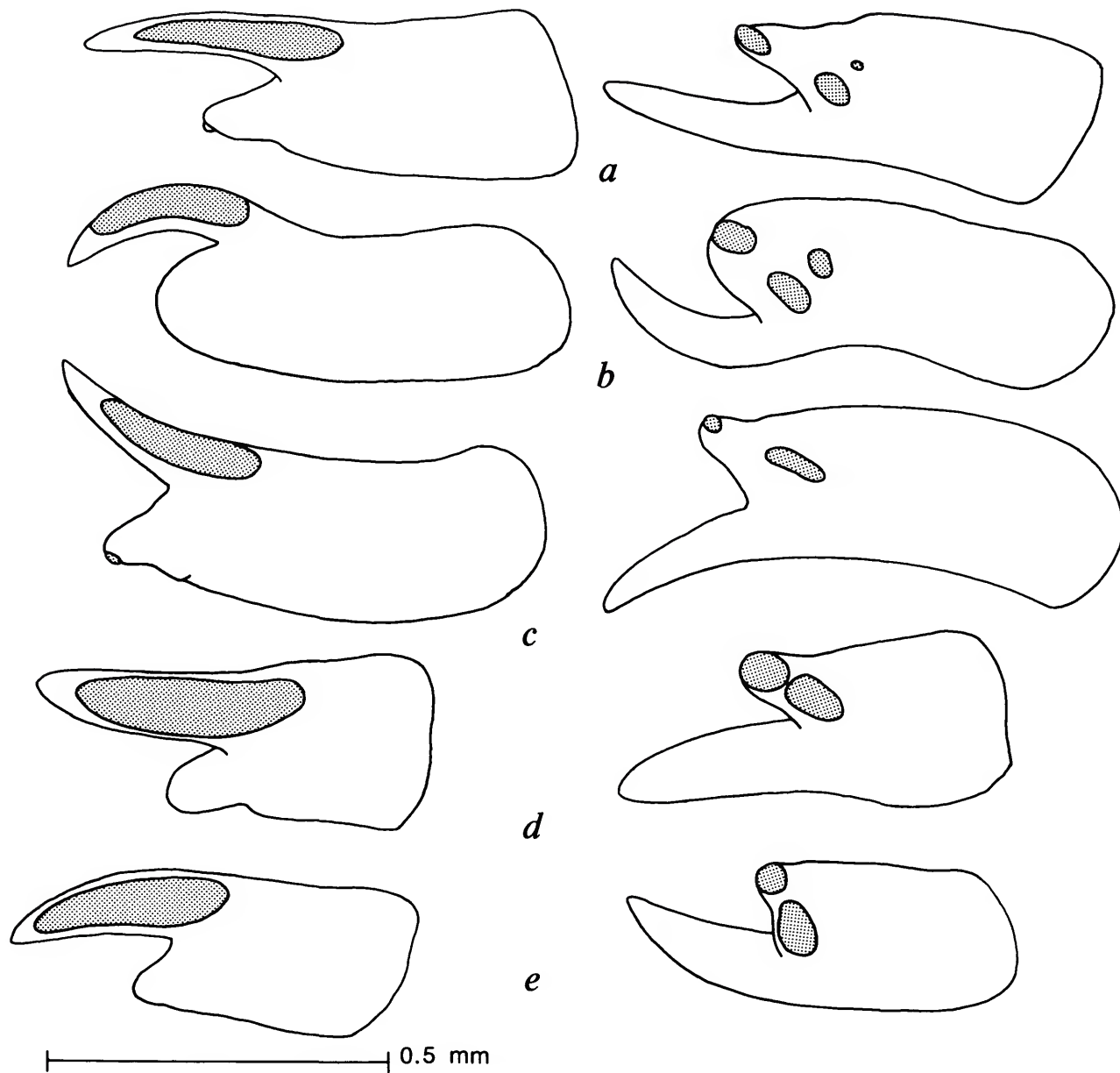


FIGURE 13.—Penial variations of *P. deserta* (Pilsbry): *a,c*, USNM 847239, spring on Red Hill, Washington County, Utah; *b*, USNM 847244, spring on west side of Middleton, Washington County, Utah; *d,e*, USNM 847202, spring upstream on Virgin River from Littlefield, Mohave County, Utah. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

aperture (Figure 11*a,b*). Shape variation evident not only among, but also within populations, with enlarged conical specimens sometimes forming a distinct size class. Sexual dimorphism significant (males larger than females) in one of two populations studied. Aperture often partly or completely

loosened from body whorl. Umbilicus either absent or chink-like to entirely open.

Melanic pigmentation of head-foot varying from dark throughout (except for tentacle and snout tips, and sole of foot) in some populations, to a light dusting on all surfaces or even

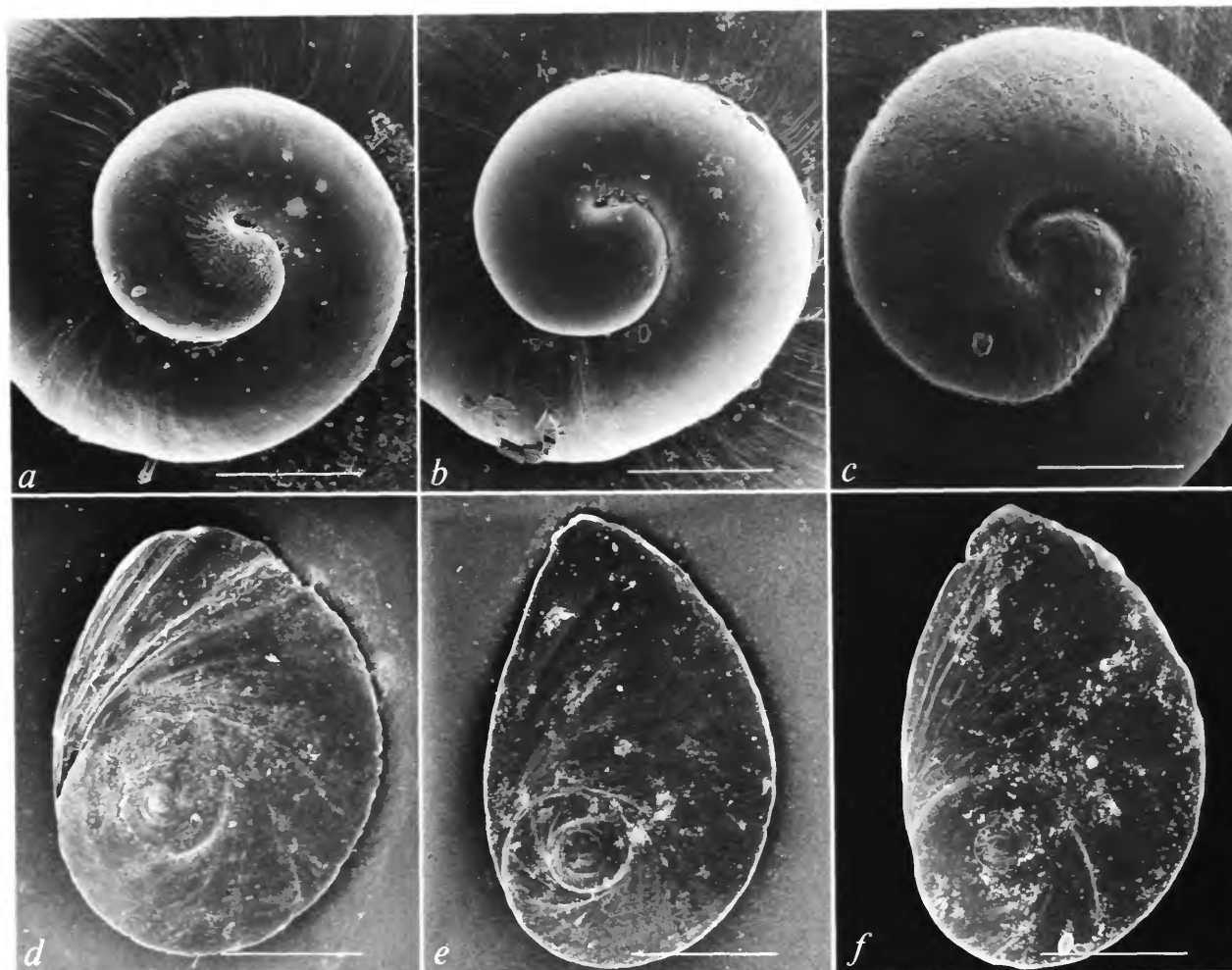


FIGURE 14.—Protoconchs and opercula of Arizona hydrobiids: *a*, protoconch, *P. montezumensis*, new species, USNM 847233, Montezuma Well, Yavapai County, Arizona, bar = 136  $\mu$ m; *b*, protoconch, *P. bacchus*, new species, USNM 847203, Grapevine Spring, Mohave County, Arizona, bar = 136  $\mu$ m; *c*, protoconch, *Tryonia gilae*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona, bar = 75  $\mu$ m; *d*, operculum, *P. montezumensis*, same lot as above, bar = 0.33 mm; *e*, operculum, *P. san Carlosensis*, new species, USNM 847226, springs W of Tom Niece Springs, Graham County, Arizona, bar = 0.27 mm; *f*, operculum, *T. gilae*, same lot as above, bar = 176  $\mu$ m.

absent in others. Penial filament pigmentation ranging from dark throughout to near-absent.

Ctenidial filaments few, seven to 10. Radula (Figure 12) characterized by relatively few cusps on central and marginal teeth. Testis relatively small (31% of body length); prostate gland relatively large (20% of body length). Penis elongate (Figure 13), filament 74% of penis length, extending beyond tip of penial lobe, and fairly thickened (length/width, 42%). Lobe relatively small, sometimes tapering. Glandular ridges, three to four. Ridges on ventral surface positioned on or just behind penial lobe. Bursa (Figure 10c) enlarged (84% of albumen gland length). Seminal receptacle small (40%) relative

to bursa length.

REMARKS.—This snail does not closely resemble any other Arizona form, but is similar to an undescribed species also from Virgin River drainage, southwestern Utah.

TYPE-LOCALITY.—Pilsbry (1916:111) gave the type-locality as "Washington County, Utah." We suspect that the spring in Middleton (USNM 847210) may actually be the type-locality, as specimens from the spring very closely resemble the holotype.

DISTRIBUTION.—Springs along Virgin River in southwestern Utah and northwestern Arizona.

*Pyrgulopsis bacchus* Hershler, new species

Grand Wash springsnail

FIGURES 10d, 11e-g, 12d-f, 14b, 15

*Fontelicella* species.—Williams et al., 1985:32.

MATERIAL EXAMINED.—ARIZONA. *Mohave County*: Grapevine Spring, USNM 859037 (holotype), 859038 (4 paratypes), 847203, J.J. Landye, 4 Jun 1980.

DIAGNOSIS.—A large size (shell height, 2.3 to 3.1 mm), ovate-shelled species. Penis small (13% of body length), with thickened, unpigmented filament; penial lobe enlarged and often bifurcate. One to three glandular ridges on ventral penial surface, along distal edge of penial lobe. Holotype (Figure 11e) height, 2.41 mm; width, 1.78 mm; whorls, 4.0.

DESCRIPTION.—Shell (Figures 11d-e, 14b) with 4.0 to 4.25 moderately rounded, unshouldered whorls. Sexual dimorphism not significant. Aperture usually separate from body whorl. Umbilicus open.

Head-foot usually darkly pigmented throughout, except for tentacles and a broad central patch on sides of head-foot, which are either lightly dusted or unpigmented.

Ctenidium relatively small (19% of body length), with 16 to 21 filaments, Radula (Figure 12d-f) with relatively few cusps on lateral teeth and numerous cusps on outer marginals. Testis large, filling 54% of body length. Penis (Figure 15) stout. Penial filament extending beyond tip of penial lobe, width of filament/length, 55%. Glandular ridges, one to three. Capsule gland (Figure 10d) small (76%) relative to albumen gland. Seminal receptacle 42% of bursa length.

REMARKS.—This species has a distinctive penis shape and glandular ridge pattern that is most similar to those of *P. conicus*, described next, but differs in having a complex penial lobe and single, elongate or several circular glandular ridges on the ventral penial surface.

TYPE-LOCALITY.—Grapevine Spring, Mohave County, Arizona.

DISTRIBUTION.—Grapevine and Whisky Springs in Grand Wash, north of Lake Mead.

ETYMOLOGY.—Named after Bacchus, the Greek god of wine, and referring to abundance of wild grapes (*Vitis arizonica*) in vicinity of Grand Wash springs.

*Pyrgulopsis conicus* Hershler, new species

Kingman springsnail

FIGURES 10e, 16a-d, 17, 18

*Tryonia* new species.—Landye, 1973:42

MATERIAL EXAMINED.—ARIZONA. *Mohave County*: Burns Spring, USNM 847208, J.J. Landye and J. King, 20 Apr 1972, USNM 847215, J.J. Landye, 1 Sep 1972, USNM 847216, J.J. Landye, 12 May 1980, USNM 847204, R. Hershler and J.J.

Landye, 18 Aug 1985; Dripping Springs, USNM 859039 (holotype), 859040 (3 paratypes), 847237, J.J. Landye, 9 May 1980; Cool Spring, USNM 847201, 6 Apr 1981.

DIAGNOSIS.—A moderate size species (shell height, 1.8 to 2.7 mm), having an ovate-conic shell. Penis small (15% of body length), with short filament and single glandular ridge near tip of penial lobe. Holotype (Figure 16a) height, 2.67 mm; width, 1.69 mm; whorls, 4.25.

DESCRIPTION.—Shells (Figure 16a-d) with 3.5 to 4.5 whorls, either well rounded with distinct shoulders or only mildly convex, without shoulders. Sexual dimorphism significant (females larger than males) in one of two populations studied. Aperture often loosened from body whorl. Umbilicus open.

Head-foot usually unpigmented, or with light dusting on snout; subepithelial pigment absent. Penial filament pigmentation light.

Ctenidial filaments, 17 to 21. Central radular teeth (Figure 17) with only four anterior cusps on either side of enlarged, central cusp. Penis (Figure 18) elongate; filament half as long as penis, sometimes extending beyond penial lobe. Penial lobe simple and elongate, with single glandular ridge positioned at or just proximal to tip of lobe on ventral surface. Less than half (42%) of bursa posterior to albumen gland (Figure 10e); seminal receptacle 59% of bursa length.

REMARKS.—The somewhat elongate shell of this species led to initial assignment of the Burns Spring population to *Tryonia* by Landye (1973, 1981).

TYPE-LOCALITY.—Dripping Springs, Mohave County, Arizona.

DISTRIBUTION.—Dripping, Cool, and Burns springs in Black Mountains near Kingman.

ETYMOLOGY.—From Greek *konikos*, referring to the conical shape of shell in this species.

*Pyrgulopsis morrisoni* Hershler, new species

Page springsnail

FIGURES 10f, 16e-h, 19, 20

*Fontelicella* species.—Williams, 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Yavapai County*: Tavasci Springs, USNM 847220, J.J. Landye and D. Belk, 2 Oct 1973; Page Springs, USNM 859041 (holotype), 859042 (4 paratypes), 847231, J.J. Landye and D. Belk, 2 Oct 1973.

DIAGNOSIS.—A medium size species (shell height, 1.8 to 2.9 mm) with ovate or ovate-conic shell. Penis moderate size, with narrow filament of medium length, penial lobe relatively large. Single glandular ridge positioned on ventral surface near tip of penial lobe. Holotype (Figure 16e) height, 2.00 mm; width, 1.49 mm; whorls, 4.0.

DESCRIPTION.—Shell (Figure 16e-h) with 3.75 to 4.50 slightly convex whorls. Sexual dimorphism significant (females larger than males) in one of two populations studied. Inner lip thin and usually adnate to body whorl. Aperture less

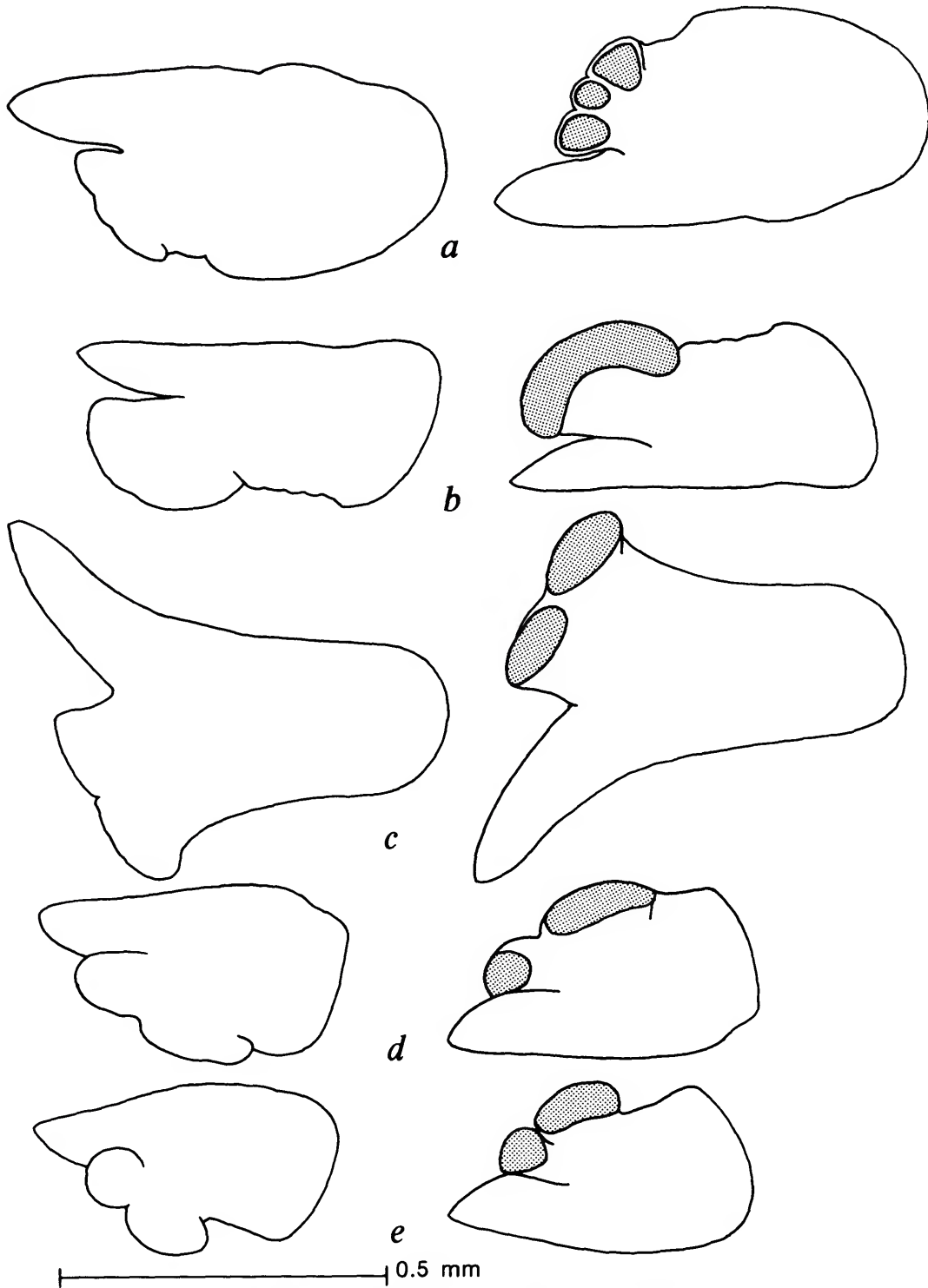


FIGURE 15.—Penial variation of *P. bacchus*, new species, USNM 847203, Grapevine Spring, Mohave County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

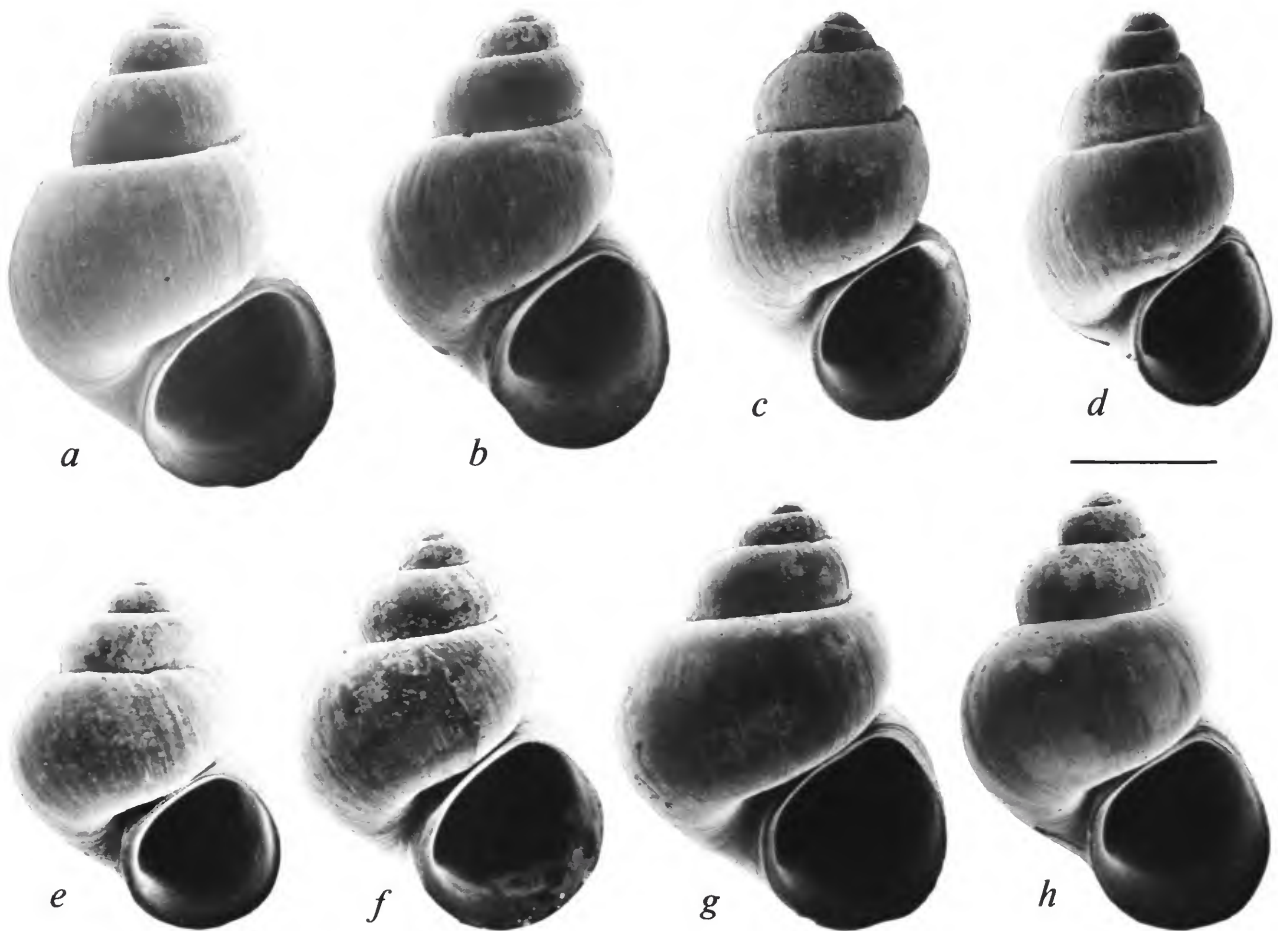


FIGURE 16.—*P. conicus*, new species: *a*, holotype, USNM 859039, Dripping Springs, Mohave County, Arizona; *b*, USNM 847203, same locality; *c,d*, USNM 847204, Burns Spring, Mohave County, Arizona. *P. morrisoni*, new species: *e*, holotype, USNM 859041, Page Springs, Yavapai County, Arizona; *f*, USNM 847231, same locality; *g,h*, USNM 847220, Tavasci Springs, Yavapai County, Arizona. (Bar = 0.75 mm.)

than half of body whorl height. Umbilicus open.

Pigment either absent from head-foot or consisting of light to moderate dusting throughout (except tentacles). Penial filament either pigmented along entire length (sometimes darkly) or unpigmented.

Ctenidial filaments, 15 to 19. Radula (Figure 19) distinguished by large numbers of cusps on central and inner marginal teeth (Table 2). Testis filling 46% to 54% of body length. Penis (Figure 20) elongate; filament only rarely extending beyond enlarged penial lobe. All specimens seen had sole glandular ridge on ventral surface of lobe. Seminal receptacle 88% to 105% of bursa length.

REMARKS.—The distinctive penis of this species, with a large lobe, slender filament, and single glandular ridge, is most similar to that of *P. sancarlosensis* (described below), but differs in lacking glandular ridges on the dorsal surface.

TYPE-LOCALITY.—Page Springs, Yavapai County, Arizona.

DISTRIBUTION.—Page and several nearby (within one km) springs in Verde Valley. The Tavasci Spring population is probably extinct.

ETYMOLOGY.—Named after the late Dr. J.P.E. Morrison for his contributions to study of Hydrobiidae.

#### *Pyrgulopsis montezumensis* Hershler, new species

Montezuma Well springsnail

FIGURES 10g, 13a,d, 21a–c, 22, 23

*Amnicola palomasensis* Pilsbry.—Smith, 1953:9.

*Fontelicella* species.—Williams et al., 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Yavapai County*: Montezuma Well (swallet), USNM 859043 (holotype), 859044 (3



FIGURE 17.—Radula of *P. conicus*, new species: *a*, centrals, bar = 12.0  $\mu\text{m}$ ; *b*, laterals, bar = 8.6  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 16.2  $\mu\text{m}$ ; *d*, outer marginals, bar = 6.0  $\mu\text{m}$ .

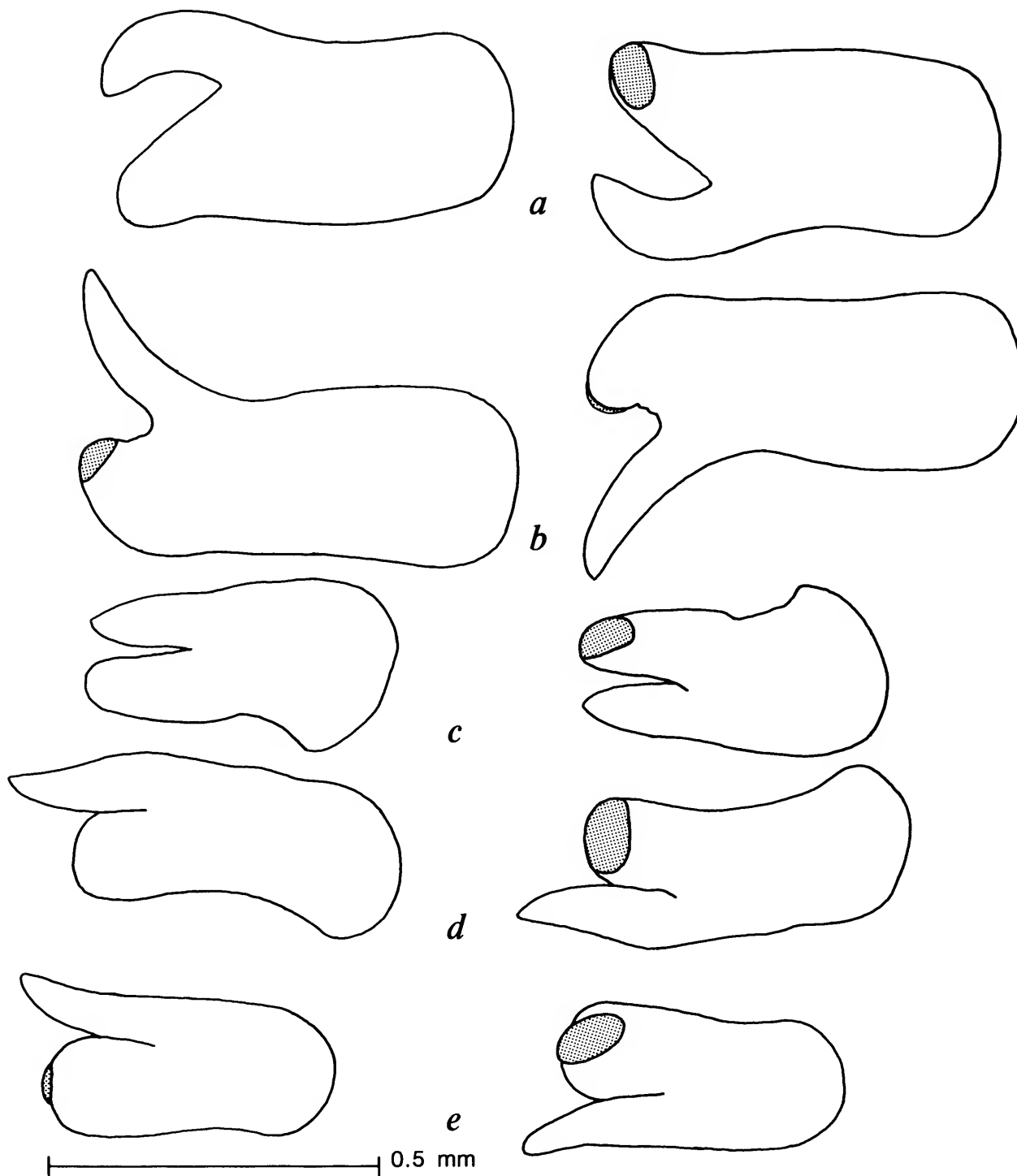


FIGURE 18.—Penial variation of *P. conicus*, new species: *a*, USNM 847204, Burns Spring, Mohave County, Arizona; *b–d*, USNM 847237, Dripping Springs, Mohave County, Arizona; *e*, USNM 847201, Cool Spring, Mohave County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)



FIGURE 19.—Radula of *P. morrisoni*, new species: *a*, centrals, laterals, inner marginals, bar = 13.6  $\mu$ m; *b*, centrals, bar = 12.0  $\mu$ m; *c*, inner marginals, bar = 13.6  $\mu$ m; *d*, inner and outer marginals, bar = 23.1  $\mu$ m.



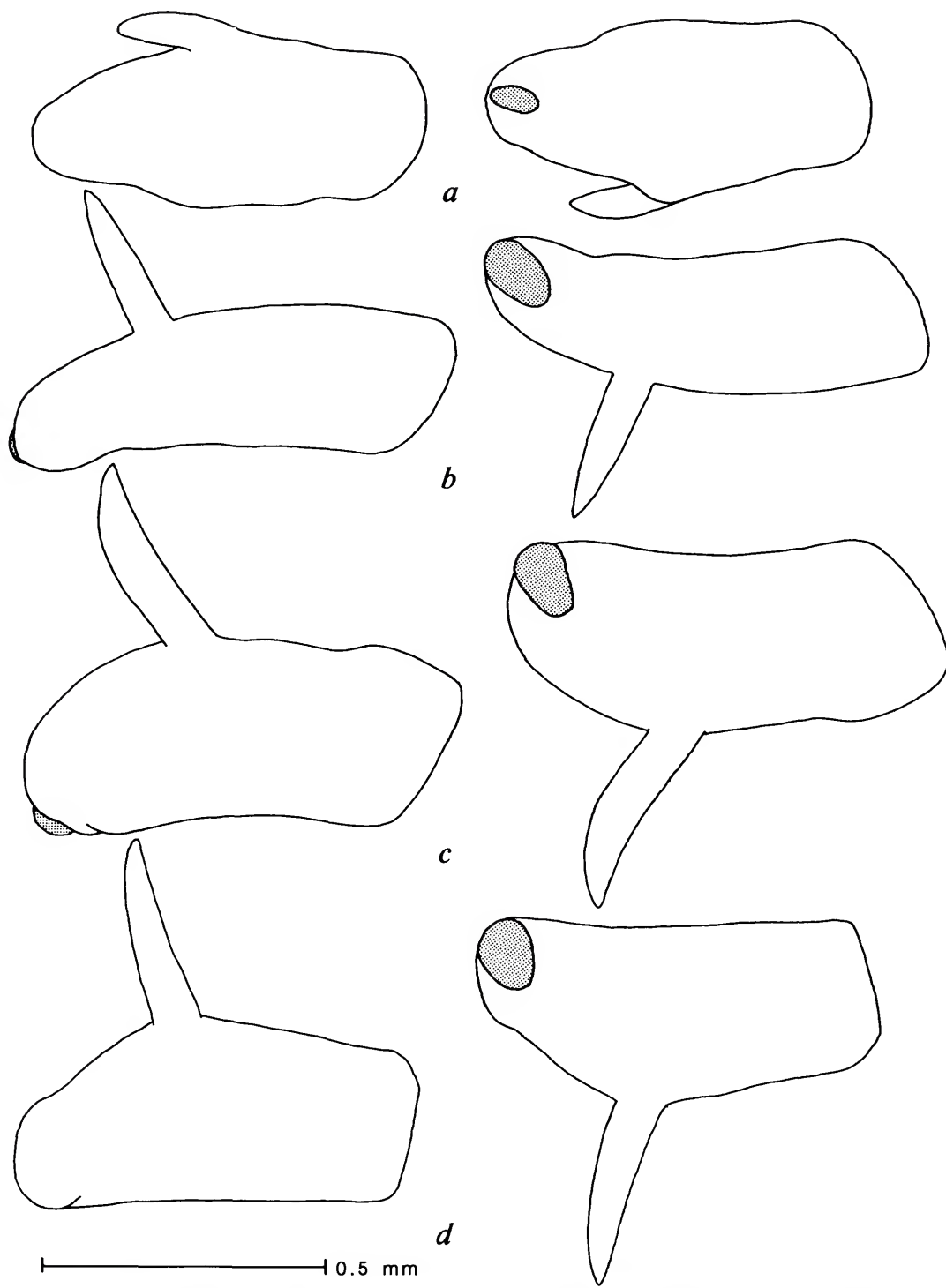


FIGURE 20.—Penial variation of *P. morrisoni*, new species: *a, b*, USNM 847231, Page Springs, Yavapai County, Arizona; *c, d*, USNM 847220, Tavasci Springs, Yavapai County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

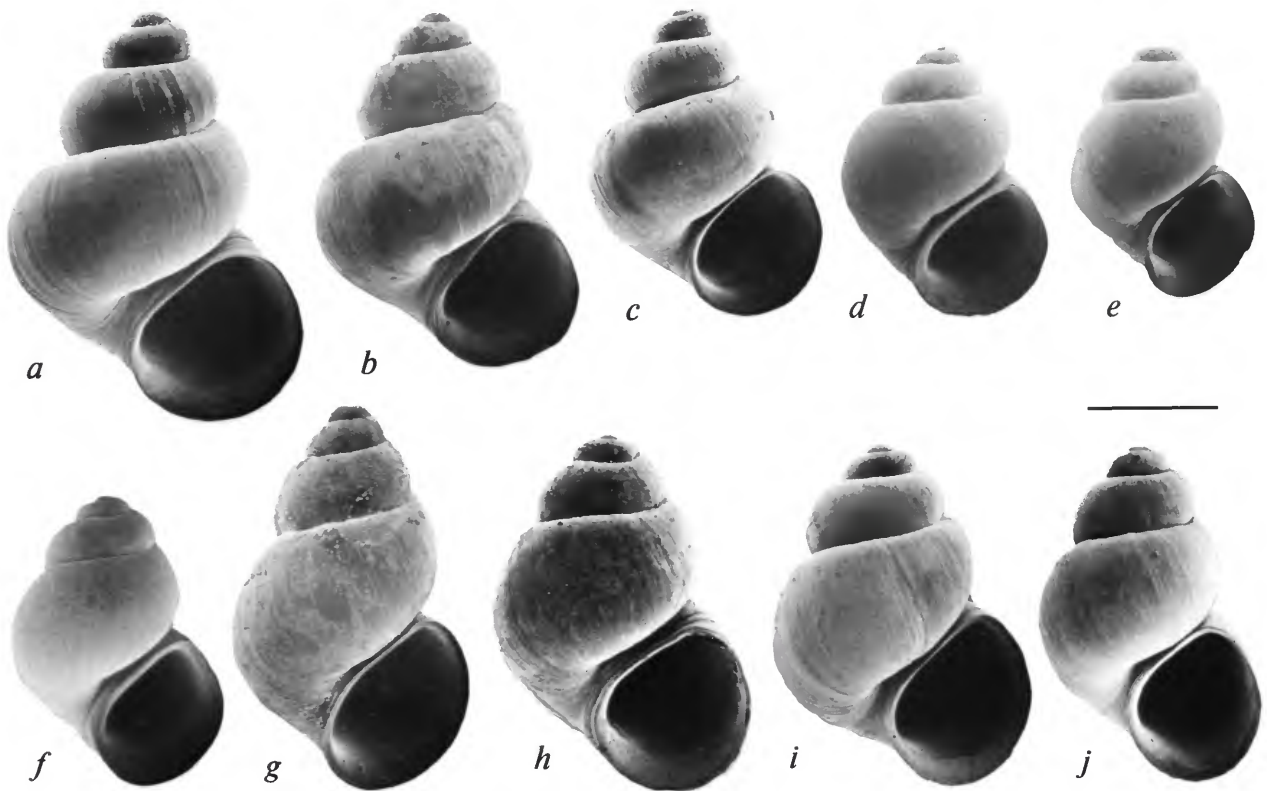


FIGURE 21.—*P. montezumensis*, new species: *a*, USNM 859043, holotype, Montezuma Well, Yavapai County, Arizona; *b,c*, USNM 847233, same locality. *P. solus*, new species: *d*, USNM 859045, holotype, Brown Spring, Yavapai County, Arizona; *e,f*, USNM 850290, same locality. *P. simplex*, new species: *g*, USNM 859049, holotype, spring near Strawberry, Gila County, Arizona; *h*, USNM 847236, locality as above; *i,j*, USNM 847222, Fossil Springs, Yavapai County, Arizona. (Bar = 0.75 mm.)

paratypes), 847233, J.J. Landye and G. Edwards, 10 May 1970; Montezuma Well (canal at outflow), USNM 847230, J.J. Landye, 10 May 1970.

**DIAGNOSIS.**—A moderate size species (shell height, 1.7 to 2.7 mm). Shell ovate to ovate-conic, with slightly loosened whorls. Distinctive dark pigmentation on snout. Penis large (29% of body length). Penial filament short, lobe enlarged. Dorsal penial surface with two elongate glandular ridges (one on base of filament), one or two additional ridges present on tip of lobe and on ventral surface. Holotype (Figure 21*a*) height, 2.65 mm; width, 1.78 mm; whorls, 4.5.

**DESCRIPTION.**—Shell (Figures 14*a*, 21*a-c*) with 3.5 to 4.5 highly convex whorls, with indented sutures. Loosening of whorls along axis noticeable in most specimens. Body whorl 73% to 74% of shell height. Sexual dimorphism significant (females larger than males) in one of two populations studied. Aperture relatively wide. Inner lip thin, and either just touching or with much of length fused to body whorl. Umbilicus open. Operculum (Figure 14*d*) ovate.

Entire snout, distal half of snout, or just distal lips with very dark, purple melanin. Tentacles, sides of head/foot, anterior edge of foot with somewhat lighter pigment. Penial filament unpigmented or with small pigment patch near base.

Ctenidial filaments, 15 to 19. Lateral angles on central tooth widely diverging (Figure 22). Central and marginal teeth with large numbers of cusps (Table 2). Penis (Figure 23) moderately elongate. Filament only 30% of penial length, rarely extending beyond penial lobe. Width of filament 40% of length. Glandular ridges, two to four. Two elongate ridges on dorsal surface positioned on or just proximal to filament, and near center of penis. In addition to elongate ridge along (ventral) edge of lobe, small ridge sometimes present on central portion of ventral surface. Seminal receptacle 64% of bursa length (Figure 10*g*).

**REMARKS.**—The characteristic slight loosening of shell coiling in this species is unique among Arizona *Pyrgulopsis*.

**TYPE-LOCALITY.**—Montezuma Well, Yavapai County, Arizona.



FIGURE 22.—Radula of *P. montezumensis*, new species, USNM 847233, Montezuma Well, Yavapai County, Arizona: *a*, centrals, bar = 12.0  $\mu\text{m}$ ; *b*, laterals, bar = 8.6  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 16.2  $\mu\text{m}$ ; *d*, outer marginals, bar = 4.3  $\mu\text{m}$ .

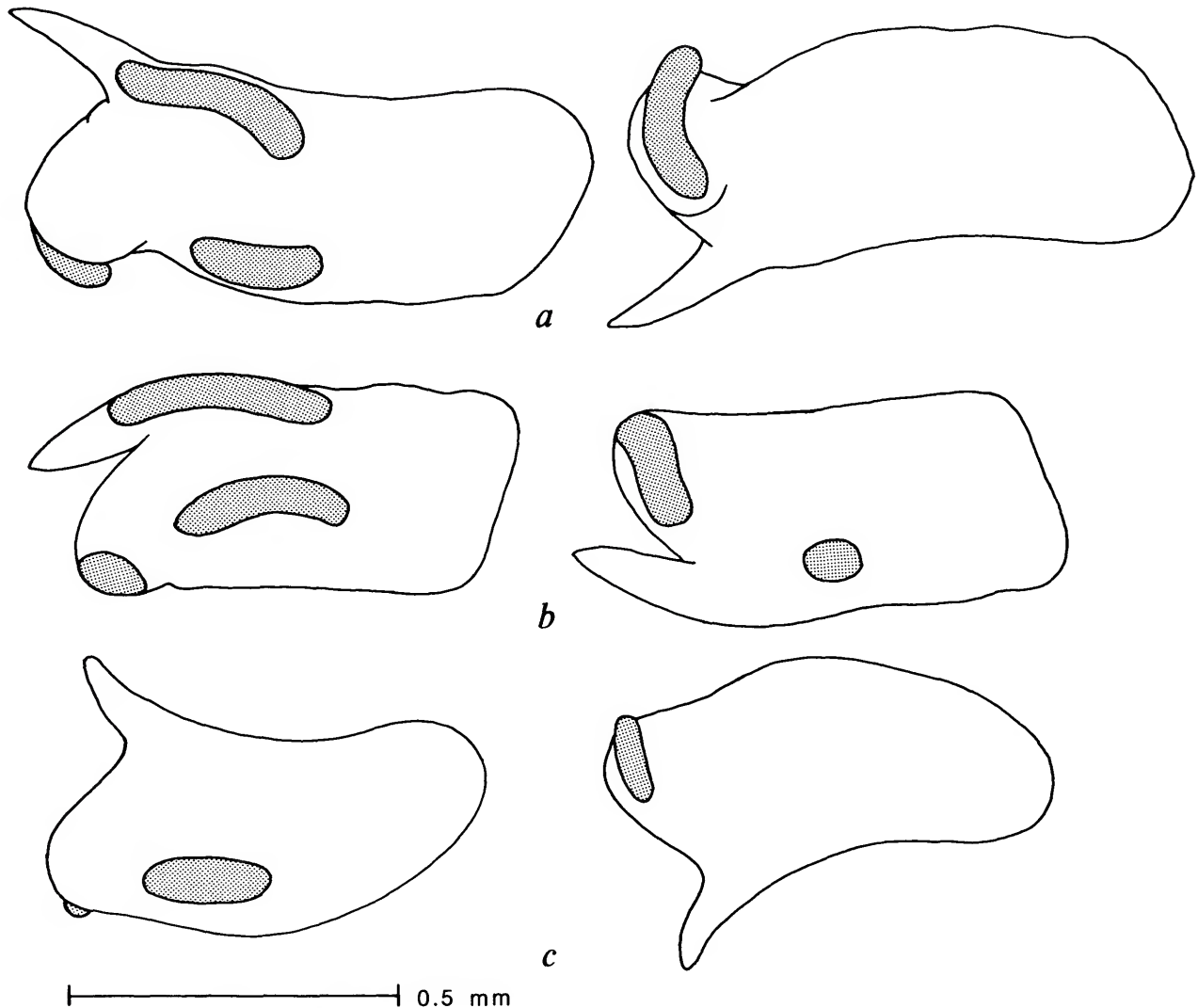


FIGURE 23.—Penial variation of *P. montezumensis*, new species: *a, b*, USNM 847233, Montezuma Well, Yavapai County, Arizona; *c*, USNM 847230, locality as above (but from spring outflow). (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

DISTRIBUTION.—Endemic to Montezuma Well and its upper 100 m of outflow, Montezuma Well National Monument, Verde Valley.

ETYMOLOGY.—Referring to the type-locality.

***Pyrgulopsis solus* Hershler, new species**

Brown springsnail

FIGURES 21*d-f*, 24, 25, 26*a*

MATERIAL EXAMINED.—ARIZONA. *Yavapai County*: Brown Spring, USNM 859045 (holotype), 859046 (3 paratypes),

850290, J.J. Landye, 4 Feb 1986.

DIAGNOSIS.—Shell ovate, small (shell height, 1.4 to 2.0 mm). Penis small (12% of body length), with enlarged, bifurcate lobe. Elongate glandular ridge along lobe's edge, smaller ridge on ventral surface. Holotype (Figure 21*d*) height, 1.69 mm; width, 1.29 mm; whorls, 3.5.

DESCRIPTION.—Shell (Figure 21*d-f*) with 3.5 to 4.0 moderately convex whorls. Body whorl relatively large (83% of shell height). Sexual dimorphism significant (females larger than males). Inner lip moderately thickened, fused to or slightly separated from body whorl. Umbilicus open.

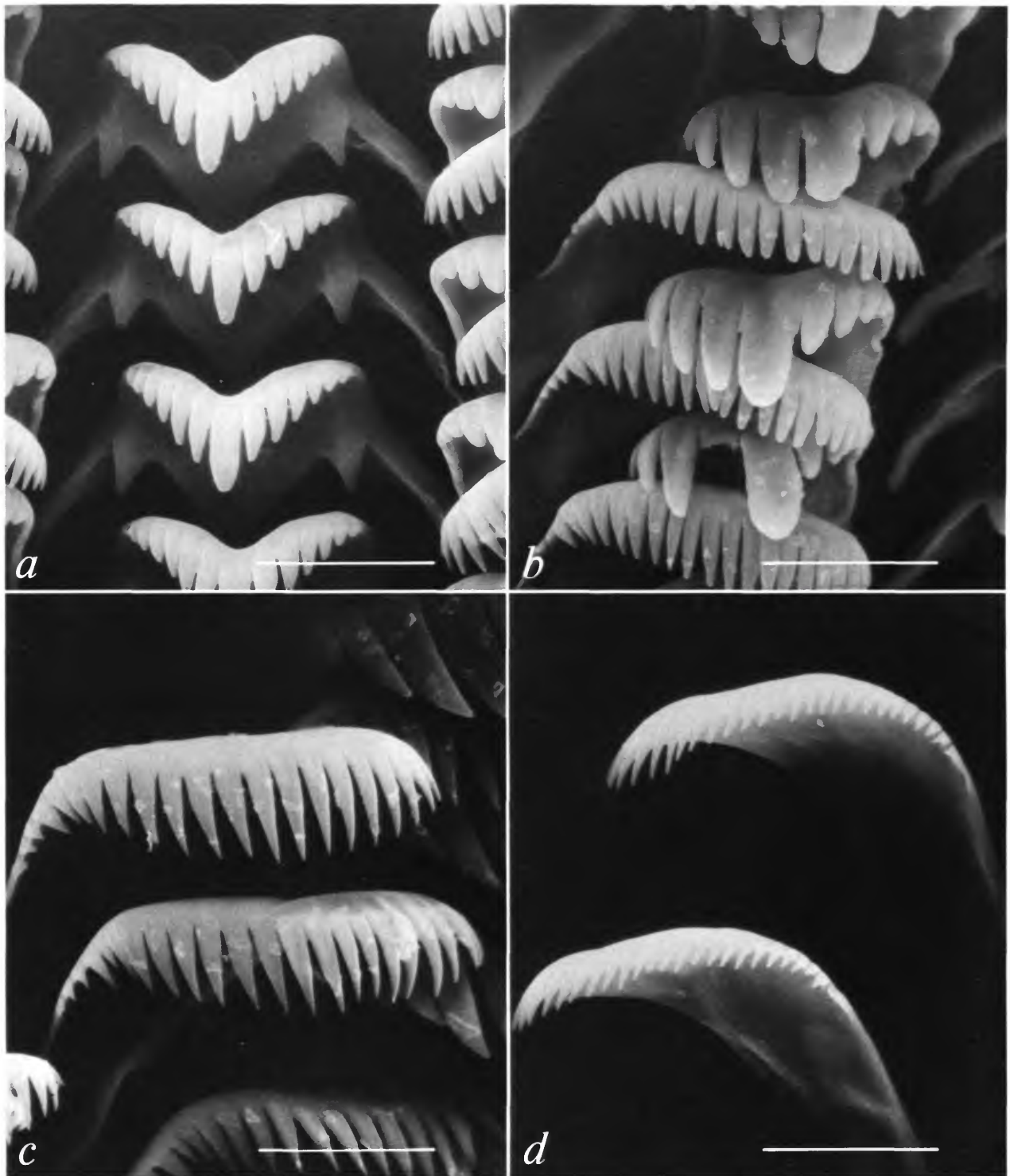


FIGURE 24.—Radula of *P. solus*, new species, USNM 850290, Brown Spring, Yavapai County, Arizona: *a*, centrals, bar = 8.6  $\mu\text{m}$ ; *b*, laterals and inner marginals, bar = 7.5  $\mu\text{m}$ ; *c*, inner marginals, bar = 6.0  $\mu\text{m}$ ; *d*, outer marginals, bar = 6.0  $\mu\text{m}$ .

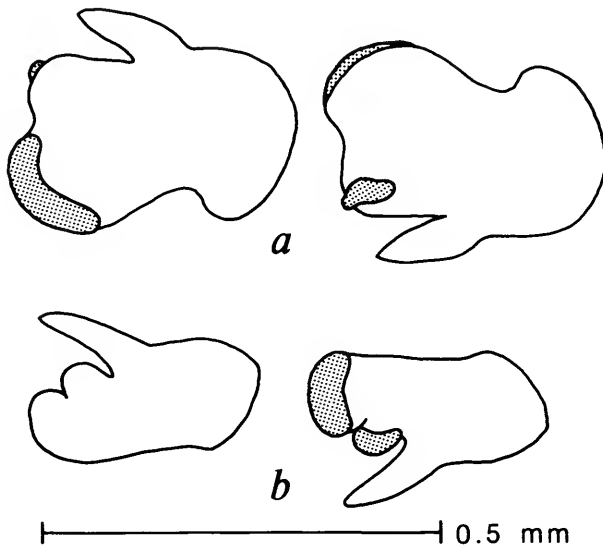


FIGURE 25.—Penial variation of *P. solus*, new species, USNM 850290, Brown Spring, Yavapai County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

Pigment on head/foot may be absent, or range from very light to dark dusting on all surfaces. Penial filament darkly pigmented.

Ctenidial filaments few, 11 to 14. Radula shown in Figure 24. Penis (Figure 25) almost square in shape and very small, not extending beyond mantle collar. Filament positioned at only two-thirds of penis length, moderate in length (46% of penis length), and rarely extending beyond penial lobe. Width of filament/length, 40%. Bursa (Figure 26a) only 36% of albumen gland length. Seminal receptacle 83% of bursa length.

REMARKS.—No close relationship is apparent between *P. solus* and other Arizona congeners as the minute, squat penis of this species is unique among southwestern *Pyrgulopsis*.

TYPE-LOCALITY.—Brown Spring, in southern end of Verde Valley, Yavapai County, Arizona.

DISTRIBUTION.—Endemic to type-locality.

ETYMOLOGY.—From Latin *solus*, meaning alone or single, and referring to endemism of species in a single spring.

### *Pyrgulopsis simplex* Hershler, new species

Fossil springsnail

FIGURES 21g–j, 26b, 27, 28

*Fontelicella* species.—Williams et al., 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Yavapai County*: Fossil Springs, USNM 847222, J.J. Landye, 5 Apr 1972. *Gila County*: spring near Strawberry, USNM 859049 (holotype), 859050 (4 paratypes), 847236, J.J. Landye, 16 Oct 1971.

DIAGNOSIS.—A moderate size species (shell height, 2.0 to 2.5 mm) with ovate-conic shell. Penis moderate size, with narrow filament of moderate length and single glandular ridge on ventral surface of penial lobe. Holotype (Figure 21g) height, 2.41 mm; width, 1.49 mm; whorls, 4.5.

DESCRIPTION.—Shell (Figure 21 g–j) with 3.5 to 4.25 unshouldered and moderately convex whorls. Shell relatively elongate for genus (shell height/shell width, 150%), with some specimens conical in shape. Sexual dimorphism significant (females larger than males) in one of two populations studied. Aperture usually separate from body whorl. Umbilicus open.

Snout unpigmented, sides of head/foot with light dusting of melanin. Penial filament darkly pigmented along virtual entirety of length.

Ctenidium relatively large (27% to 31% of body length), with 16 to 19 filaments. Radula shown in Figure 27. Penis (Figure 28) very elongate. Filament 57% of penis length, projecting well beyond tip of penial lobe. Width of filament only 28% of length. Variably sized, single, glandular ridge positioned near distal edge of simple penial lobe. Ovary only 12% of body length. Over half (56%) of bursa posterior to albumen gland. Seminal receptacle 65% of bursa length.

REMARKS.—*P. simplex* may be closely allied with other Arizona species having a relatively simple penis, including *P. conicus*, *P. morrisoni*, and *P. sancarlosensis*. The penial filament of *P. simplex* is shorter than that of *P. sancarlosensis*, but longer than those of the other two species.

TYPE-LOCALITY.—Spring near Strawberry, Gila County, Arizona.

DISTRIBUTION.—Restricted to a number of springs forming the perennial portion of Fossil Creek, which flows into Verde River south of Verde Valley.

ETYMOLOGY.—From Latin *simplex*, referring to simple condition of penis, with few glandular ridges.

### *Pyrgulopsis confluentis* Hershler, new species

Three Forks springsnail

FIGURES 3d–g, 26c, 29, 30

New genus, new species.—Landye, 1973:49.

New genus, new species.—Landye, 1981:27.

MATERIAL EXAMINED.—ARIZONA. *Apache County*: spring on N side of Blanket Creek at Three Forks, USNM 859053 (holotype), 859054 (4 paratypes), 847234, J.J. Landye, 15 Sep 1977; spring at Three Forks, USNM 847229, J.J. Landye, 7 Oct 1973.

DIAGNOSIS.—Shell low ovate to ovate-conic, variable in size (shell height, 1.5 to 4.8 mm). Penis moderate size, with small filament; elongate, tapering lobe; and enlarged ventral accessory crest. Glandular ridges numerous on both penial surfaces. Holotype (Figure 3d) height, 2.80 mm; width, 1.96 mm; whorls, 4.5.

DESCRIPTION.—Shell with 3.5 to 4.75 unshouldered and

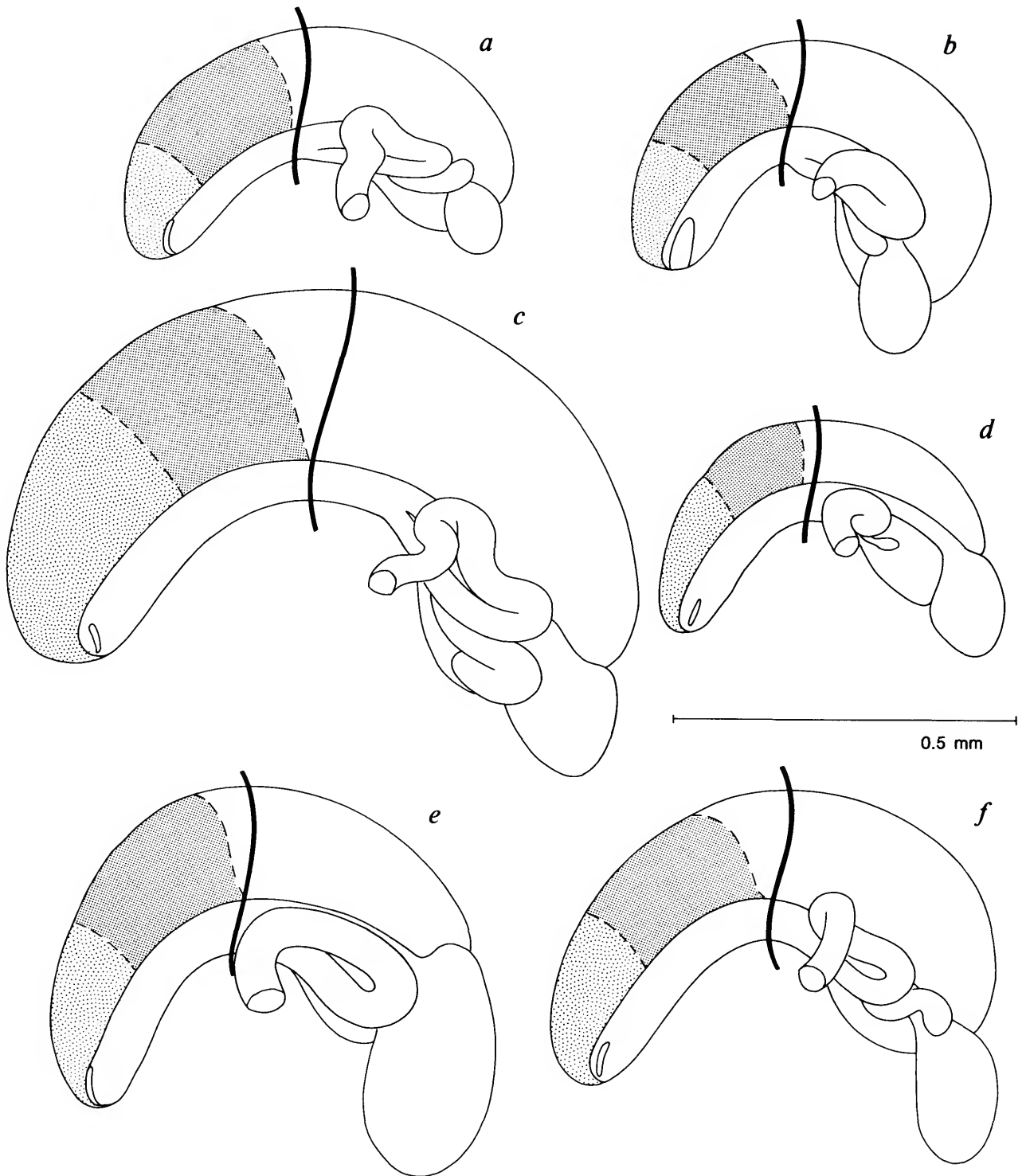


FIGURE 26.—Pallial oviducts of *Pyrgulopsis* species: a, *P. solus*, new species, USNM 850290, Brown Spring, Yavapai County, Arizona; b, *P. simplex*, new species, USNM 847236, spring near Strawberry, Gila County, Arizona; c, *P. confluentis*, new species, USNM 847234, spring on N side of Blanket Creek at Three Forks, Apache County, Arizona; d, *P. cochisi*, new species, USNM 847218, Springs at San Bernardino Ranch, Cochise County, Arizona; e, *P. sancarlosensis*, new species, USNM 847226, springs W of Tom Niece Springs, Graham County, Arizona; f, *P. thompsoni*, new species, USNM 847238, Peterson Ranch Springs, Santa Cruz County, Arizona.



FIGURE 27.—Radula of *P. simplex*, new species, USNM 847236, spring near Strawberry, Gila County, Arizona: *a*, centrals, bar = 12.0  $\mu\text{m}$ ; *b*, laterals, bar = 13.6  $\mu\text{m}$ ; *c*, inner marginals, bar = 10.0  $\mu\text{m}$ ; *d*, outer marginals, bar = 7.5  $\mu\text{m}$ .



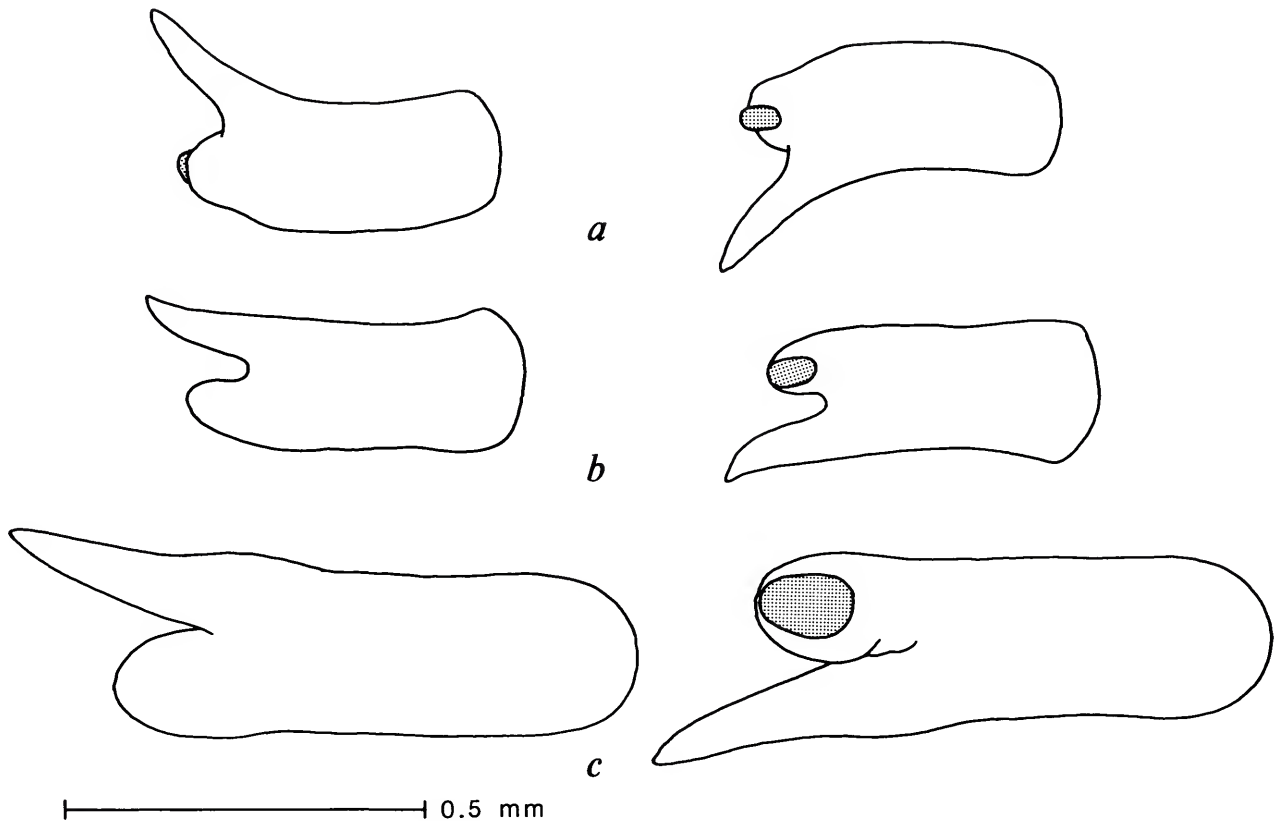


FIGURE 28.—Penial variation of *P. simplex*, new species: *a, b*, USNM 847236, spring near Strawberry, Gila County, Arizona; *c*, USNM 847222, Fossil Springs, Yavapai County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

well-rounded whorls. Note shell size and shape difference among the two known populations (Figure 3*d-g*). Sexual dimorphism significant (females larger than males) in one population. Dark, thickened periostracum covering entire shell surface. Inner lip thin. Umbilicus chink-like to open.

Dark pigment on snout and tentacles characteristic, pigment somewhat lighter on sides of head/foot. Proximal half of penial filament darkly pigmented, with pigment sometimes extending into penis as well.

Ctenidial filaments, 17 to 23. Ctenidium only 19% to 21% of body length. Radula shown in Figure 29. Inner marginals with as many or more cusps as outers (Table 2). Testis 46% of body length. Penis elongate (Figure 30); filament only 27% of penis length, not projecting beyond tip of penial lobe. Filament relatively stout at base (width/length, 47%). Lobe sometimes with narrow, terminal process. Accessory crest on ventral surface swollen. Glandular ridges, four to six, rarely enlarged or elongate. One ridge (sometimes absent) on proximal (dorsal) half of filament; two on dorsal portion of lobe (or just proximal to lobe); one just proximal to tip of lobe (ventral); and one or two on accessory crest. Ovary only 11%

of body length. Oviduct coil complex, coil diameter only 30% of albumen gland length (Figure 26*c*). Half of bursa posterior to albumen gland. Seminal receptacle 70% of bursa length.

REMARKS.—This species links with the *P. glandulosus*-group on the basis of penial morphology, but differs in lacking accessory crests.

TYPE-LOCALITY.—Spring on N side of Blanket Creek at Three Forks, Apache County, Arizona.

DISTRIBUTION.—Several springs at Three Forks feeding Black River.

ETYMOLOGY.—From Latin *confluens*, meaning a place where streams meet, and referring to occurrence of species at Three Forks.

### *Pyrgulopsis sancarlosensis* Hershler, new species

Bylas springsnail

FIGURES 13*e*, 26*e*, 31*a-g*, 32, 33

*Fontlicella* [sic.] species.—Meffe and Marsh, 1983:369.

*Fontlicella* species.—Williams et al., 1985:19.



FIGURE 29.—Radula of *P. confluentis*, new species, USNM 847234, spring on N side of Blanket Creek at Three Forks, Apache County, Arizona: *a*, centrals, bar = 12.0  $\mu\text{m}$ ; *b*, laterals and inner marginals, bar = 12.0  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 13.6  $\mu\text{m}$ ; *d*, outer marginals, bar = 7.5  $\mu\text{m}$ .

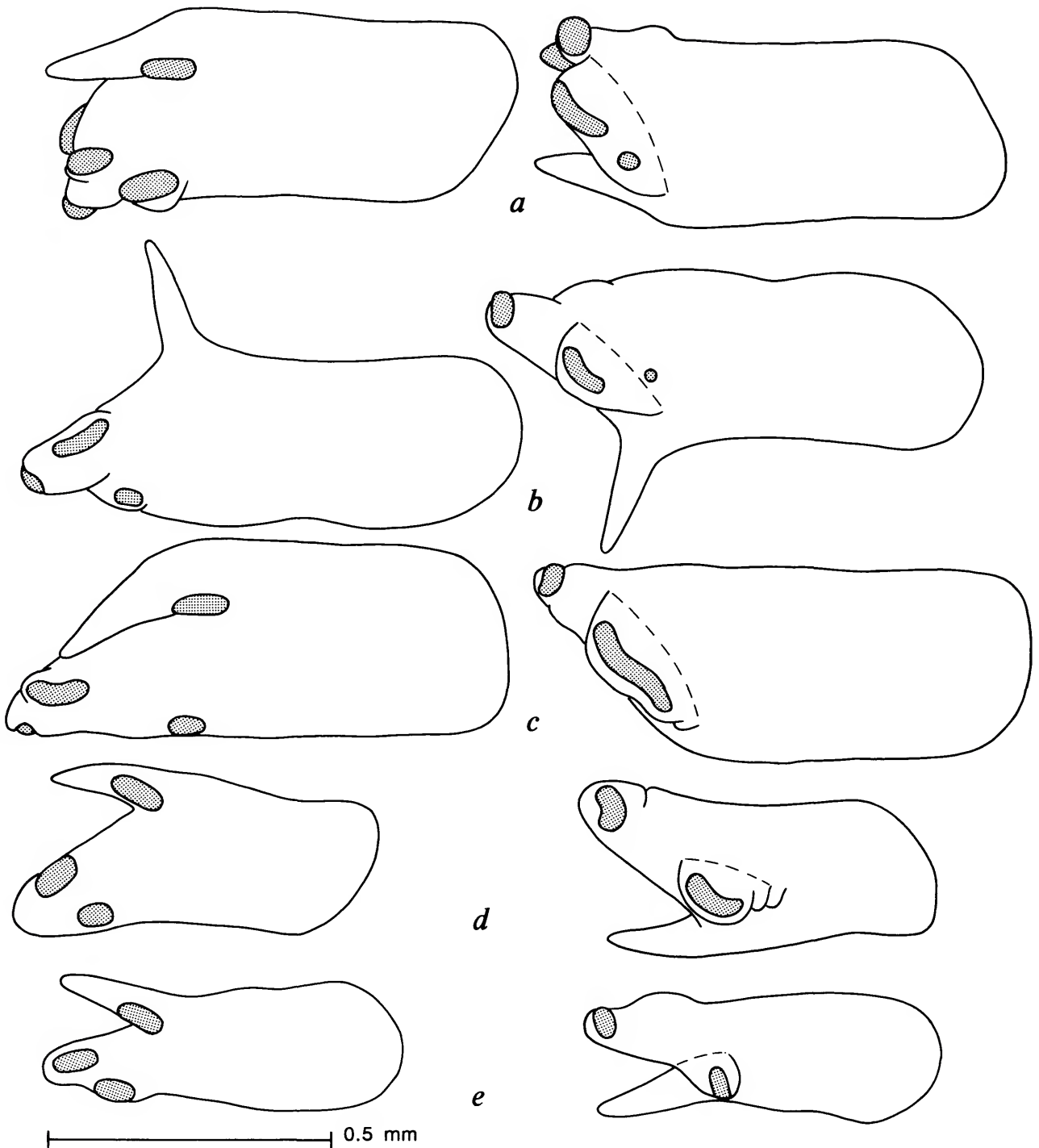


FIGURE 30.—Penial variation of *P. confluentis*, new species: *a-d*, USNM 847234, spring on N side of Blanket Creek at Three Forks, Apache County, Arizona; *e*, USNM 847229, spring at Three Forks, Apache County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

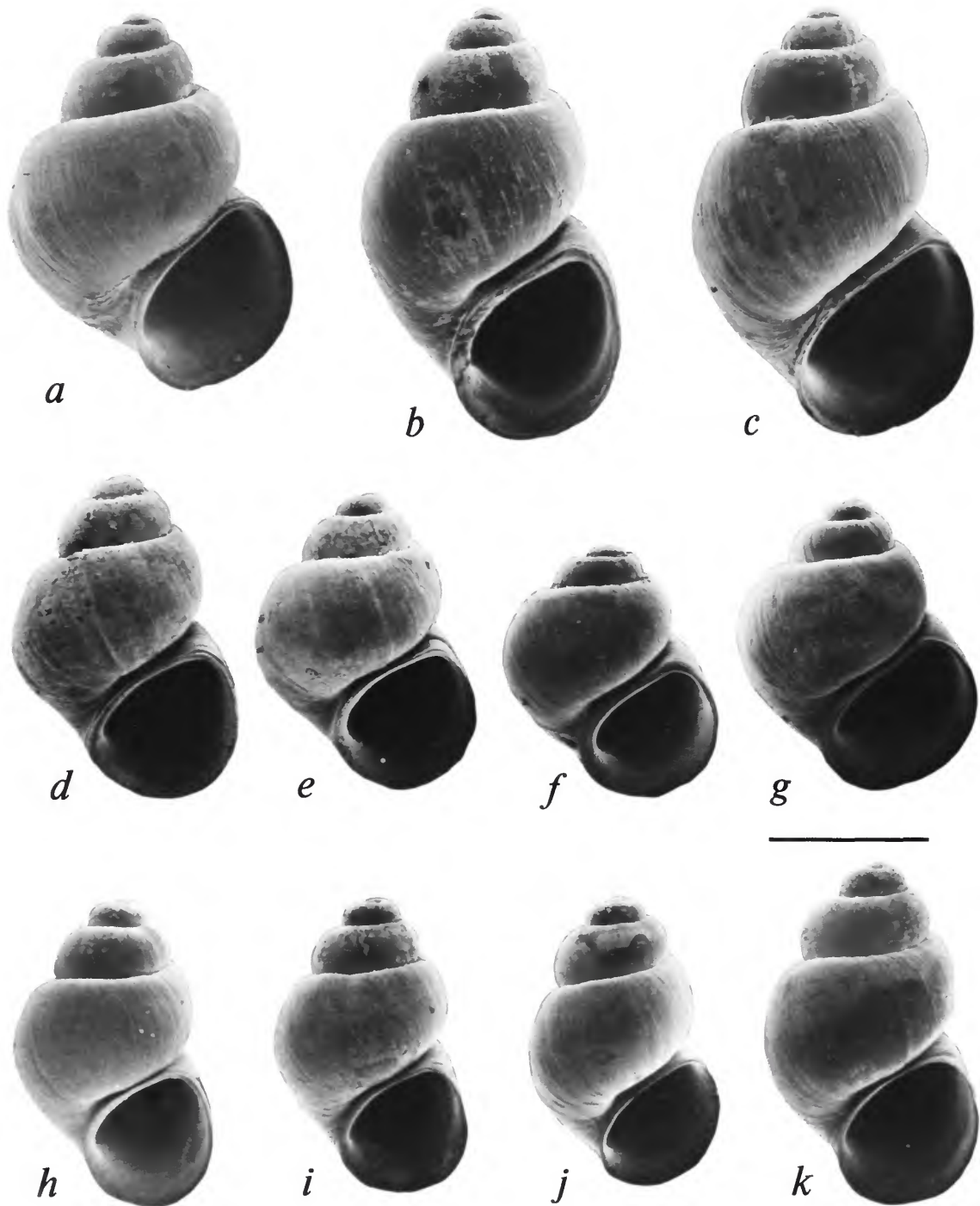


FIGURE 31.—*P. sancarlosensis*, new species: *a*, USNM 859051, holotype, springs W of Tom Niece Springs, Graham County, Arizona; *b,c*, same locality, USNM 847226; *d,e*, USNM 847224, large spring N of Bylas, Graham County, Arizona; *f,g*, USNM 847217, small spring near Bylas, Graham County, Arizona. *P. cochisi*, new species: *h*, holotype, USNM 859055, springs at San Bernardino Ranch, Cochise County, Arizona; *i-k*, same locality, USNM 847218. (Bar = 0.75 mm.)

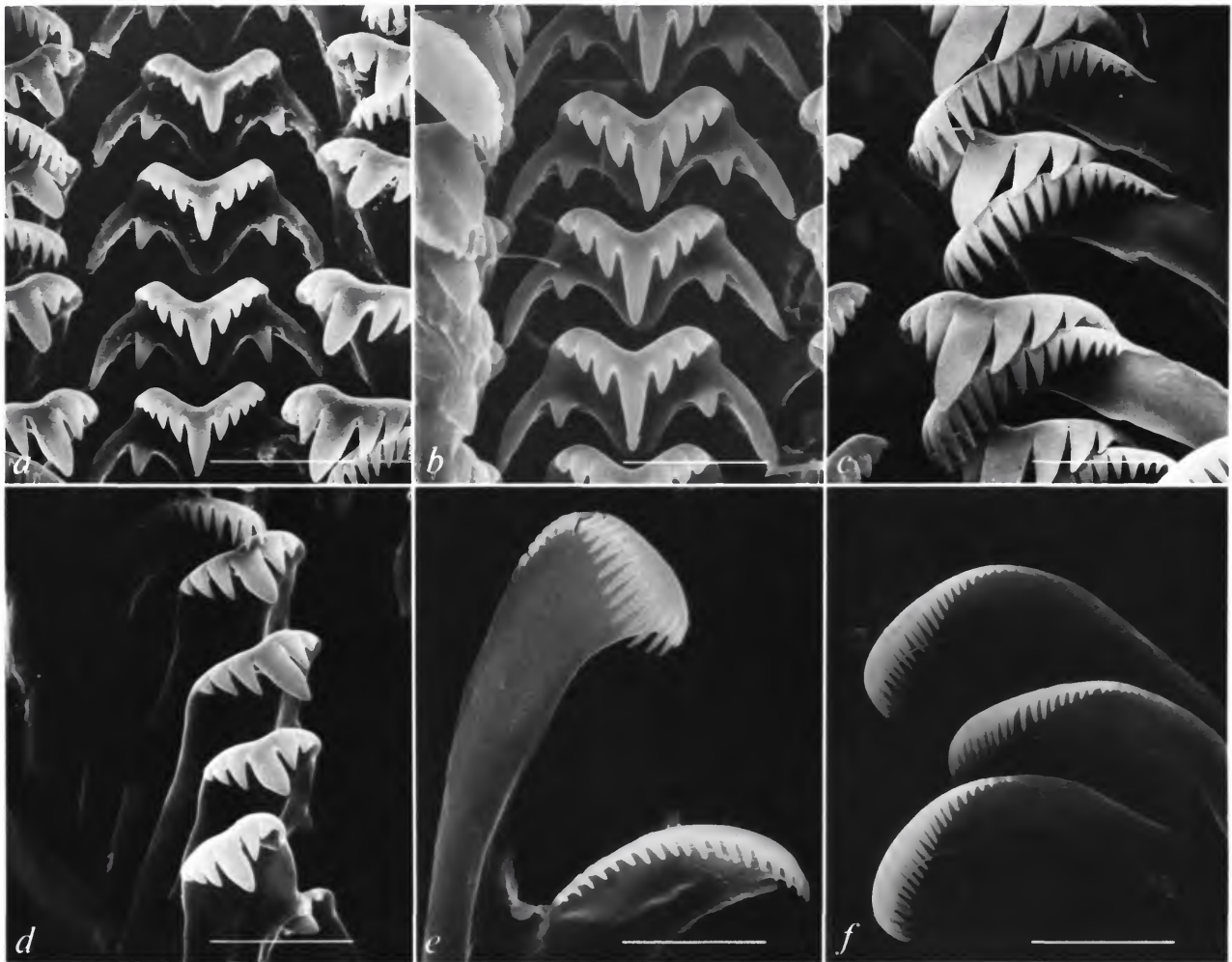


FIGURE 32.—Radula of *P. sancarlosensis*, new species, USNM 847226, springs W of Tom Niece Springs, Graham County, Arizona: *a, b*, centrals, bars = 15.0, 12.0  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 8.6  $\mu\text{m}$ ; *d*, laterals, bar = 15.0  $\mu\text{m}$ ; *e*, inner marginals, bar = 6.0  $\mu\text{m}$ ; *f*, outer marginals, bar = 8.6  $\mu\text{m}$ .

**MATERIAL EXAMINED.**—ARIZONA. *Graham County*: small spring near Bylas, USNM 847217, J.J. Landye, 20 May 1971; spring near Gila River bridge NW of Bylas, USNM 847213, J.J. Landye, 30 Jan 1971; large spring N of Bylas, USNM 847224, J.J. Landye and D.W. Taylor, 20 Apr 1971; springs W of Tom Niece Springs, USNM 859051 (holotype), 859052 (4 paratypes), 847226, J.J. Landye, 29 Jun 1973; seeps W of Tom Niece Springs, USNM 847225, J.J. Landye, 27 Jun 1973.

**DIAGNOSIS.**—Shell small (height, 1.1 to 2.4 mm), varying in shape from globose to elongate-conic. Penis large (25% to 33% of body length), with elongate filament and up to three glandular ridges. Seminal receptacle absent. Holotype (Figure 31*a*) height, 1.90 mm; width, 1.29 mm; whorls, 4.0.

**DESCRIPTION.**—Shell height, 1.1 to 2.4 mm; whorls, 3.25 to

4.25, moderately rounded. Diversity in shell size and shape shown in Figure 31*a–g*. Both shell forms sometimes present in single population, with conical specimens usually enlarged (often female). Sexual dimorphism not significant. Small globose specimens with relatively large apertures (50% to 55% of shell height); larger, conical shells with smaller apertures (48% of shell height). Aperture usually separated, sometimes greatly so, from body whorl. Umbilicus open. Operculum shown in Figure 13*e*.

Snout darkly (black) pigmented, tentacles and sides of head/foot with lighter pigment, central section of latter sometimes unpigmented. Penial filament either darkly pigmented along entire length or unpigmented.

Ctenidial filaments, 12 to 20. Radula shown in Figure 32.

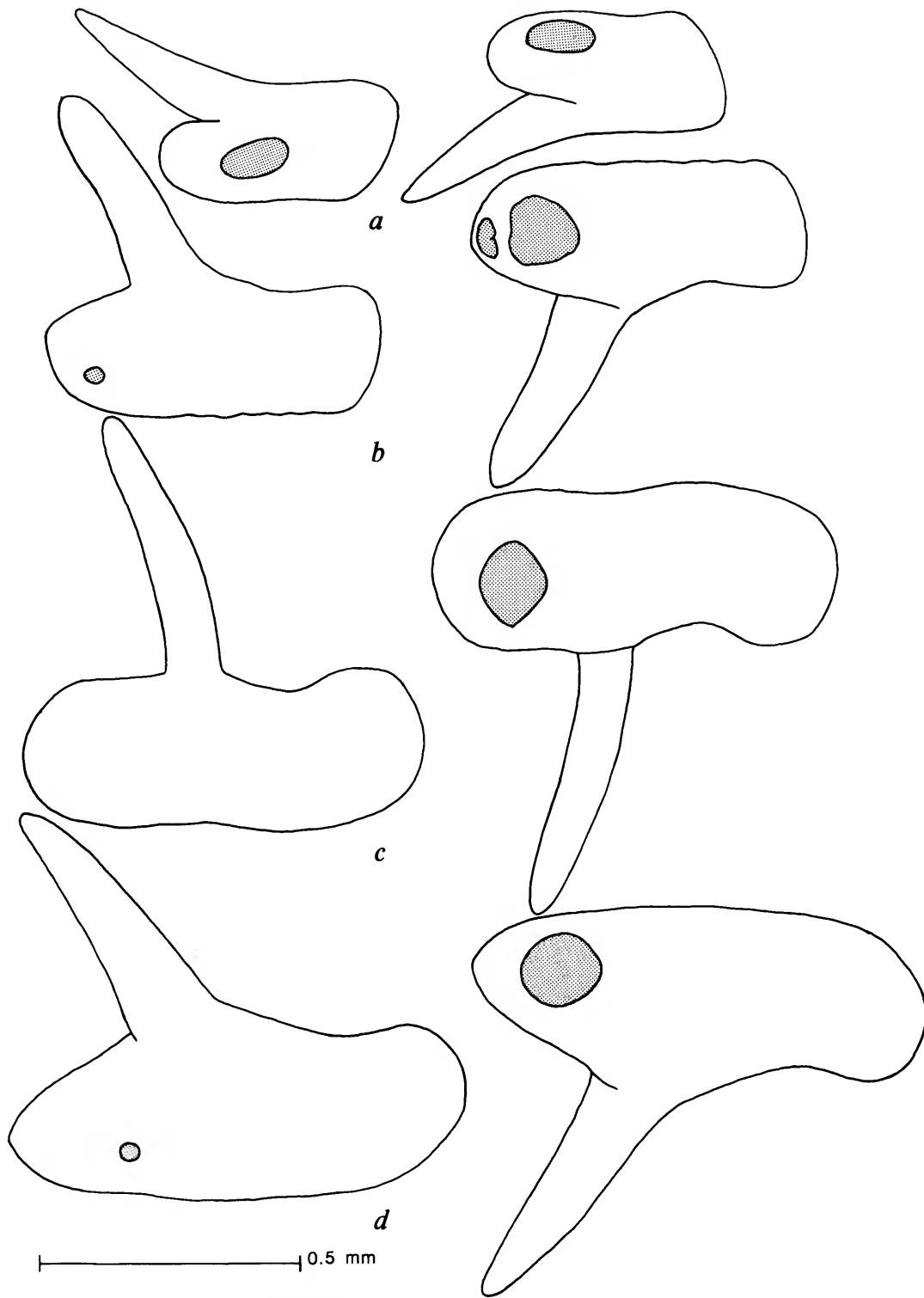


FIGURE 33.—Penial variation of *P. sancarlosensis*, new species: *a*, USNM 847217, small spring near Bylas, Graham County, Arizona; *b–d*, USNM 847226, springs W of Tom Niece Springs, Graham County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

Penial filament relatively narrow (width/length, 26% to 29%) and elongate (67% to 84% of penis length), but usually projecting perpendicular to penis length and therefore not extending beyond tip of penial lobe. Enlarged lobe usually untapered. Glandular ridges, one to three. Dorsal surface of penis with or without single ridge; ventral surface with single enlarged ridge and sometimes an additional smaller one. Capsule gland (Figure 26e) consistently longer than albumen gland. Oviduct coil diameter large (81% to 82%) relative to albumen gland length. Bursa 60% to 99% of albumen gland length. Note that duct exits lateral to bursa tip.

REMARKS.—Absence of seminal receptacle is not known for any congener, although size of structure does vary greatly and is greatly reduced in forms such as *P. cochisi* (described next). Loss of seminal receptacle may represent the end point of a reduction trend, with sperm storage function presumably assumed by the thickened coiled section of oviduct.

TYPE-LOCALITY.—Springs W of Tom Niece Springs, Graham County, Arizona.

DISTRIBUTION.—Springs along north side of Gila River between Bylas and Pima.

ETYMOLOGY.—Named after San Carlos Apache Indian Reservation near Bylas.

### *Pyrgulopsis cochisi* Hershler, new species

San Bernardino springsnail

FIGURES 25d, 30h-k, 33, 34

*Fonticella* species.—Williams et al., 1985:50.

MATERIAL EXAMINED.—ARIZONA. *Cochise County*: Springs at San Bernardino Ranch, USNM 859055 (holotype), 859056 (2 paratypes), 847218, J.J. Landye, 20 Mar 1971.

DIAGNOSIS.—A small size species (1.3 to 1.7 mm) having ovate-conic shell. Penis moderate size, without lobe; filament elongate. Dorsal and ventral penial surfaces each with single glandular ridge. Holotype (Figure 31h) height, 1.55 mm; width, 1.04 mm; whorls, 3.5.

DESCRIPTION.—Shell (Figure 32h-k) with 3.25 to 4.0 slightly convex whorls, with sutures only very slightly indented. Sexual dimorphism significant (females larger than males). Inner lip thin. Umbilicus open.

Snout with light to dark dusting of pigment. Sides of head/foot somewhat less pigmented than snout, although operculigerous lobe often quite dark. Penial filament darkly pigmented along entire length.

Ctenidial filaments, 12 to 15. Anterior portion of central tooth with few cusps (4-1-4) (Figure 34). Inner and outer marginals with roughly same number of cusps (Table 2). Prostate 11% of body length. Penis fairly elongate (Figure 35). Penial filament 61% of penis length, extending distal to anterior tip of penis. Filament three times as long as wide. Glandular ridges, two. Ridges positioned just proximal to base

of filament. Capsule gland slightly longer (108%) than albumen gland. Seminal receptacle body minute, length of receptacle (body plus duct) 67% of bursa length.

REMARKS.—*Pyrgulopsis cochisi* is most similar to *P. thompsoni*, which also have small penes with reduced penial lobe (absent in the former) and single glandular ridge, but is smaller and has a glandular ridge on both penial surfaces.

TYPE-LOCALITY.—Spring at San Bernardino Ranch, Cochise County, Arizona.

DISTRIBUTION.—Restricted to type-locality and nearby small seeps at San Bernardino Ranch.

ETYMOLOGY.—Named after Apache chief Cochise.

### *Pyrgulopsis thompsoni* Hershler, new species

Huachuca springsnail

FIGURES 26f, 36, 37, 38

*Paludestrina stearnsiana*.—Pilsbry and Ferriss, 1909:516.

"Undescribed...hydrobiid."—Minckley, 1969:6.

*Fonticella* species.—Bequaert and Miller, 1973:214.

*Fonticella* species.—Williams et al., 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Santa Cruz County*: Cottonwood Springs, USNM 847221, J.J. Landye, 19 Aug 1973; Monkey Spring, USNM 847223, J.J. Landye and D. Belk, 2 Dec 1969; Canelo Hills Cienega, USNM 847228, J.J. Landye, 14 Nov 1978; Sheehy Spring, USNM 847235, J.J. Landye, 18 Apr 1976, USNM 847227, 14 Nov 1978; Peterson Ranch Springs, USNM 859057 (holotype), 859058 (3 paratypes), 847238, J.J. Landye, 19 Aug 1973. SONORA (Mexico): Ojo Caliente, USNM 847251, J.J. Landye and D.W. Taylor, 7 Apr 1971.

DIAGNOSIS.—A moderate to large size species (1.7 to 3.2 mm) having ovate or ovate-conic shell. Penis moderate size, with elongate filament and single, small glandular ridge on ventral surface of penial lobe. Holotype (Figure 36a) height, 2.57 mm; width, 1.63 mm; whorls, 4.25.

DESCRIPTION.—Shell (Figure 36) with 3.25 to 5.0 moderately convex, slightly shouldered whorls. Sexual dimorphism significant in two of four populations studied, with males larger in one of these and females larger in other. Inner lip thin. Aperture fused to or separate from body whorl. Umbilicus chink-like or open.

Snout and anterior portion of foot (dorsal surface) with light to fairly dark pigment. Remainder of head/foot usually unpigmented. Penial filament darkly pigmented throughout.

Ctenidial filaments, 11 to 20. Radula shown in Figure 37. Testis 37% to 54% of body length. Prostate 7% to 8% of body length. Penis squat to elongate. Penis filament centered at 80% to 93% of penis length. Filament 35% to 103% of penis length, and only slightly thickened (width/length, 27% to 46%). Penis lobe simple. Glandular ridge usually located near tip of lobe. Oviduct coil relatively complex in that initial turn of loop bends



FIGURE 34.—Radula of *P. cochisi*, new species, USNM 847218, springs at San Bernardino Ranch, Cochise County, Arizona: *a*, centrals, bar = 9.1  $\mu\text{m}$ ; *b*, laterals, bar = 5.0  $\mu\text{m}$ ; *c*, laterals and inner marginals, bar = 6.7  $\mu\text{m}$ ; *d*, outer marginals, bar = 6.0  $\mu\text{m}$ .



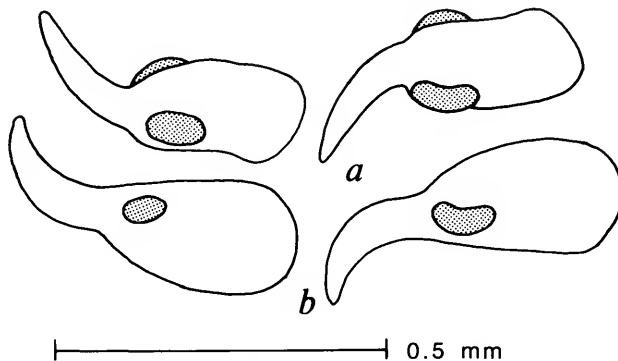


FIGURE 35.—Penial variation of *P. cochisi*, new species, USNM 847218, springs at San Bernardino Ranch, Cochise County, Arizona. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

back on itself (Figure 26f). Most of bursa length (55% to 85%) posterior to albumen gland. Seminal receptacle 53% to 72% of bursa length.

TYPE-LOCALITY.—Peterson Ranch Springs, Santa Cruz County, Arizona.

DISTRIBUTION.—Six springs in Southern Santa Cruz County, Arizona, United States, and northern Sonora, Mexico.

ETYMOLOGY.—Named after Dr. F.G. Thompson, in recognition of his contributions to study of North American Hydrobiidae.

### Genus *Tryonia* Stimpson, 1865

DIAGNOSIS.—Shell elongate-conic to turreted, 1.7 to 7.0 mm high. Aperture simple, umbilicus narrow or absent. Teleoconch smooth or with spiral lines or collabral striations or varices. Penis with enlarged glandular lobe at base and one to four smaller glandular lobes on inner curvature. Females ovoviviparous, with young brooded in capsule gland. Thin-walled capsule gland reflected posteriorly, albumen gland greatly reduced in size. Bursa copulatrix and seminal receptacle small (relative to pallial oviduct), spermathecal duct short.

REMARKS.—Hershler and Thompson (1987) provided a detailed description for the genus. *Hyalopyrgus* Thompson, 1968 is regarded by them to be a synonym of *Tryonia*. The genus has a disjunct distribution, occurring in much of Florida as well as a large part of the arid Southwest. These snails are related to a group of genera, including *Aphaostracan* Thompson, 1968, *Littoridinops* Pilsbry, 1952, *Mexipyrgus* Taylor, 1966, and *Pyrgophorus* Ancy, 1888 that have elongate-conic shells and glandular (mammiiform) penial lobes. *Tryonia* differs from the above by its turreted shell and unique position of penial lobes. The genus contains ten described species as well as numerous undescribed species from the Southwest.

### *Tryonia gilae* Hershler, new species

#### *Gila tryonia*

FIGURES 14c,f, 39a–e, 40, 41a–c, 42, 43d–i, 44, 45, 46a, 47b

*Tryonia* species.—Meffe and Marsh, 1983:369.

*Tryonia* species.—Williams et al., 1985:19.

MATERIAL EXAMINED.—ARIZONA. *Graham County*: small spring near Bylas, USNM 859059 (holotype), 859060 (4 paratypes), 847257, J.J. Landye, 30 Jan 1971; spring near Gila River bridge NW of Bylas, USNM 847255, J.J. Landye, 30 Jan 1971; large spring N of Bylas, USNM 847258, J.J. Landye and D.W. Taylor, 20 May 1971; springs W of Tom Niece Springs, USNM 847254, J.J. Landye, 27 Jun 1973; seeps W of Tom Niece Springs, USNM 847252, J.J. Landye, 27 Jan 1973; Cold Springs, USNM 847253, J.J. Landye, 27 Jan 1973.

DIAGNOSIS.—A moderately large size species (1.9 to 3.3 mm) with elongate-conic to turreted shell. Cephalic tentacles with well-defined linear tracts of hypertrophied cilia. Penis with two glandular lobes on inner curvature near distal tip and enlarged lobe on outer curvature at base. Outer curvature distal to lobes with hypertrophied ciliary tuft. Bursa relatively large. Holotype (Figure 39a) height, 3.25 mm; width, 1.45 mm; whorls, 6.0.

DESCRIPTION.—Shell (Figure 39a–e) clear, transparent, and without periostracum. Shell often twice as tall as wide; whorls, 4.5 to 6.0, slightly to moderately convex with indented sutures. Sexual dimorphism pronounced, with females larger than males. Protoconch (Figure 14c) smooth and flat (sometimes slightly depressed), with 1.0 to 1.25 whorls. Embryonic shell with as many as 1.5 whorls. Body whorl 57% to 74% of shell height. Aperture simple, occupying less than half of shell height, longer than wide, slightly angled above and rounded below, and either fused to or separate from body whorl. Inner lip fairly straight, slightly thickened and reflected; outer lip rounded and thin. Apertural plane slightly tilted from coiling axis (somewhat advanced adapically) with long axis inclined 25° to 30° to coiling axis. Umbilicus open. Teleoconch with strong growth lines. Operculum (Figure 14f) amber, paucispiral, over one and a half times longer than wide, and with three whorls.

Snout (Figure 40) longer than wide, terminating with fleshy lips. Cephalic tentacles (Figures 40, 41a,b) narrow, slightly expanded at tips, and moderately elongate (slightly extending beyond snout tip). Ciliary tracts on tentacles shown in Figure 41a–c. Snout and “neck” with scattered ciliary tufts. Black eyes located in slightly bulging outer edges of tentacle bases. Foot elongate, with anterior edge almost straight and posterior portion expanded and rounded. Anterior pedal glands, 12 to 18.

Head/foot lightly dusted with epithelial melanin throughout, except for tentacles. Narrow strip extending down sides of head/foot very lightly pigmented or unpigmented. Dorsal surfaces of style sac and stomach darkly pigmented. Ovary with light dusting, testis very darkly pigmented. Section of

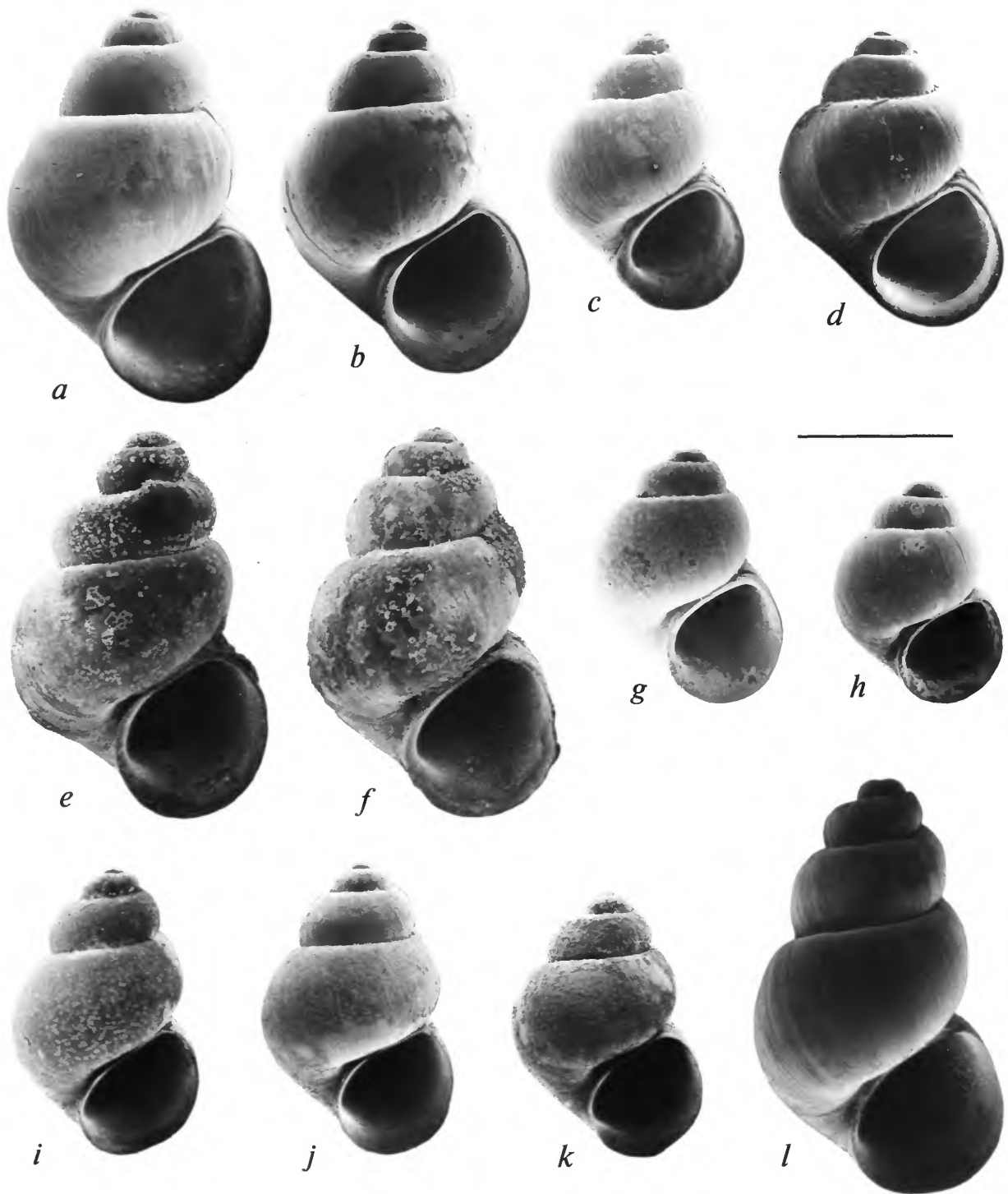


FIGURE 36.—*P. thompsoni*, new species: *a*, holotype, USNM 859057, Peterson Ranch Springs, Santa Cruz County, Arizona; *b*, USNM 847238, same locality; *c,d*, USNM 847221, Cottonwood Springs, Santa Cruz County, Arizona; *e,f*, USNM 847228, Canelo Hills Cienega, Santa Cruz County, Arizona; *g,h*, USNM 847223, Monkey Springs, Santa Cruz County, Arizona; *i-k*, USNM 847227, Sheehy Spring, Santa Cruz County, Arizona; *l*, USNM 847251, Ojo Caliente, Sonora, Mexico. (Bar = 0.75 mm.)

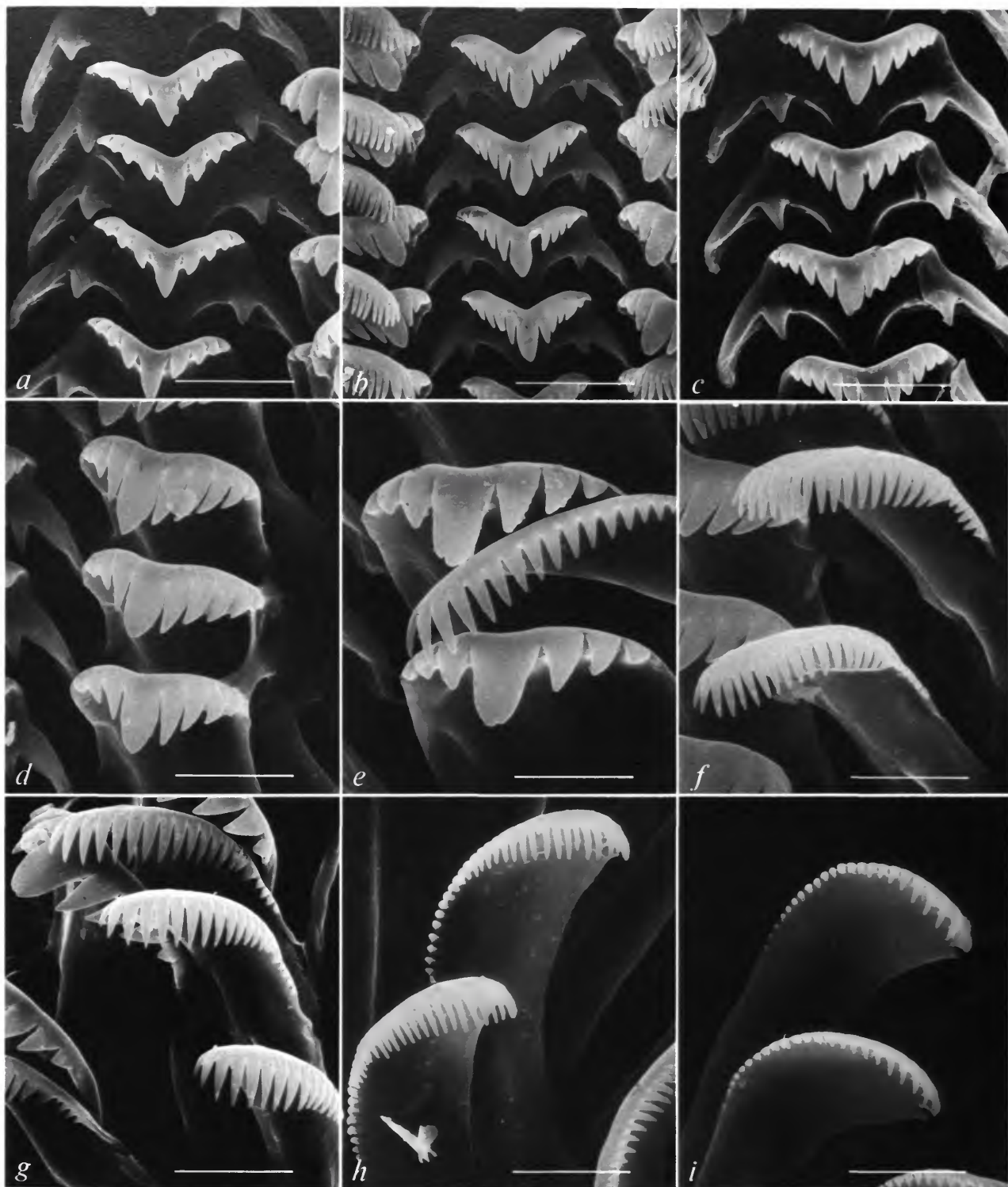


FIGURE 37.—Radula of *P. thompsoni*, new species: *a*, centrals, USNM 847238, Peterson Ranch Springs, Santa Cruz County, Arizona, bar = 12.0  $\mu$ m; *b*, centrals, USNM 847221, Cottonwood Springs, Santa Cruz County, Arizona, bar = 12.0  $\mu$ m; *c*, centrals, USNM 847227, Sheehy Spring, Santa Cruz County, Arizona, bar = 10.0  $\mu$ m; *d*, laterals, USNM 847238, bar = 8.6  $\mu$ m; *e,f*, laterals and inner marginals, USNM 847238, bars = 6.7, 7.5  $\mu$ m; *g*, inner marginals, USNM 847238, bar = 10.0  $\mu$ m; *h,i*, outer marginals, USNM 847238, bars = 6.0  $\mu$ m.

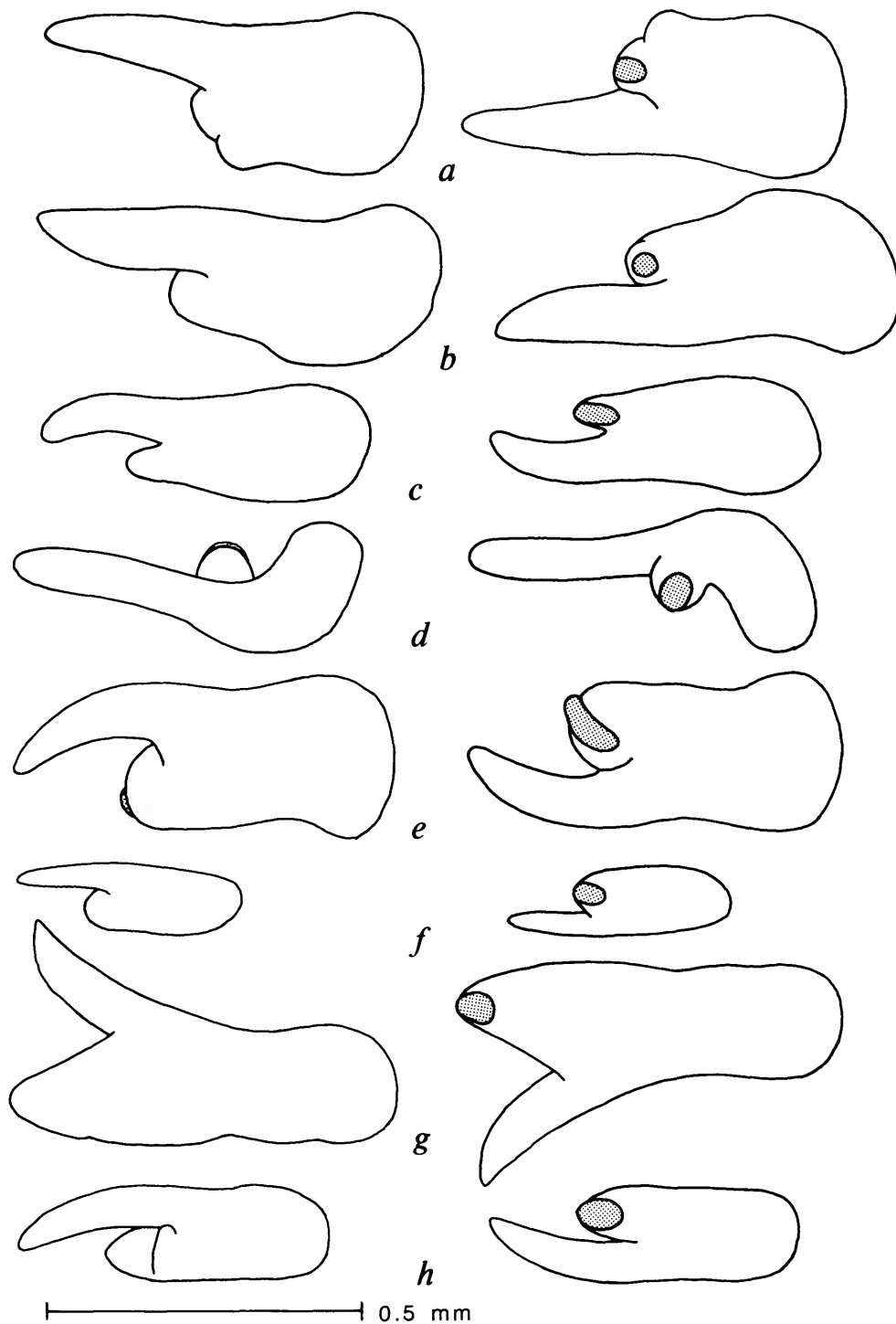


FIGURE 38.—Penial variation of *P. thompsoni*, new species: *a,b*, USNM 847238, Peterson Ranch Springs, Santa Cruz County, Arizona; *c,d*, USNM 847228, Canelo Hills Cienega, Santa Cruz County, Arizona; *e*, USNM 847221, Cottonwood Springs, Santa Cruz County, Arizona; *f*, USNM 847223, Monkey Spring, Santa Cruz County, Arizona; *g*, USNM 847227, Sheehy Spring, Santa Cruz County, Arizona; *h*, USNM 847251, Ojo Caliente, Sonora, Mexico. (Left = dorsal aspect; right = ventral aspect; screened areas = glandular ridges.)

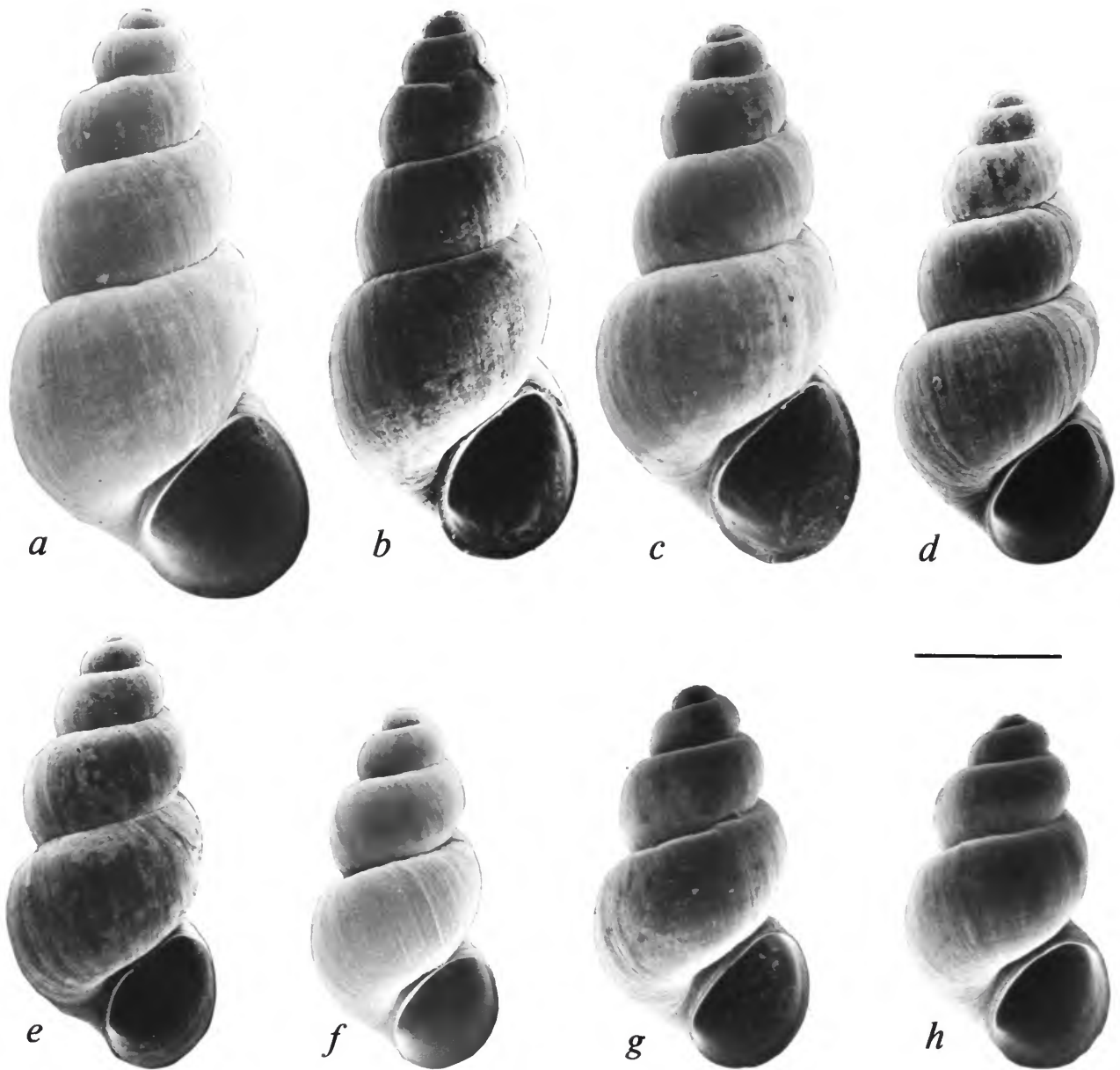


FIGURE 39.—*Tryonia gilae*, new species: *a*, holotype, USNM 859059, small spring near Bylas, Graham County, Arizona; *b, c*, same locality, USNM 847257; *d, e*, USNM 847253, Cold Springs, Graham County, Arizona. *T. quitobaquiae*, new species: *f*, holotype, USNM 859061, Quitobaquito Springs, Pima County, Arizona; *g, h*, same locality, USNM 847256. (Bar = 0.75 mm.)

pallial cavity roof above ctenidium darkly pigmented in males. Penis with dark pigment patch near distal tip (see Hershler, 1985, fig. 44) and smaller pigment streaks at bases of small penial lobes and elsewhere on dorsal surface. Dark subepithelial pigment concentrated on right side of mantle collar. Large, dull grey glandular clusters in "neck" proximal to tentacles.

Bases of tentacles with white glandular clusters.

Ctenidium (Figure 42, Ct) elongate, filling most of pallial cavity. Ctenidial filaments, 20 to 25. Filaments broad. Osphradium (Figure 42, Os) small relative to ctenidium length. Kidney (Figure 44a, Ki) with small opening fringed by obvious lips (Figure 44a, Oki).

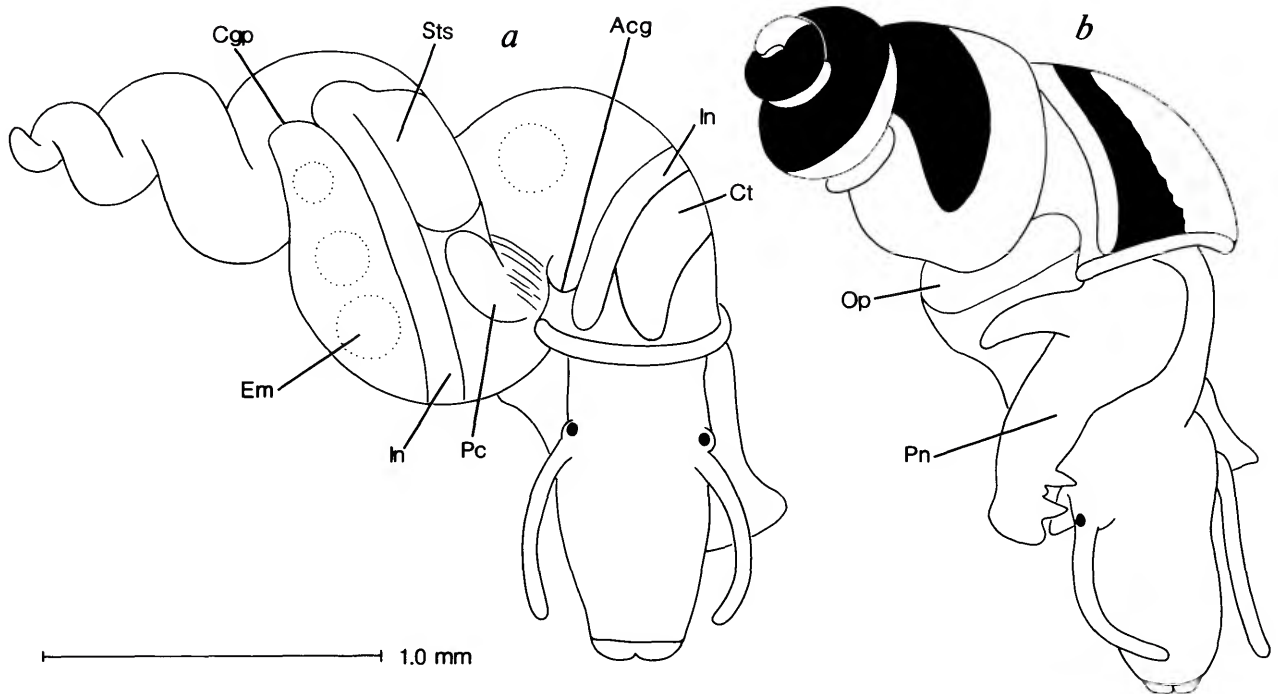


FIGURE 40.—Dorsal aspect (without shell) of relaxed *T. gilae*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona: *a*, female; *b*, male. (Abbreviations: Acg = anterior end of capsule gland; Cgp = posterior end of capsule gland; Ct = ctenidium; Em = brooded embryo; In = intestine; Op = operculum; Pc = pericardium; Pn = penis; Sts = style sac.)

Buccal mass small (about 13%) relative to snout. Radula (Figure 43*d-i*) typically taenioglossate, with broadly trapezoidal central teeth having two pairs of basal cusps. Lateral angles of centrals widely divergent, narrow basal process characteristic. Central teeth with enlarged central cusp; central cusp of laterals sometimes not enlarged (Figure 43*g*). Inner and outer marginals similarly shaped; outers with only a few more cusps than inners. Stomach (Figure 44*b*, Ast, Pst) and style sac (Sts) about equal in length; the former having a broad caecal chamber (Cc) along its posterior margin. Posterior stomach chamber with single opening to digestive gland (Dgo). Digestive gland covering posterior half of stomach and extending (ventral to testis) almost to tip of visceral coil.

Testis large, overlapping most of posterior stomach chamber. Prostate gland (Figure 44*a*, Pr) small, flat, near-circular in outline, positioned largely or totally posterior to pallial cavity. Vas deferens enters posterior end of prostate gland and exits near anterior tip.

Penis (Figure 40, Pn) flattened, elongate, large relative to snout, extending forward from attachment area without coiling. Two small penial lobes (Figure 46*a*, Pl) on inner curvature centered at about two-thirds of penis length. Lobe on outer

curvature massive, and usually folded back against penis near base. All penial lobes bearing mammiform glands distally. Tip of penis with pronounced swelling on inner curvature (Figure 46*a*, Ics). Vas deferens undulating in penis, terminating in eversible papilla lateral to swelling (Figure 46*a*, Vd). Penis surface, especially at base, well endowed with dense glandular clusters of several types. Penial ciliation shown in Figure 45. Dense tuft of cilia at penis tip extending along outer curvature to level of base of distal lobe, and along inner curvature to distal end of swelling (Figure 45*a,b*). Three or four distinctive strips of cilia cross penis surface proximal to enlarged lobe (Figure 45*c,d*). Remainder of penis surface with scattered, small ciliary tufts.

Ovary very small relative to body length, non-lobular. Capsule gland (Figure 40*a*, Cg) enlarged (covering entirety of style sac), containing three or four shelled embryos. Brooded young darkly pigmented. Capsule gland with narrow muscular sphincter (Figure 42, Cg) at anterior end as well as posterior bend (Figure 47*b*, Cg) which extends (partly ventral to distal section of capsule gland) almost to anterior end of pallial cavity. Albumen gland (Figure 47*c*, Ag) comprising very small, narrow section of pallial oviduct, terminating ventral to

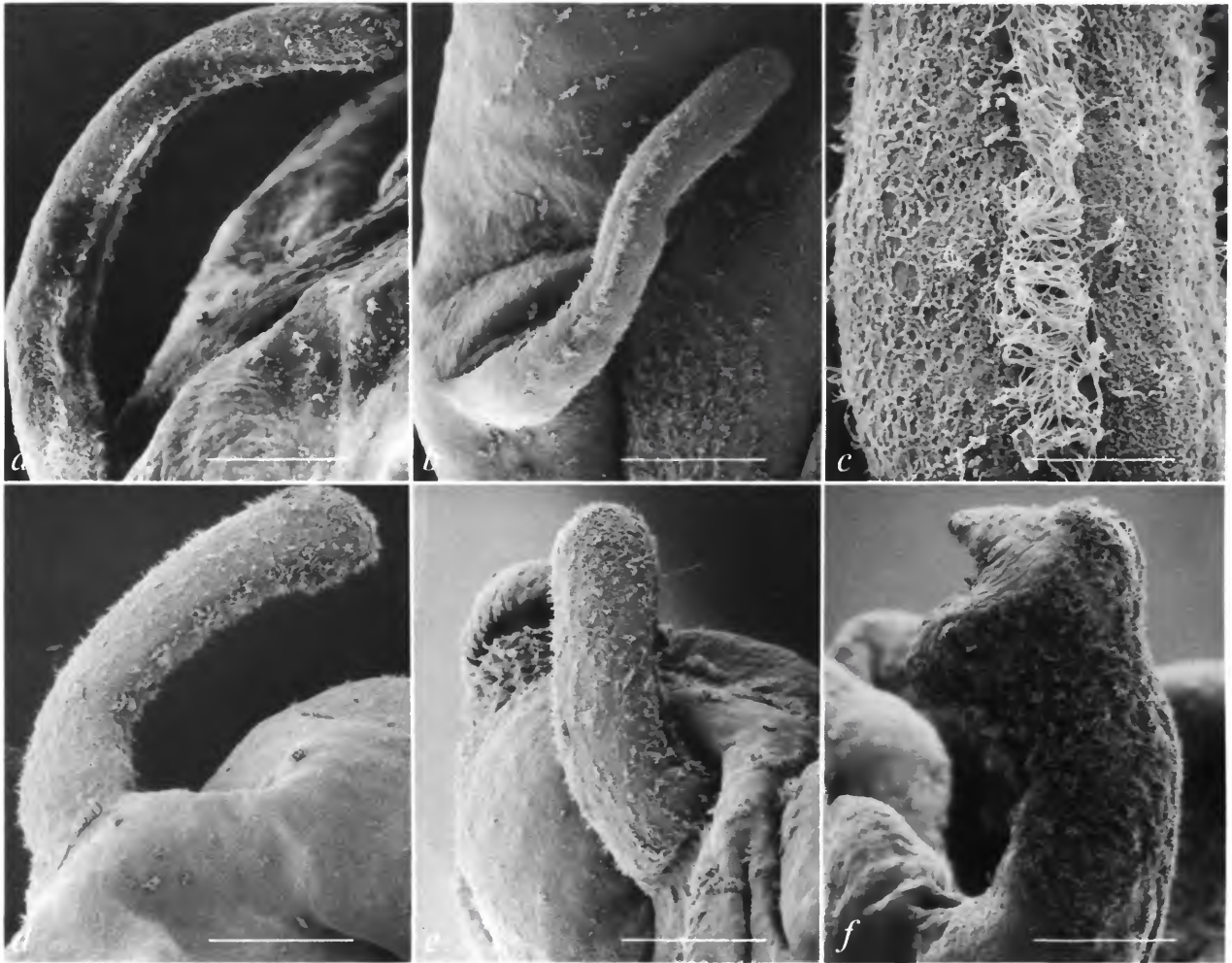


FIGURE 41.—SEM micrographs of cephalic tentacles of *Tryonia gila*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona: *a*, left tentacle, bar = 100  $\mu$ m; *b*, right tentacle, bar = 120  $\mu$ m; *c*, close-up of ciliation on tentacle, bar = 20.0  $\mu$ m. *T. quitobaquiae*, new species: *d*, left tentacle, bar = 75  $\mu$ m; *e*, right tentacle, bar = 75  $\mu$ m; *f*, distal half of penis, showing dense ciliation, bar = 50  $\mu$ m.

bursa copulatrix (Bu) at entry of renal oviduct. Oviduct (Ov) with simple coil (ventral to bursa) proximal to opening into albumen gland (Oov). Bursa club-shaped, small relative to pallial oviduct, and largely obscured anteriorly by albumen gland. Bursa gradually narrows anteriorly to give rise to spermathecal duct (Sd) just posterior to end of pallial cavity. Seminal receptacle (Sr) minute, with short duct connecting to oviduct. After this juncture duct (Dsr) coils several times ventral to bursa before looping back to open into dorsal surface of bursa at or just proximal to origin of spermathecal duct (Osr). Spermathecal duct pressed to ventral surface (columellar side) of capsule gland. Duct narrow, non-muscular, and short, opening just anterior to posterior end of pallial

cavity (Figure 42).

REMARKS.—This species is not very similar to either *T. quitobaquiae* from Arizona (described next) or undescribed taxa from New Mexico (Taylor, 1983). Its affinities may lie instead with Nevada species having relatively many penial lobes.

TYPE-LOCALITY.—Small spring near Bylas, Graham County, Arizona.

DISTRIBUTION.—Springs along north side of Gila River between Bylas and Pima.

ETYMOLOGY.—Referring to distribution of this species along Gila River.

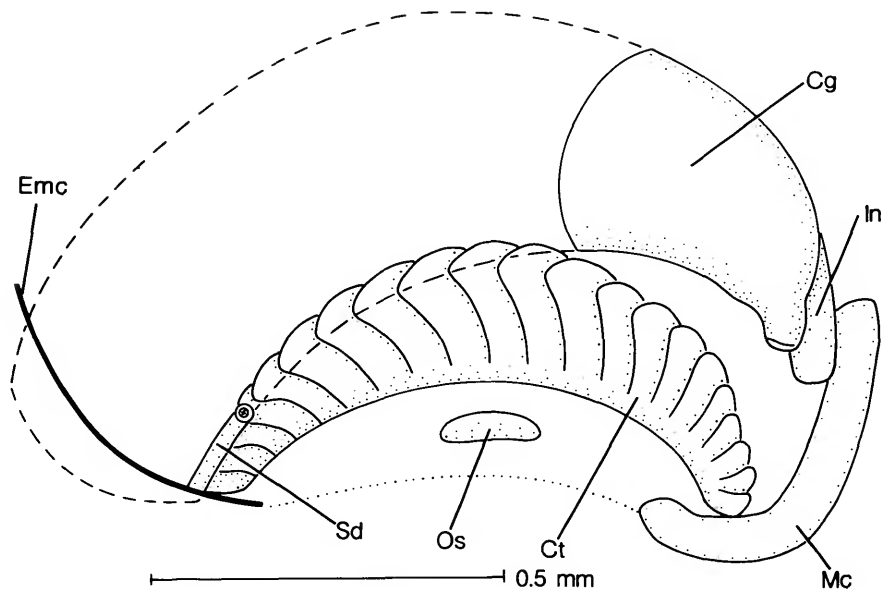


FIGURE 42.—Pallial cavity (viewed from right) of *T. gilae*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona: Most of capsule gland removed (position indicated by dashed lines) to reveal ctenidium and spermathecal duct. (Abbreviations: Cg = capsule gland; Ct = ctenidium; Emc = posterior end of pallial cavity; In = intestine; Mc = mantle collar; Os = osphradium; Sd = spermathecal duct.)

### *Tryonia quitobaquitae* Hershler, new species

#### Quitobaquito tryonia

FIGURES 39f–h, 41d–f, 43a–c, 46a, 47a

*Tryonia imitator* (Pilsbry).—Bequaert and Miller, 1973:213.

**MATERIAL EXAMINED.**—ARIZONA. *Pima County*: Quitobaquito Springs, USNM 859061 (holotype), 859062 (4 paratypes), 847256, J.J. Landye, 13 Mar 1971.

**DIAGNOSIS.**—A minute size species (1.4 to 1.8 mm), with ovate-conic to turreted shell. Cephalic tentacles without well-defined ciliary tracts. Penis with two lobes on inner curvature, a small one just distal to midpoint and a somewhat larger one near the base. Much of distal portion of penis with dense cover of cilia. Bursa very small relative to pallial oviduct. Holotype (Figure 39f) height, 1.96 mm; width, 0.96 mm; whorls, 4.5.

**DESCRIPTION.**—Shell (Figure 39f–h) with 3.5 to 4.5 highly convex whorls with deep sutures. Apertural lip thin. Inner lip only slightly reflected and usually fused to body whorl. Umbilicus chink-like.

Dark pigmentation on visceral coil near uniform. Snout and operculigerous lobe usually darkly pigmented, elsewhere head/foot having light dusting of melanin, with broad central section on sides of head/foot sometimes having distinctively light coating. Penial tip with pigment patch.

Scattered ciliary tufts on cephalic tentacles shown in Figure 41d,e. Central teeth of radula (Figure 43a) with single pair of

basal cusps. Lateral teeth (Figure 43b) with enlarged central cusp. Marginals shown in Figure 43b,c.

Elongate penis shown in Figure 46b. Note that vas deferens undulates only slightly in penis. Extensive penial ciliation shown in Figure 41f. Ciliation extending on both outer and inner curvatures to level of base of distal lobe. Bursa copulatrix complex shown in Figure 47a,b. Bursa (Bu) minute, not greatly overlapped by albumen gland.

**REMARKS.**—The reduced lobation of *T. quitobaquitae* is shared by two large undescribed congeners from New Mexico (Taylor, 1983).

**TYPE-LOCALITY.**—Quitobaquito Springs, Organ Pipe National Monument, Pima County, Arizona.

**DISTRIBUTION.**—Type-locality, Burro Spring and an unnamed spring, all within the national monument.

**ETYMOLOGY.**—Referring to the type-locality.

#### Morphometrics

Results of discriminant analyses based on shell and anatomical data are in Tables 3–5, with scores on the first two discriminant functions plotted in Figures 48 and 49. Correct classification to species for grouped cases, representing topotypes for each species, was 89% (overall) for the analysis based on male shell data (ranging from 80% to 100% among groups), 93% for the analysis based on female shell data (63% to 100%), and 100% for analyses using anatomical data (Table 6). Runs using subsets of taxa, such as the Verde Valley





FIGURE 43.—Radula of *Tryonia quitobaquia*, new species, USNM 847256, Quitobaquito Springs, Pima County, Arizona: *a*, centrals, bar = 8.6  $\mu$ m; *b*, laterals and inner marginals, bar = 6.7  $\mu$ m; *c*, outer marginals, bar = 5.0  $\mu$ m. *T. gilae*, new species: *d*, centrals, USNM 847257, small spring near Bylas, Graham County, Arizona, bar = 10.0  $\mu$ m; *e*, centrals, USNM 847253, Cold Springs, Graham County, Arizona, bar = 7.5  $\mu$ m; *f*, laterals, USNM 847257, bar = 6.0  $\mu$ m; *g*, laterals, USNM 847253, bar = 5.0  $\mu$ m; *h*, inner marginals, USNM 847253, bar = 12.0  $\mu$ m; *i*, outer marginals, USNM 847257, bar = 7.5  $\mu$ m.

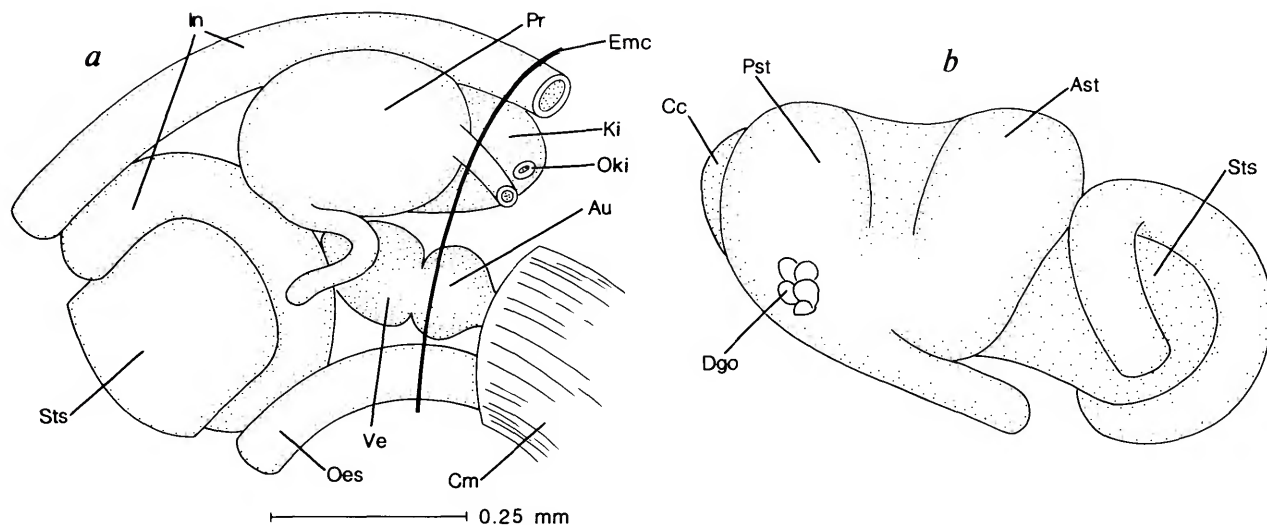


FIGURE 44.—Anatomy of *T. gilae*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona: *a*, right aspect of prostatic gland and adjacent organs and structures; *b*, right aspect of stomach. (Abbreviations: Ast = anterior stomach chamber; Au = auricle; Cc = caecal chamber; Cm = columellar muscle; Dgo = opening of digestive gland into stomach; Emc = posterior end of pallial cavity; In = intestine; Ki = kidney; Oes = oesophagus; Oki = kidney opening; Pr = prostatic gland; Pst = posterior stomach chamber; Sts = style; Ve = ventricle.)

species, did not yield superior classification.

The somewhat lower level of successful classification based on shell data is reflected in plots of scores on the first two discriminant functions (Figure 48), which collectively explain 68.8% (male) and 78.7% (female) of total variance. Note that groups are not well separated, especially in the analysis of female shell data (Figure 48*b*) in which each is overlapped by at least one other. Significant separation of closest groups (7, *P. simplex*; 3, *P. conicus*) was not achieved even after all steps were completed ( $p = 0.33$ ): note that all points representing the former are enclosed within the latter. For the analysis of male data (Figure 48*b*), significant separation of closest groups was achieved ( $p = 0.04$ ), yet all except two exhibit overlap.

Interpretation of the two discriminant functions (based on loadings and correlations in Table 3) suggests that function 1 represents size in both (decreasing along axis in male plot, increasing in female plot) while function 2 correlates with relative shell height (increasing along axis in male plot, decreasing in female plot). Note that most separation of groups occurs along the size-correlated axis. The two non-overlapped groups in the male plot (1, *P. deserta*, separated on axis II; 12, *P. cochisi*, separated on axis I) are unusually globose-shelled and small, respectively. Classification of ungrouped cases was highly variable, ranging from 0% for several populations of *P. thompsoni* to 70% for an additional population of that species.

A superior classification resulting from analyses based on

anatomical data is reflected in relatively separated groups in plots of scores on the first two discriminant functions (collectively explaining 64% (male) and 67.6% (female) of total variance), with six (male) and three (female) groups non-overlapped (Figure 49*a,b*). Significant ( $p > .005$ ) separation of closest groups was achieved after the final step (in both).

In the plot based on analysis of male anatomical data, separation of groups is fairly good along both axes (especially 1), and largely interpretable in terms of penial morphology and body size. Function 1 has particularly high loadings of GLR and WFI (Table 4). Species with low scores on this axis, such as *P. thompsoni* (11), have penes with thickened filaments and few (usually one) glandular ridges (see Figure 38), while those with higher scores (9, *P. confluentis*; 8, *P. glandulosus*; 5, *P. montezumensis*) have penes with narrow filaments and more than two ridges (see Figures 8, 9, 23, 30). The second axis has high loadings of other penial variables (L2, L3/L2, LFI) as well as a size component (note high loading of BL). Species with low scores on this axis have relatively long penial filaments and/or lobes (Figures 14, 28, 31, 35) (10, *P. sancarlosensis*; 7, *P. simplex*; 1, *P. deserta*; 12, *P. cochisi*), while species with high scores, such as *P. bacchus* (2), have shortened filaments and/or lobes (Figure 15). Note that ungrouped specimens are fairly tightly clustered and positioned close to topotypes of their species (especially *P. sancarlosensis*), but rarely overlap with them (Figure 49*a*). For these ungrouped specimens, classification ranged from 0% (two

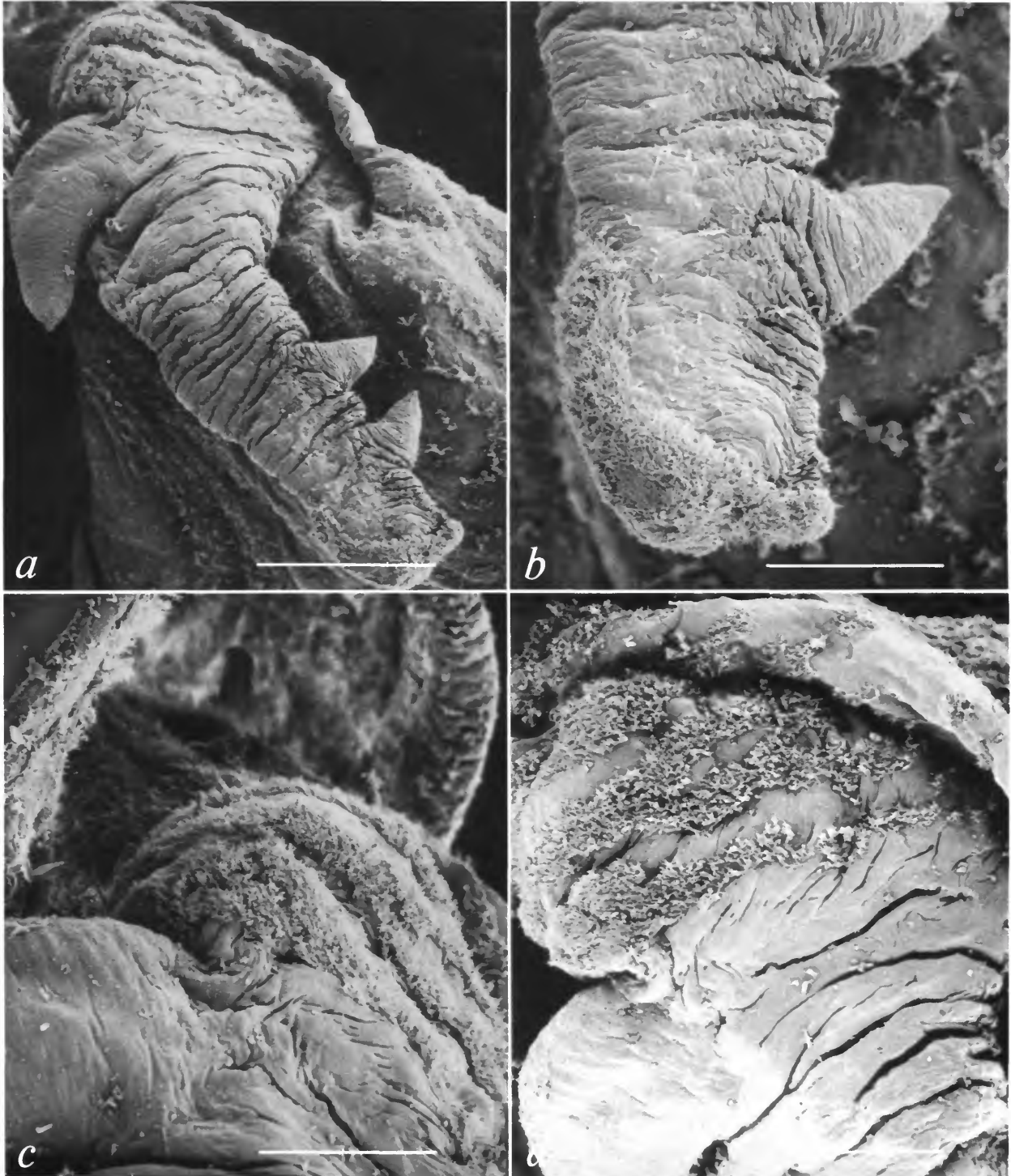


FIGURE 45. SEM micrographs of penis of *T. gilae*, new species, USNM 847257, small spring near Bylas, Graham County, Arizona: *a*, dorsal aspect of penis, bar = 200  $\mu\text{m}$ ; *b*, close-up of distal end of above, bar = 75  $\mu\text{m}$ ; *c,d*, dorsal aspect of penis base, bars = 86, 100  $\mu\text{m}$ .

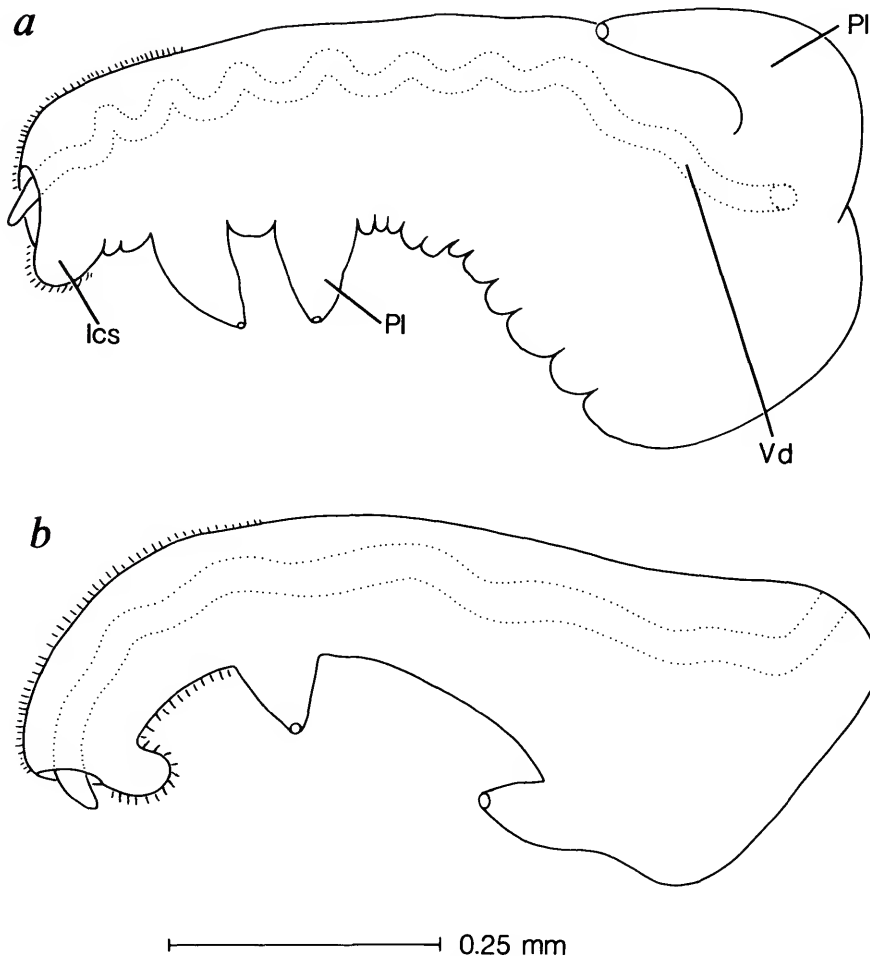


FIGURE 46.—Penis of *T. gilae*, new species: *a*, (above) USNM 847257, small spring near Bylas, Graham County, Arizona. *T. quitobaquiae*, new species: *b*, Quitobaquito Springs, Pima County, Arizona. (Abbreviations: lcs = swelling on inner curvature; PI = penial lobe; Vd = vas deferens.

populations of *P. thompsoni*) to 100% (a third population of the same).

In the plot based on analysis of female data (Figure 49*b*), group separation is largely effected by scores on the first discriminant function, which is clearly size-correlated, given high loadings of CTL, OSL, OCT, and BDW on it (Table 5). The second discriminant function has high loadings of OSL/CTL, BUW, COP, and SRL/BUL. The particularly low scores of *P. sancarlosensis* (10) on this axis probably result from absence of a seminal receptacle in this species. Ungrouped specimens (especially *P. sancarlosensis* and *P. morrisoni*) are generally more separated from appropriate topotypes than in the male plot. Also note the large variance on the first discriminant function for specimens representing *P. thompsoni*. For ungrouped cases, classification

ranged from 0 to 40%.

### Discussion

Results of the discriminant analyses support division of Arizona *Pyrgulopsis* into 12 species, in that these appear well differentiated, with discriminant equations based on four separate data sets for grouped topotypes nearly always correctly classifying them.

Discriminant analyses using anatomical data provide classifications slightly superior to those generated by shell data, and yield greater species separation on plots (especially based on male anatomical data) of the first two discriminant function scores, suggesting the former data set discriminates these species somewhat better than the latter. This may be partly due

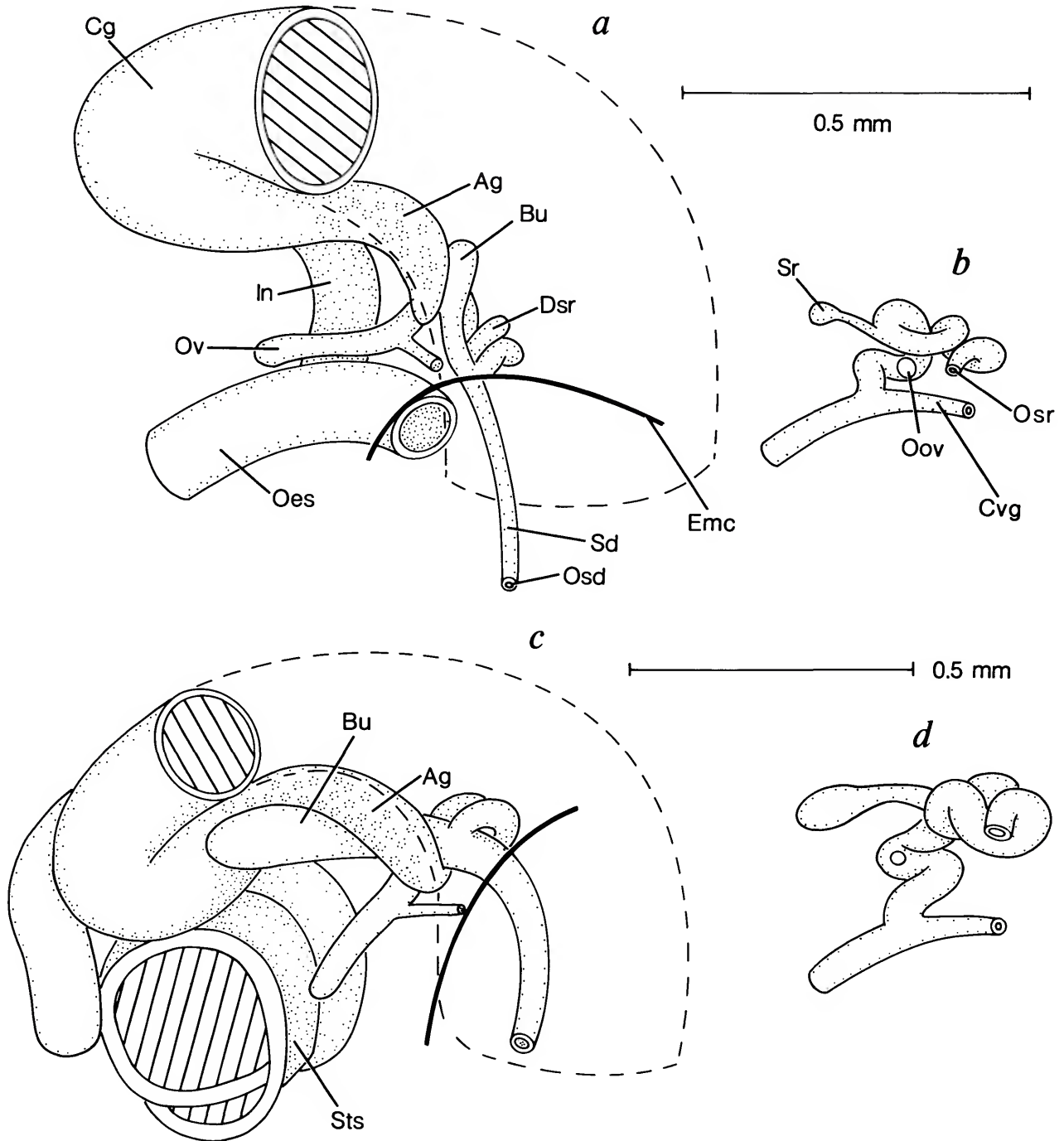
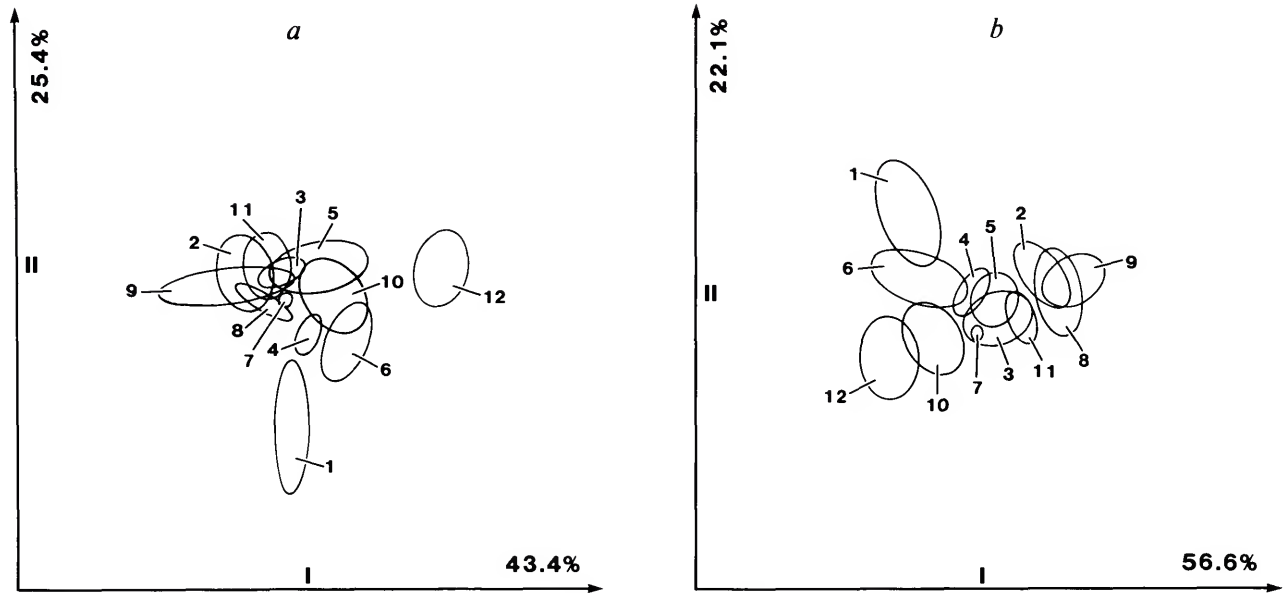


FIGURE 47.—Bursa copulatrix complex (viewed from right) of *T. quitobaquiae*, new species: *a,b* USNM 847256, Quitobaquito Springs, Pima County, Arizona, and *T. gilae*, new species: *c,d* USNM 847257, small spring near Bylas, Graham County, Arizona; much of pallial oviduct cut away (position indicated by dashed lines) to reveal underlying structures; visceral ganglion connective tightly pressed against oviduct. (Abbreviations: Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cvg = visceral ganglion connective; Dsr = duct of seminal receptacle; Emc = posterior end of pallial cavity; In = intestine; Oes = oesophagus; Oov = opening of oviduct into albumen gland; Osd = opening of spermathecal duct; Osr = opening of seminal receptacle duct into spermathecal duct; Ov = oviduct; Sd = spermathecal duct; Sr = seminal receptacle; Sts = style sac.)



FIGURES 48, 49—Plots of scores on first two discriminant functions derived from *Pyrgulopsis* shell data (Figure 48, above) and anatomical data (Figure 49, below); percent variation explained by each function is indicated on respective axes; ellipses encircle positions of toptypical specimens for each species; positions of ungrouped specimens (from additional populations) for three species are indicated by symbols in Figure 49 (*a* = male; *b* = female; 1 = *P. deserta*; 2 = *P. bacchus*; 3 = *P. conicus*; 4 = *P. morrisoni*; 5 = *P. montezumensis*; 6 = *P. solus*; 7 = *P. simplex*; 8 = *P. glandulosus*; 9 = *P. confluentis*; 10 = *P. sancarlosensis*; 11 = *P. thompsoni*; 12 = *P. cochisi*.)

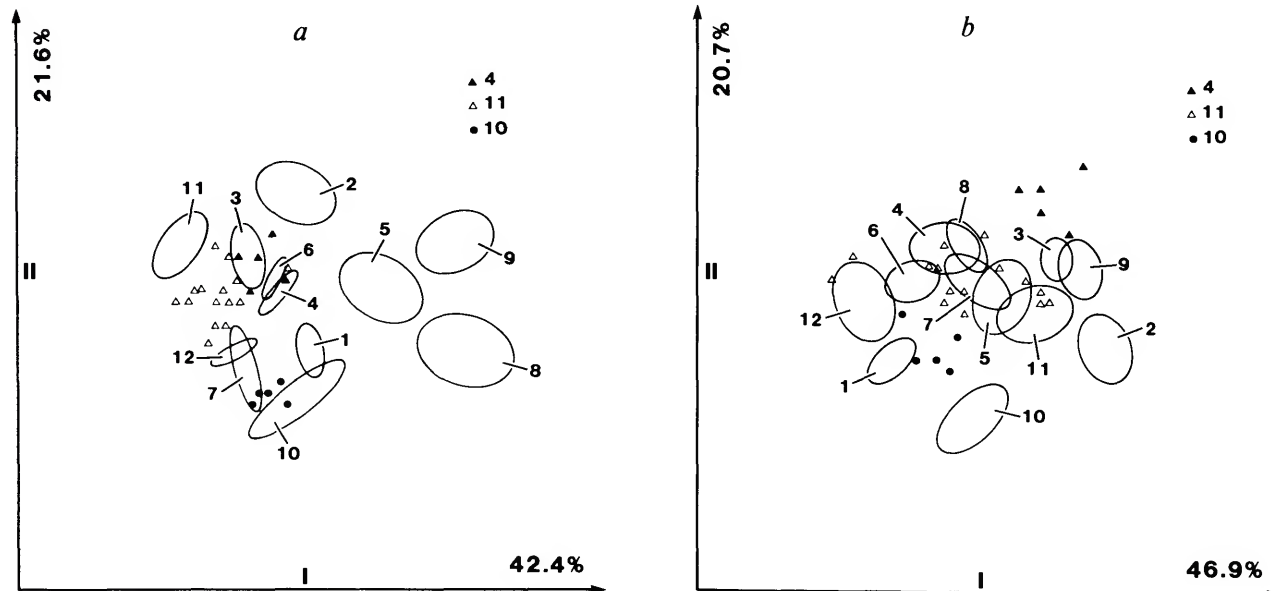


TABLE 3.—Results of stepwise discriminant function analysis on thirteen shell variables in terms of standardized weights and correlation of variable with discriminant function.

Variable	Males				Females			
	Function 1		Function 2		Function 1		Function 2	
SH	0.56	-0.61	2.44	0.53	-2.21	0.51	2.59	-0.13
SW	2.38	-0.72	1.10	0.27	1.12	0.82	-0.65	0.15
AH	3.91	-0.69	5.54	0.36	-0.91	-3.57	0.10	0.04
AW	-0.21	-0.73	0.46	0.37	-0.08	0.68	0.41	0.10
LBW	-6.93	-0.69	-5.21	0.48	1.38	0.72	2.57	-0.10
WBW	-0.62	-0.79	0.01	0.40	0.89	0.82	0.46	0.03
CD	-0.69	-0.30	-0.86	0.38	-1.17	0.31	-0.36	0.01
AB	0.55	-0.55	1.11	0.50	0.64	0.55	-0.71	-0.20
NW	-0.12	-0.36	0.27	0.48	0.13	0.33	-0.15	-0.32
SH/SW	1.83	0.06	1.35	0.61	0.56	0.08	-1.44	-0.43
AH/SH	-2.52	0.01	-3.28	-0.54	0.58	-0.15	2.98	0.43
LBW/SH	2.61	0.09	1.59	-0.46	-1.08	-0.16	-1.58	0.26
CD/AB	0.64	0.08	1.04	0.10	0.83	0.01	0.45	0.17

TABLE 4.—Results of stepwise discriminant function analysis on eleven male anatomical variables in terms of standardized weights and correlation of variable with discriminant function.

Variable	Function 1		Function 2	
	CTW	0.10	0.05	0.21
TS/BL	-0.04	-0.08	0.78	0.44
L2	0.48	0.44	-0.88	-0.04
BL	0.17	0.03	0.81	0.65
L3/L2	-0.58	-0.06	-0.85	-0.05
GLR	0.87	0.68	0.05	0.03
LFI	-0.21	-0.03	-0.49	-0.25
WFI	-0.46	0.05	0.20	0.04
CTL	-0.05	0.12	-0.31	0.37
LPR/BL	0.56	0.16	-0.06	-0.30
L3	0.28	0.28	1.24	-0.04

TABLE 5.—Results of stepwise discriminant function analysis of thirteen female anatomical variables in terms of standardized weights and correlation of variable with discriminant function.

Variable	Function 1		Function 2	
	CTL	-0.59	0.49	0.40
BAG	-0.26	0.12	-0.19	-0.40
BUW	0.16	0.23	-0.70	-0.29
COP	-0.28	0.15	0.73	0.31
CGW	0.26	0.33	0.14	0.03
FI	0.25	0.39	0.19	0.17
AGL	0.49	0.40	-0.27	0.09
OV	0.29	0.26	-0.29	-0.09
SRL/BUL	-0.07	-0.01	0.70	0.52
OSL	1.01	0.29	-0.19	0.16
BDW	0.62	0.36	0.34	0.03
OCT	0.56	0.38	-0.11	0.01
OSL/CTL	-1.29	-0.11	0.70	0.08

TABLE 6.—Classification results of discriminant function analyses expressed as per cent of specimens correctly classified.

Data set	Grouped cases	Ungrouped cases
Male shell	89 (n = 113)	14 (n = 104)
Female shell	93 (108)	15 (103)
Male anatomy	100 (60)	29 (28)
Female anatomy	100 (60)	19 (27)

to differences in sample size: more shells per group were measured than animals (seven to eleven vs. five), which results in increased variance in discriminant function scores for the former.

Superior separation of groups based on the first two discriminant functions for male anatomical data reflects relative diversity and ease of quantification of penial morphology compared to shell and female anatomy. Morphologic diversity among shells of the congeners, apart from size and general form, is slight (Figures 3, 11, 16, 21, 31, 36). In addition, shell variables used, consisting of those traditionally employed by malacologists, are admittedly unsuited for accurate quantification of shell form, which is far better achieved using parameters developed by Raup (1961, 1966). Female reproductive morphology is similarly conservative, with little variation in pallial oviduct and bursa copulatrix complex apart from size (and absence of seminal receptacle in *P. sancarlosensis*) (Figures 10, 26). Penial variation is more pronounced, and involves easily quantified features that include number of glandular ridges and relative sizes of lobe and filament (Figures 8, 9, 13, 15, 18, 20, 23, 25, 28, 30, 33, 35, 38).

The relatively high frequency of misclassification of ungrouped specimens is partly a result of interpopulation

variation within species. Significant variation in shell size and general form is evident in several species (Figures 3d–g, 21g–i, 31a–g, 36) and even occurs among samples of *P. montezumensis* from Montezuma Well proper and its upper outflow, with classification of the latter only 33% for either sex. Similar levels of anatomical variation were not readily apparent to us (note only slight variation in penes among six populations of *P. thompsoni*, Figure 38), yet misclassification was still

frequent. This reflects occurrence of subtle variation among conspecific populations involving complex combinations of variables. An additional explanation is inflated variation within populations due to small sample sizes (five to eleven). Regardless of its cause, existence of such variation suggests that discriminant function equations solely based on data from topotypes do not consistently correctly classify specimens from additional populations.

### Addendum

A recent (Taylor, 1987) monograph of springsnails of New Mexico and vicinity, published subsequent to correction of proofs of this paper, includes descriptions of a few of the species that we name herein and we recognize the following cases of synonymy: *Tryonia gilae* Hershler is a junior primary homonym (and junior subjective synonym) of *Tryonia gilae* Taylor; and *Pyrgulopsis confluentis* Hershler, *P. sancarlosensis* Hershler, and *P. cochisi* Hershler are junior subjective synonyms of *Fontelicella trivialis* Taylor, *Apachecoccus bernardinus* Taylor, and *Yaquicoccus bernardinus* Taylor, respectively. Discussion of generic allocations provided by Taylor for some of the above is tabled for a forthcoming paper by one of us (RH).



# Appendices

Appendix 1. Shell data for species of *Pyrgulopsis*. USNM catalog numbers are given for localities. Sample sizes are given in parentheses (#males, #females). Asterisked localities have significant (two tailed t-test,  $p < .05$ ) sexual dimorphism in shell height (SH). Measurements are in mm.  $\bar{X}$  = mean, S = standard deviation.

Species and locality	Parameters																		
	SH		SW		AH		AW		LBW		WBW		CD		AB		NW		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
<u><i>P. glandulosus</i></u> *847205 (n = 8,7)	$\bar{X}$	2.24	2.56	1.67	1.93	1.13	1.28	1.03	1.12	1.84	2.13	1.42	1.60	0.18	0.19	0.68	0.78	3.78	3.89
	S	0.18	0.15	0.13	0.08	0.09	0.10	0.10	0.06	0.14	0.18	0.13	0.10	0.05	0.01	0.07	0.05	0.16	0.13
<u><i>P. deserta</i></u> *847202 (n = 8,9)	$\bar{X}$	1.51	1.41	1.28	1.20	0.85	0.80	0.75	0.74	1.30	1.24	1.05	0.95	0.09	0.12	0.41	0.40	3.44	3.28
	S	0.17	0.13	0.12	0.10	0.06	0.06	0.05	0.06	0.11	0.12	0.10	0.07	0.01	0.03	0.04	0.05	0.18	0.20
847206 (n = 8)	$\bar{X}$	1.47	1.76	1.15	1.36	0.74	0.87	0.71	0.82	1.22	1.41	0.99	1.16	0.13	0.12	0.42	0.50	3.47	3.69
	S	0.13	0.15	0.06	0.04	0.04	0.03	0.04	0.05	0.08	0.09	0.04	0.06	0.10	0.02	0.04	0.06	0.16	0.29
<u><i>P. bacchus</i></u> 84203 (n = 10)	$\bar{X}$	2.57	2.54	1.79	1.84	1.23	1.23	1.13	1.14	2.02	2.02	1.58	1.58	0.20	0.18	0.78	0.74	4.18	4.15
	S	0.23	0.16	0.08	0.07	0.05	0.05	0.05	0.07	0.12	0.11	0.08	0.06	0.03	0.03	0.11	0.06	0.12	0.18
<u><i>P. conicus</i></u> 847237 (n = 9,8)	$\bar{X}$	2.36	2.31	1.54	1.57	1.11	1.11	0.96	0.96	1.83	1.81	1.29	1.33	0.13	0.15	0.68	0.66	4.11	4.09
	S	0.17	0.14	0.11	0.09	0.07	0.08	0.07	0.06	0.12	0.10	0.08	0.09	0.02	0.02	0.07	0.04	0.13	0.13
*847201 (n = 7,9)	$\bar{X}$	2.17	2.47	1.43	1.65	1.01	1.11	0.84	0.98	1.66	1.88	1.23	1.37	0.13	0.15	0.61	0.69	4.07	4.25
	S	0.21	0.13	0.14	0.10	0.09	0.07	0.08	0.05	0.12	0.06	0.10	0.05	0.01	0.02	0.04	0.04	0.31	0.13
<u><i>P. morrisoni</i></u> *847231 (n = 9)	$\bar{X}$	1.89	2.08	1.43	1.54	0.92	0.98	0.83	0.91	1.49	1.63	1.14	1.26	0.11	0.12	0.56	0.59	3.78	4.00
	S	0.10	0.14	0.07	0.11	0.07	0.08	0.05	0.07	0.10	0.10	0.05	0.08	0.02	0.02	0.03	0.05	0.15	0.13
847220 (n = 8,10)	$\bar{X}$	2.29	2.37	1.64	1.68	1.11	1.12	0.97	0.99	1.80	1.82	1.39	1.43	0.15	0.14	0.67	0.66	4.13	4.03
	S	0.19	0.18	0.10	0.11	0.10	0.07	0.08	0.06	0.14	0.12	0.08	0.08	0.02	0.01	0.07	0.06	0.19	0.22
<u><i>P. montezumensis</i></u> *847233 (n = 10,8)	$\bar{X}$	2.12	2.18	1.41	1.51	0.95	0.99	0.87	0.93	1.55	1.65	1.25	1.32	0.15	0.17	0.59	0.62	4.00	4.06
	S	0.28	0.15	0.20	0.09	0.14	0.05	0.10	0.08	0.19	0.09	0.14	0.08	0.03	0.02	0.05	0.05	0.20	0.26
*847230 (n = 10,9)	$\bar{X}$	2.06	2.41	1.42	1.66	0.93	1.07	0.81	0.95	1.54	1.74	1.17	1.40	0.11	0.15	0.56	0.65	4.05	4.14
	S	0.24	0.14	0.12	0.06	0.07	0.06	0.07	0.04	0.19	0.08	0.12	0.09	0.02	0.02	0.06	0.65	0.37	0.13
<u><i>P. solus</i></u> *850290 (n = 8,10)	$\bar{X}$	1.57	1.72	1.17	1.29	0.78	0.87	0.73	0.82	1.29	1.45	1.00	1.08	0.11	0.11	0.46	0.50	3.50	3.73
	S	0.08	0.16	0.04	0.12	0.03	0.08	0.03	0.07	0.05	0.14	0.03	0.08	0.02	0.02	0.04	0.05	0.13	0.18
<u><i>P. simplex</i></u> *847236 (n = 9,10)	$\bar{X}$	2.08	2.31	1.43	1.55	1.01	1.08	0.87	0.94	1.67	1.80	1.18	1.27	0.13	0.14	0.59	0.63	3.81	4.00
	S	0.12	0.09	0.11	0.07	0.07	0.07	0.06	0.06	0.09	0.10	0.08	0.08	0.01	0.02	0.04	0.05	0.21	0.20
847222 (n = 10,9)	$\bar{X}$	2.18	2.21	1.42	1.56	0.97	1.05	0.87	0.90	1.65	1.68	1.25	1.26	0.13	0.13	0.63	0.67	4.03	4.00
	S	0.19	0.16	0.11	0.11	0.09	0.11	0.007	0.06	0.15	0.08	0.08	0.06	0.01	0.02	0.07	0.11	0.18	0.18
<u><i>P. confluentis</i></u> 847234 (n = 10)	$\bar{X}$	2.81	3.01	1.80	1.92	1.18	1.24	1.10	1.16	2.09	2.18	1.65	1.76	0.19	0.24	0.82	0.85	4.30	4.35
	S	0.29	0.68	0.16	0.15	0.10	0.10	0.11	0.09	0.18	0.19	0.14	0.18	0.03	0.07	0.09	0.14	0.20	0.32
*847229 (n = 10)	$\bar{X}$	1.62	1.83	1.30	1.42	0.83	0.93	0.77	0.84	1.36	1.50	1.08	1.21	0.14	0.15	0.50	0.53	3.73	3.68
	S	0.12	0.80	0.09	0.06	0.06	0.04	0.04	0.03	0.09	0.10	0.08	0.06	0.02	0.03	0.05	0.04	0.14	0.21
<u><i>P. sancarlosensis</i></u> 847226 (n = 13)	$\bar{X}$	1.90	2.01	1.28	1.33	0.92	0.93	0.82	0.85	1.56	1.66	1.09	1.15	0.15	0.15	0.56	0.62	3.90	4.06
	S	0.19	0.20	0.08	0.11	0.07	0.06	0.05	0.04	0.14	0.90	0.08	0.07	0.02	0.03	0.07	0.06	0.26	0.17
847217 (n = 10)	$\bar{X}$	1.34	1.54	1.06	1.20	0.74	0.83	0.67	0.75	1.17	1.34	0.83	0.67	0.08	0.11	0.40	0.46	3.40	3.65
	S	0.17	0.34	0.10	0.16	0.07	0.11	0.06	0.11	0.12	0.21	0.10	0.15	0.01	0.02	0.05	0.11	0.21	0.27
847224 (n = 9)	$\bar{X}$	1.50	1.62	1.11	1.20	0.75	0.82	0.73	0.77	1.28	1.40	0.95	1.02	0.11	0.13	0.45	0.48	3.33	3.53
	S	0.06	0.82	0.04	0.09	0.03	0.05	0.03	0.05	0.05	0.11	0.03	0.08	0.02	0.03	0.03	0.07	0.13	0.36
<u><i>P. cochisi</i></u> *847218 (n = 9)	$\bar{X}$	1.41	1.54	0.89	1.10	0.63	0.69	0.57	0.63	1.11	1.21	0.81	0.88	0.11	0.12	0.43	0.48	3.56	3.69
	S	0.09	0.12	0.05	0.09	0.03	0.05	0.03	0.05	0.05	0.08	0.04	0.05	0.01	0.02	0.03	0.04	0.21	0.17
<u><i>P. thompsoni</i></u> *847238 (n = 10,9)	$\bar{X}$	2.67	2.41	1.68	1.59	1.20	1.12	1.05	1.00	2.03	1.90	1.43	1.42	0.18	0.14	0.77	0.70	4.53	4.14
	S	0.24	0.17	0.11	0.09	0.08	0.08	0.07	0.07	0.13	0.12	0.08	0.11	0.02	0.02	0.06	0.05	0.18	0.13
847221 (n = 8,9)	$\bar{X}$	1.97	2.08	1.43	1.43	0.97	0.97	0.87	0.87	1.60	1.59	1.18	1.18	0.12	0.13	0.58	0.59	4.03	4.03
	S	0.08	0.18	0.06	0.12	0.04	0.06	0.04	0.05	0.08	0.10	0.05	0.08	0.01	0.01	0.02	0.04	0.21	0.20
*847228 (n = 10)	$\bar{X}$	2.15	2.51	1.40	1.62	0.96	1.12	0.90	1.01	1.64	1.89	1.29	1.47	0.14	0.15	0.62	0.73	4.05	4.35
	S	0.25	0.31	0.10	0.11	0.09	0.08	0.07	0.08	0.15	0.17	0.10	0.10	0.02	0.01	0.07	0.07	0.23	0.29
847227 (n = 8,9)	$\bar{X}$	1.91	1.85	1.19	1.23	0.83	0.87	0.75	0.76	1.43	1.47	1.09	1.13	0.14	0.14	0.54	0.57	3.91	3.89
	S	0.19	0.19	0.08	0.05	0.06	0.04	0.07	0.04	0.12	0.07	0.07	0.06	0.04	0.02	0.05	0.05	0.38	0.18

Appendix 2. Female anatomical data for species of *Pyrgulopsis*. USNM catalog numbers are given for the localities. For all samples, n = 5. Measurements are in mm.  $\bar{X}$  = mean, S = standard deviation.

Species and locality	Parameters																					
	BL	OV	OSL	OSW	OCT	CTL	CTW	FI	CGL	CGW	AGL	AGW	COL	COP	COD	BUL	BUW	BDW	BAG	SRL	SRW	
<u><i>P. glandulosus</i></u> 847205	$\bar{X}$ S	4.22 0.36	0.72 0.09	0.24 0.04	0.29 0.44	0.22 0.03	1.00 0.07	0.20 0.19	18.80 1.30	0.59 0.06	0.29 0.02	0.62 0.07	0.38 0.02	0.27 0.08	0.20 0.02	0.09 0.02	0.27 0.02	0.18 0.05	0.18 0.01	0.26 0.04	0.08 0.07	0.02
<u><i>P. deserta</i></u> 847202	$\bar{X}$ S	2.70 0.26	0.58 0.21	0.16 0.04	0.06 0.01	0.18 0.04	0.70 0.05	0.17 0.02	12.40 0.90	0.39 0.02	0.27 0.05	0.50 0.09	0.33 0.04	0.18 0.02	0.13 0.04	0.06 0.01	0.42 0.07	0.22 0.03	0.05 0.01	0.30 0.05	0.16 0.04	0.07 0.01
<u><i>P. bacchus</i></u> 847203	$\bar{X}$ S	6.07 0.55	0.97 0.08	0.28 0.02	0.08 0.01	0.31 0.02	1.15 0.05	0.25 0.05	17.40 1.67	0.62 0.05	0.37 0.02	0.82 0.06	0.44 0.04	0.35 0.06	0.12 0.04	0.11 0.02	0.39 0.06	0.29 0.04	0.12 0.01	0.25 0.06	0.16 0.05	0.07 0.02
<u><i>P. conicus</i></u> 847237	$\bar{X}$ S	5.07 0.52	0.89 0.13	0.29 0.02	0.06 0.00	0.30 0.02	1.10 0.07	0.23 0.03	20.00 1.00	0.57 0.05	0.30 0.03	0.70 0.10	0.38 0.04	0.29 0.03	0.16 0.03	0.09 0.01	0.29 0.04	0.18 0.20	0.08 0.01	0.12 0.04	0.17 0.03	0.09 0.02
<u><i>P. morrisoni</i></u> 847231	$\bar{X}$ S	3.78 0.14	0.74 0.20	0.25 0.02	0.09 0.01	0.20 0.04	0.82 0.14	0.18 0.02	16.40 1.14	0.49 0.06	0.27 0.02	0.47 0.07	0.32 0.05	0.24 0.01	0.07 0.06	0.09 0.01	0.24 0.04	0.16 0.03	0.08 0.01	0.17 0.04	0.20 0.05	0.06 0.00
847220	$\bar{X}$ S	5.36 0.41	0.89 0.11	0.36 0.06	0.10 0.01	0.25 0.05	1.21 0.17	0.25 0.03	18.20 0.84	0.67 0.08	0.41 0.01	0.86 0.12	0.52 0.09	0.24 0.05	0.25 0.05	0.09 0.01	0.24 0.03	0.18 0.03	0.08 0.02	0.12 0.06	0.26 0.04	0.10 0.02
<u><i>P. montezumensis</i></u> 847233	$\bar{X}$ S	4.63 0.16	0.60 0.08	0.26 0.04	0.10 0.02	0.26 0.03	1.06 0.02	0.20 0.02	17.40 1.52	0.60 0.03	0.34 0.04	0.68 0.04	0.41 0.04	0.27 0.04	0.20 0.03	0.10 0.01	0.33 0.05	0.25 0.04	0.07 0.01	0.22 0.04	0.21 0.03	0.07 0.02
<u><i>P. solus</i></u> 850290	$\bar{X}$ S	3.44 0.23	0.51 0.08	0.19 0.02	0.07 0.01	0.18 0.03	0.78 0.07	0.17 0.01	12.60 0.89	0.46 0.04	0.27 0.04	0.50 0.06	0.32 0.03	0.22 0.03	0.12 0.01	0.07 0.01	0.18 0.01	0.17 0.04	0.05 0.01	0.10 0.00	0.15 0.02	0.06 0.00
<u><i>P. simplex</i></u> 847236	$\bar{X}$ S	3.87 0.32	0.45 0.22	0.21 0.02	0.09 0.03	0.24 0.06	1.03 0.09	0.16 0.01	17.60 0.14	0.49 0.08	0.23 0.02	0.54 0.10	0.30 0.03	0.22 0.02	0.10 0.02	0.08 0.00	0.29 0.12	0.14 0.01	0.07 0.01	0.15 0.05	0.17 0.04	0.05 0.01
<u><i>P. confluentis</i></u> 847234	$\bar{X}$ S	6.15 0.56	0.91 0.13	0.33 0.02	0.06 0.02	0.30 0.03	1.43 0.20	0.20 0.04	20.60 1.52	0.82 0.03	0.40 0.03	0.87 0.06	0.47 0.05	0.34 0.07	0.19 0.02	0.08 0.01	0.39 0.04	0.27 0.04	0.08 0.01	0.25 0.04	0.37 0.07	0.11 0.02
<u><i>P. sarcarlosensis</i></u> 847226	$\bar{X}$ S	3.96 0.18	0.85 0.14	0.23 0.05	0.06 0.02	0.22 0.01	0.92 0.01	0.19 0.01	17.80 1.30	0.54 0.06	0.26 0.02	0.49 0.01	0.37 0.04	0.40 0.04	0.01 0.01	0.09 0.01	0.49 0.05	0.26 0.03	0.06 0.02	0.29 0.02	0.00 0.00	0.00
847217	$\bar{X}$ S	2.66 0.26	0.41 0.03	0.22 0.05	0.07 0.02	0.19 0.03	0.73 0.09	0.17 0.02	17.20 1.79	0.37 0.05	0.23 0.02	0.37 0.03	0.28 0.02	0.30 0.02	0.00 0.00	0.10 0.02	0.22 0.03	0.18 0.02	0.07 0.01	0.17 0.02	0.00 0.00	0.00
<u><i>P. cochisi</i></u> 847218	$\bar{X}$ S	2.69 0.27	0.39 0.04	0.19 0.01	0.55 0.02	0.17 0.03	0.62 0.05	0.13 0.03	14.20 0.84	0.44 0.02	0.20 0.02	0.41 0.06	0.26 0.02	0.14 0.02	0.05 0.02	0.05 0.01	0.17 0.03	0.15 0.02	0.04 0.01	0.11 0.03	0.11 0.01	0.02
<u><i>P. thompsoni</i></u> 847238	$\bar{X}$ S	5.19 0.94	0.72 0.14	0.19 0.03	0.07 0.03	0.32 0.02	1.07 0.13	0.22 0.02	18.20 1.30	0.68 0.16	0.33 0.06	0.73 0.15	0.40 0.05	0.31 0.06	0.13 0.07	0.07 0.01	0.32 0.06	0.20 0.03	0.07 0.02	0.26 0.06	0.23 0.06	0.06
847227	$\bar{X}$ S	5.67 0.36	0.68 0.11	0.33 0.03	0.10 0.02	0.38 0.04	0.31 0.11	0.26 0.003	19.80 1.30	0.63 0.06	0.34 0.04	0.69 0.10	0.44 0.05	0.22 0.04	0.17 0.04	0.07 0.01	0.31 0.05	0.15 0.04	0.05 0.02	0.27 0.06	0.16 0.02	0.06 0.01

Appendix 3. Male anatomical data for species of *Pyrgulopsis*. USNM catalog numbers are given for the localities. For all samples, n = 5. Measurements are in mm.  $\bar{X}$  = mean, S = standard deviation.

Species and Locality		Parameters															
		BL	TS	OSL	OSW	OCT	CTL	CTW	FI	LPR	WPR	L2	L3	PW	LFI	WFI	GLR
<u><i>P. glandulosus</i></u>	$\bar{X}$	3.44	0.88	0.31	0.11	0.18	0.96	0.20	17.40	0.56	0.26	1.42	1.10	0.43	0.36	0.11	4.80
847205	S	0.32	0.04	0.04	0.02	0.02	0.04	0.03	0.55	0.04	0.04	0.21	0.20	0.07	0.08	0.02	0.45
<u><i>P. deserta</i></u>	$\bar{X}$	2.44	0.75	0.18	0.07	0.15	0.55	0.18	11.20	0.48	0.21	0.53	0.45	0.34	0.39	0.16	3.00
847202	S	0.14	0.13	0.03	0.001	0.03	0.09	0.02	0.84	0.04	0.05	0.04	0.04	0.03	0.03	0.02	0.00
<u><i>P. bacchus</i></u>	$\bar{X}$	6.06	3.29	0.31	0.09	0.29	1.17	0.30	17.80	0.81	0.39	0.77	0.64	0.35	0.32	0.17	2.00
847203	S	0.25	0.38	0.05	0.02	0.03	0.10	0.03	1.92	0.15	0.06	0.15	0.17	0.02	0.07	0.03	0.71
<u><i>P. conicus</i></u>	$\bar{X}$	4.68	1.92	0.26	0.08	0.24	1.04	0.25	18.60	0.47	0.28	0.69	0.49	0.36	0.34	0.12	1.00
847237	S	0.53	0.36	0.06	0.02	0.01	0.12	0.04	1.14	0.07	0.04	0.20	0.21	0.03	0.05	0.01	0.00
<u><i>P. morrisoni</i></u>	$\bar{X}$	3.45	1.60	0.24	0.09	0.16	0.69	0.17	16.20	0.38	0.22	1.02	0.72	0.37	0.30	0.09	1.00
847231	S	0.17	0.24	0.04	0.02	0.02	0.07	0.01	0.84	0.07	0.03	0.12	0.18	0.06	0.04	0.01	0.00
847220	$\bar{X}$	4.69	2.54	0.31	0.10	0.26	0.97	0.23	17.20	0.56	0.31	1.11	0.85	0.44	0.53	0.14	1.00
	S	0.57	0.26	0.03	0.02	0.02	0.03	0.03	2.39	0.08	0.03	0.13	0.17	0.05	0.07	0.01	0.00
<u><i>P. montezumensis</i></u>	$\bar{X}$	3.92	1.82	0.28	0.09	0.21	0.99	0.23	15.80	0.59	0.29	1.09	0.92	0.49	0.32	0.13	3.60
847233	S	0.26	0.40	0.04	0.02	0.02	0.18	0.02	0.84	0.04	0.03	0.12	0.13	0.02	0.07	0.01	0.55
<u><i>P. solus</i></u>	$\bar{X}$	3.14	1.38	0.20	0.07	0.17	0.72	0.14	12.60	0.34	0.20	0.40	0.27	0.23	0.18	0.07	2.00
850290	S	0.23	0.23	0.03	0.01	0.03	0.09	0.02	1.14	0.03	0.01	0.05	0.09	0.03	0.03	0.01	0.00
<u><i>P. simplex</i></u>	$\bar{X}$	3.14	0.89	0.22	0.09	0.21	0.93	0.16	17.40	0.37	0.22	0.67	0.52	0.25	0.38	0.10	1.00
847236	S	0.80	0.32	0.05	0.02	0.03	0.04	0.03	1.14	0.04	0.04	0.08	0.13	0.04	0.12	0.01	0.00
<u><i>P. confluentis</i></u>	$\bar{X}$	5.52	2.53	0.35	0.08	0.26	1.24	0.21	19.40	0.55	0.31	1.24	0.83	0.49	0.33	0.15	5.40
847234	S	0.38	0.28	0.02	0.03	0.03	0.08	0.06	1.82	0.06	0.02	0.14	0.12	0.09	0.04	0.07	0.55
<u><i>P. sarcarlosensis</i></u>	$\bar{X}$	3.34	0.89	0.23	0.07	0.20	0.96	0.18	18.00	0.56	0.26	1.09	0.78	0.44	0.72	0.19	1.80
847226	S	0.32	0.22	0.04	0.01	0.03	0.06	0.02	2.00	0.10	0.05	0.12	0.11	0.03	0.08	0.03	0.84
847217	$\bar{X}$	2.64	0.71	0.24	0.06	0.14	0.74	0.15	14.00	0.46	0.20	0.67	0.56	0.34	0.56	0.16	2.00
	S	0.41	0.07	0.03	0.02	0.03	0.13	0.02	1.58	0.04	0.03	0.09	0.12	0.07	0.06	0.02	0.00
<u><i>P. cochisi</i></u>	$\bar{X}$	2.50	0.94	0.17	0.06	0.15	0.58	0.12	13.40	0.28	0.17	0.45	0.45	0.23	0.27	0.09	2.00
847218	S	0.24	0.05	0.01	0.01	0.02	0.04	0.02	1.34	0.01	0.03	0.03	0.03	0.02	0.03	0.01	0.00
<u><i>P. thompsoni</i></u>	$\bar{X}$	5.47	2.96	0.20	0.08	0.29	1.12	0.23	19.00	0.37	0.26	0.47	0.41	0.42	0.46	0.15	1.00
847238	S	0.89	0.39	0.04	0.01	0.05	0.15	0.04	0.71	0.10	0.04	0.11	0.11	0.08	0.06	0.02	0.00
847221	$\bar{X}$	3.80	2.01	0.26	0.07	0.20	0.93	0.19	16.40	0.3	0.22	0.69	0.56	0.32	0.27	0.08	1.00
	S	0.27	0.31	0.02	0.02	0.04	0.09	0.02	0.90	0.03	0.04	0.08	0.10	0.06	0.05	0.02	0.00
847228	$\bar{X}$	5.12	2.14	0.30	0.09	0.33	1.14	0.24	17.60	0.34	0.25	0.50	0.46	0.28	0.39	0.10	1.00
	S	0.58	0.19	0.07	0.01	0.04	0.20	0.06	1.52	0.03	0.03	0.06	0.05	0.09	0.05	0.02	0.00
847227	$\bar{X}$	3.64	1.35	0.24	0.08	0.26	0.87	0.19	15.60	0.25	0.17	0.82	0.66	0.28	0.29	0.13	1.00
	S	0.35	0.18	0.05	0.01	0.04	0.12	0.01	1.34	0.02	0.03	0.07	0.04	0.04	0.04	0.01	0.00

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