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New species and records of springsnails (Caenogastropoda: Cochliopidae: *Tryonia*) from the Chihuahuan Desert (Mexico and United States), an imperiled biodiversity hotspot

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Abstract

We describe 13 new, narrowly localized species of the aquatic gastropod genus *Tryonia* from springs in the Chihuahuan Desert (Chihuahua and Texas): *T. allendae* **n. sp.**, *T. angosturae* **n. sp.**, *T. chuviscarae* **n. sp.**, *T. contrerasi* **n. sp.**, *T. julimesensis* **n. sp.**, *T. metcalfi* **n. sp.**, *T. minckleyi* **n. sp.**, *T. molinae* **n. sp.**, *T. oasiensis* **n. sp.**, *T. ovata* **n. sp.**, *T. peregrina* **n. sp.**, *T. taylori* **n. sp.** and *T. zaragozae* **n. sp.**. These novelties are distinguished by shell and other morphologic characters and are well differentiated genetically from each other and from other congeners (mtCOI sequence divergence ≥1.9%). We also provide two new records for *T. seemani* (Frauenfeld, 1863), which is distributed near the southern limit of the Chihuahuan Desert (Durango State) and previously had been thought to be possibly extinct. Bayesian analysis of a mtCOI dataset resolved two clades composed of novelties described herein: one (containing four species) is distributed in several drainages in Chihuahua, the other (containing three species) is a local species flock in the Río Conchos basin (also in Chihuahua) that lives in the warmest waters yet recorded for *Tryonia* (41–44°C). (The phylogenetic relationships of the other new species were not well supported.) Both of these clades contain sympatric species pairs; co-occurrence of *Tryonia* congeners previously had been reported only in Ash Meadows (southern Nevada). Some of the species described herein are from previously unsurveyed localities and may help delineate new areas of endemism within the Chihuahuan Desert. One of the new species (*T. julimesensis*) became extinct between 1991 and 2001 and another (*T. oasiensis*) disappeared from its single known locality shortly after it was first discovered in 2009 and also may be extinct. The other species treated herein are at risk of extirpation owing to the declining extent and condition of their unprotected habitats.

Key words: springs, Mexico, Texas, gastropods, mitochondrial DNA, endemism, taxonomy, conservation

Introduction

The Chihuahuan Desert (Mexico and United States) is considered a globally significant freshwater biodiversity hotspot based on its large endemic biota, which includes a flagship assemblage in the Cuatro Cienegas basin and numerous species that are scattered among other insular habitat patches within this large region (Olson *et al*. 1998, Dinerstein *et al*. 2001, Olson & Dinerstein 2002). Freshwater habitats are rapidly disappearing from the Chihuahuan Desert owing to groundwater withdrawal, urbanization and other anthropogenic activities, resulting in the decline or extinction of many endemic species (e.g., Williams *et al*. 1985, Contreras-Balderas *et al*. 2003, Howells 2003). Viewed within this context, the still incomplete process of discovery and taxonomic description of regional aquatic biota (as a necessary prelude to implementation of conservation initiatives) may be likened to a race against time. Here we contribute to the inventory of this remarkable biota by describing new species and records of narrowly localized springsnails from the region.

The genus *Tryonia* (Caenogastropoda: Cochliopidae) is composed of tiny, narrow-shelled snails which brood their young in the female genital duct; have glandular, papillae-like lobes on the edges of the penis; and typically live in springs. This genus was recently revised by Hershler (2001), who recognized 16 species in western North America, one species in Florida, and one species in Guatemala. One additional (western North American) species,

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Hydrobia seemani Frauenfeld, 1863, was subsequently transferred to the genus by Hershler *et al*. (2002a). *Tryonia* is diagnosed by an unique character state (shared within the Cochliopidae), the insertion of the visceral vas deferens into the postero-dorsal edge of the prostate gland, and is further distinguished from a suite of closely similar genera (*Chorrobius*, *Mexipyrgus*, *Minckleyella*, *Pseudotryonia*) by a unique combination of female genitalic character-states (Hershler 2001, Hershler *et al*. 2011). *Tryonia* has also been delineated as a clade (sister to *Mexipyrgus*) based on mtCOI data (e.g., Hershler *et al*. 1999a), although the results of one recent analysis suggest that it may be paraphyletic relative to the recently described monotypic Mexican genus *Minckleyella* (Hershler *et al*. 2011). *Tryonia* species differ principally in size, shell shape and sculpture, and number and arrangement of penial papillae (Taylor 1987, Hershler 2001). They are also well differentiated genetically, with pairwise sequence divergences for mtCOI ranging from 1.8% to 7.2% (Hershler *et al*. 1999a; data from 16 of 19 currently recognized congeners).

In western North America, *Tryonia* ranges south to the Chihuahuan Desert where four congeners are distributed near the northern and southern limits of this large region. In the early 1970's one of us (J.J.L.) collected undescribed *Tryonia*-like snails from a series of springs in the (Mexican) Chihuahuan Desert during the course of aquatic biotic surveys led by Wendell L. Minckley (Arizona State University).The first author and J.J.L. made further collections of these snails and discovered additional such novelties during several excursions to the Chihuahuan Desert beginning in 1990. Previously, we described five of these species which proved to be members of other, anatomically distinctive cochliopid lineages (Hershler *et al*. 2002b, 2011). Here we describe, based on morphologic and molecular (mtCOI) evidence, 13 new species of *Tryonia* from these collections (11 from Chihuahua, two from Texas) and provide two new records for a previously described regional congener, *T. seemani*, which had not been collected for more than 100 years and was thought to be possibly extinct (Thompson 2008). (Descriptions of 4–5 additional new congeners from Chihuahua for which we do not have molecular data will be published in a subsequent paper.) We briefly discuss our findings as they relate to the diversification of *Tryonia* in western North America. We also discuss the conservation status of the species treated herein.

Material and methods

The geographic locations of the species treated herein and other congeners that are distributed in the Chihuahuan Desert are shown in Figure 1. Mexican place names were obtained from 1:50,000 topographic sheets published by the Instituto Nacional de Estadistica Geografia e Informatica (INEGI). Morphological study was based on specimens that were relaxed with menthol crystals and fixed in dilute formalin prior to preservation in 70% ethanol. Snails used for mtDNA sequencing were preserved in 90% ethanol in the field. Types and other voucher material from this study were deposited in the National Museum of Natural History (USNM) collection. Relevant material from the Bell Museum of Natural History (BellMNH); Natural History Museum, London (NHMUK); and University of Texas at El Paso Centennial Museum (UTEP) was also examined during the course of this study. Unless otherwise specified, paratype lots of the new species contain large (>100 specimens) numbers of dry shells and alcohol preserved specimens.

Genomic DNA was extracted from entire snails using a CTAB protocol (Bucklin 1992). A 658-bp segment of cytochrome *c* oxidase subunit I (COI) was amplified and sequenced with primers LCO1490 and HCOI2198 (Folmer *et al*. 1994) following the protocols of Liu *et al*. (2003). Sequences were determined for both strands and then edited and aligned using Sequencher™ version 4.10. We sequenced one to seven specimens from each sample of the species treated herein. In preliminary molecular phylogenetic analyses that included a large number of cochliopid taxa the new sequences were consistently nested within a *Tryonia* + *Minckleyella* clade that in turn was sister to *Mexipyrgus*. The final analysis thus included only the species reported herein, all other species of *Tryonia* for which mtCOI sequences were available (16 of 19 species), and *Minckleyella balnearis* Hershler *et al*., 2011. Note that we recognize anatomically divergent *Minckleyella* as distinct from *Tryonia* because it was positioned outside of the *Tryonia* clade in a subset of recently published molecular phylogenetic analyses (Hershler *et al*. 2011). A taxonomic resolution of *Tryonia* is beyond the scope of this paper. *Mexipyrgus carranzae* Taylor, 1966 was used as the outgroup. Sample information, GenBank accession numbers, and ranges of pairwise COI sequence divergence for *Tryonia* species are in Table 1.

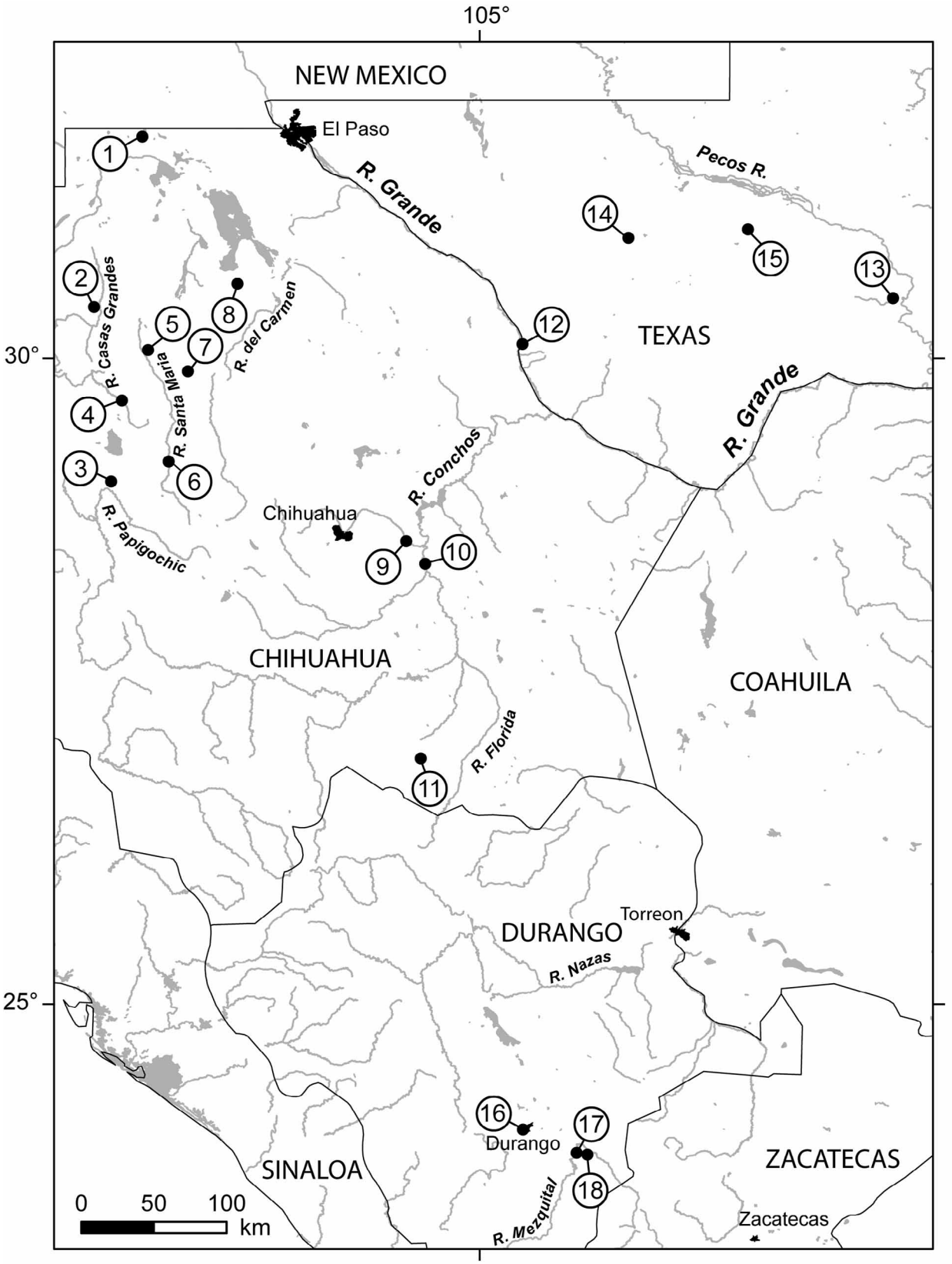

FIGURE 1. Map showing the distribution of *Tryonia* species in the Chihuahuan Desert. 1. *Tryonia hertleini*, Las Palomas. 2. *Tryonia peregrina* **sp. nov.**, Ojo Vareleño, northwest of Casas Grandes. 3. *Tryonia peregrina* **sp. nov.**, Yepomera. 4. *Tryonia zaragozae* **sp. nov.**, northeast of Ignacio Zaragoza. 5. *Tryonia angostura* **sp. nov.**, *T. ovata* **sp. nov.**, south of Galeana. 6. *Tryonia molinae* **sp. nov.**, El Molino. 7. *Tryonia taylori* **sp. nov.**, vicinity of Rancho Ojo Caliente. 8. *Tryonia contrerasi* **sp. nov.**, vicinity of Rancho Nuevo. 9. *Tryonia chuviscarae* **sp. nov.**, *T. minckleyi* **sp. nov.**, Balneario de San Diego de Alcala. 10. *Tryonia julimesensis* **sp. nov.**, south of Julimes. 11. *Tryonia allendae* **sp. nov.**, southwest of Talamantes. 12. *Tryonia metcalfi* **sp. nov.**, La Cienega, south of Candelaria. 13. *Tryonia oasiensis* **sp. nov.**, Caroline Spring, Oasis Ranch. 14. *Tryonia cheatumi*, Phantom Lake Spring. 15. *Tryonia circumstriata*, Diamond Y Draw. 16. *Tryonia seemani*, Ojo de Agua del Obispo, Durango City. 17. *Tryonia seemani*, Nombre de Dios. 18. *Tryonia seemani*, Amado Nervo.

TABLE 1. Specimen codes, localities, and GenBank accession numbers. [a]Hershler *et al*. 1999a; [b]Hershler *et al*. 1999b; [c]Hershler *et al*. 2005; [d]Hershler *et al*. 2011. COI divergence: pairwise sequence divergence among *Tryonia* species.

Species	Code	Locality	Accession number	COI divergence
T. allendae **sp. nov.**		El Ojito, southwest of Talamantes, Chihuahua	AY803039[c]	1.9–7.6%
T. angosturae **sp. nov.**		Ojos de Arrey, south of Galeana, Chihuahua	AY803037[c]	1.9–8.1%
T. chuviscarae **sp. nov.**	Try4	Balneario de San Diego de Alcala, Chihuahua	JF776782 JF776783	2.7–8.4%
	Try10		JF776788	
T. contrerasi **sp. nov.**	Try12	Ojo del Apache south of Rancho Nuevo, Chihuahua	JF776795 JF776796	3.6–7.9%
	Try13	Ojo Carbonero, southeast of Rancho Nuevo, Chihuahua	JF776793 JF776794	
T. julimesensis **sp. nov.**		Unnamed springs south-southeast of Julimes, Chihuahua	JF776789	2.7–8.2%
T. metcalfi **sp. nov.**	Try9	Unnamed seeps in La Cienega, Presidio County, Texas	JF776784 JF776785	5.8–8.9%
T. minckleyi **sp. nov.**	Try3	Balneario de San Diego de Alcala, Chihuahua	JF776780 JF776781	6.2–8.9%
T. molinae **sp. nov.**	Try5	Unnamed spring in northern part of El Molino, Chihuahua	JF776800 JF776801 JF776802 JF776803	4.3–7.9%
T. oasiensis **sp. nov.**	Try1	Caroline Spring, Terrell County, Texas	JF776797 JF776798 JF776799	4.3–8.3%
T. ovata **sp. nov.**		Ojos de Arrey, south of Galeana, Chihuahua	JF776787	3.7–7.9%
T. peregrina **sp. nov.**	Try2	Ojo Vareleño, northwest of Casas Grandes, Chihuahua	AY803035[c] AY803036[c] JF776786	1.9–8.4%
	Try6	Unnamed spring on east side of Yepomera, Chihuahua	JF776804 JF776805 JF776806 JF776807	
T. seemani (Frauenfeld)	Try10	Unnamed spring on west side of Nombre de Dios, Durango	JF786790 JF786791	2.6–6.6%
	Try11	Unnamed spring in Amado Nervo, southwest of Villa Union, Durango	JF786792	
T. taylori **sp. nov.**	Try7	Ojo Caliente at Rancho Ojo Caliente, south of Highway 10, Chihuahua	JF776808 JF776809 JF776810 JF776811 JF776812	4.2–8.1%
.	Try8	El Ojo de Servin, west of Rancho Ojo Caliente Chihuahua	JF776813 JF776814 JF776815 JF776816 JF776817 JF776818 JF776819	
T. zaragozae **sp. nov.**		Unnamed springs north-east of Ignacio Zaragoza, Chihuahua	AY803038[c]	1.9–7.7%
T. aequicostata (Pilsbry)		Lake Eustis, Lake County, Florida	AF129301[a]	2.7–6.7%
T. angulata Hershler & Sada		Big Spring, Ash Meadows, Nye County, Nevada	AF061764[b]	3.3–7.5%

..... continued

TABLE 1 (continued)

Species	Code	Locality	Accession number	COI divergence
T. cheatumi (Pilsbry)		Phantom Lake Spring outflow, Jeff Davis County, Texas	AF129305[a]	4.4–7.4%
T. circumstriata (Leonard & Ho)		Diamond Y Spring, Pecos County, Texas	AF129306[a]	2.7–7.1%
T. clathrata Stimpson		Warm Springs, Moapa Valley, Clark County, Nevada	AF061767[b]	4.0–7.4%
T. elata Hershler & Sada		Spring, Point of Rocks, Ash Meadows, Nye County, Nevada	AF061766[b]	2.3–7.9%
T. ericae Hershler & Sada		North Scruggs Spring, Ash Meadows, Nye County, Nevada	AF061768[b]	2.3–7.3%
T. gilae Taylor		Tom Niece Spring, Graham County, Arizona	AF129309[a]	4.2–8.4%
T. imitator (Pilsbry)		Moro Cojo Slough, Moss Landing, Monterey County, California	AF061770[b]	1.8–7.1%
T. margae Hershler		Grapevine Springs, Death Valley, Inyo County, California	AF061771[b]	1.9–7.8%
T. monitorae Hershler		Unnamed spring, Potts Ranch, Monitor Valley, Nye County, Nevada	AF129326[a]	1.9–7.8%
T. porrecta (Mighels)		"Oasis Spring," Salton Trough, Riverside County, California	AF061772[b]	4.9–7.7%
T. quitobaquitae Hershler		Quitobaquito Spring, Pima County, Arizona	AF129315[a]	3.7–7.9%
T. rowlandsi Hershler		Grapevine Springs, Death Valley, Inyo County, California	AF061775[b]	3.8–6.5%
T. salina Hershler		Unnamed spring, Cottonball Marsh, Death Valley, Inyo County, California	AF061776[b]	1.8–7.0%
T. variegata Hershler		Devils Hole, Ash Meadows, Nye County, Nevada	AF061778[b]	2.9–8.2%
Mexipyrgus carranzae Taylor		Mojarral West Laguna, Cuatro Cienegas basin, Coahuila	AF129325[a]	
Minckleyella balnearis Hershler *et al*.	1	Ojo de Dolores, southwest of Jimenez, Chihuahua	HM149773[d]	
	2		HM149774[d]	

Sequence divergences (uncorrected p distance) within and between species were calculated using MEGA4 (Tamura *et al*. 2007), with standard errors estimated by 1000 bootstrap replications with pairwise deletion of missing data. Base compositional differences were first evaluated using the X^2 test. MrModeltest 2.3 (Nylander 2004) was used to obtain an appropriate substitution model (using the Akaike Information Criterion) and parameter values for the analyses. Phylogenetic relationships were inferred by Bayesian analysis using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Three short runs were first conducted using the default random tree option to determine when the log-likelihood sum reached a stable value (by plotting the log-likelihood scores of sample points against generation time). Metropolis-coupled Markov chain Monte Carlo simulations were then run with four chains using the model selected through MrModeltest for 1,000,000 generations, and Markov chains were sampled at intervals of 10 generations to obtain 100,000 sample points. At the end of the analysis, the average standard deviation of split frequencies was around 0.01, indicating that the runs had reached convergence. The sampled trees with branch lengths were used to generate a 50% majority rule consensus tree with the first 5000 trees, equal to 50,000 generations, removed to ensure that the chain sampled on a stationary portion.

Series of large, adult females were used for shell measurements and illustrations, unless indicated otherwise. Whorl counts refer to the entire shell. Sexual dimorphism in shells, which is commonly observed in *Tryonia* species (Taylor 1987), could not be quantified owing to the generally small sample sizes. Variation in the number of cusps on the radular teeth (n = 5 for each sample) was assessed using the method of Hershler *et al*. (2007). Other methods of morphological study and descriptive terminology are those of Taylor (1987), Hershler (2001) and Hershler *et al*. (2002a). Shell data were analyzed using Systat for Windows 11.00.01 (SSI 2004). Bivariate (scatter) plots of pertinent shell ratios were also generated to help assess differentiation among congeners.

We used an evolutionary lineage concept in describing new species for those snails that are morphologically diagnosable as well as phylogenetically independent and substantially divergent genetically (Hershler *et al*. 2007). Inasmuch as the principal goal of our paper is to delimit species, we have only provided brief taxonomic descrip-

tions which focus on those aspects of morphology that have proven most useful in previous such studies of *Tryonia* (Taylor 1987, Hershler 2001). Internal anatomy was studied only to determine whether the species treated herein conform to *Tryonia* as currently diagnosed (Hershler 2001).

Results

Molecular analysis

Forty specimens were sequenced. New sequences were deposited in GenBank under accession numbers JF776780–JF776819 (Table 1). A total of 658 bp of COI was analyzed, of which 201 sites (35%) were variable and 156 (23.7%) were parsimony-informative. Average base frequencies were 24.8% A, 39.4% T, 17.3% C, 18.5% G. There was no significant base frequency bias among species (X^2 = 28.2, df = 189, P = 1.00).

MrModeltest selected the GTR + I + G model as the best fit for the dataset using the Akaike Information Criterion. The optimized parameters were A=0.2762, C=0.1474, G=0.1570, T=0.4194; Rmat = {0.3012 23.5625 0.1124 3.0489 15.2104}; shape of gamma distribution = 1.2379; and proportion of invariable sites = 0.6132. The new sequences reported herein formed 14 genetically differentiated (COI divergence ≥ 1.9%) and morphologically diagnosable lineages in the Bayesian tree (Fig. 2), only one of which can be referred to a previously described spe-

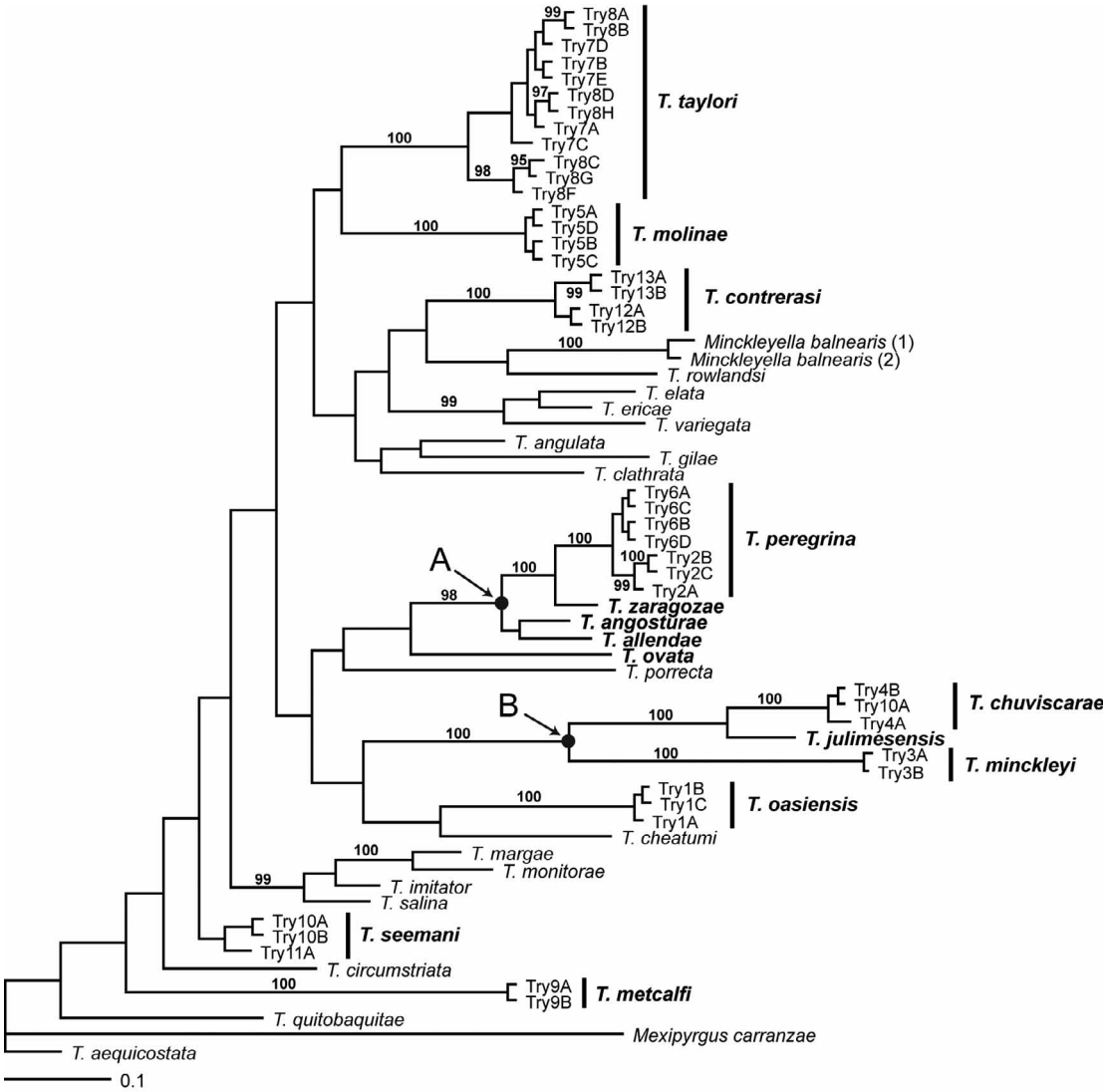

FIGURE 2. Bayesian tree based on the COI dataset. Posterior probabilities are provided when ≥95%. The names of the species treated herein are in bold face. Terminals and specimen codes are labeled as in Table 1. The two well supported clades composed of new species described herein are labeled A–B.

cies (*T. seemani*). The other 13 lineages are described below as new species. Two lineages containing novelties described herein were strongly supported in the Bayesian tree: one contains four species that are distributed in several drainages in Chihuahua (Fig. 2, clade A), the other (clade B) contains three species from the Río Conchos basin (also in Chihuahua). The relationships of the other six new species (and *T. seemani*) were not well resolved.

Systematics

Family Cochliopidae Tryon, 1866
Genus *Tryonia* Stimpson, 1865

Type Species: *Tryonia clathrata* Stimpson, 1865 (by original designation).

Diagnosis: (From Hershler 2001: 3)

The new species described below are referred to *Tryonia* on the basis of the insertion of the posterior vas deferens into the postero-dorsal edge of the prostate gland and details of female reproductive anatomy (young brooded in thin-walled albumen gland, bursa copulatrix and seminal receptacle present, sperm duct coiled and opening to bursal duct behind pallial wall; e.g., *T. peregrina*, described below, Fig. 3). They also closely conform to the genus in all other respects.

Tryonia peregrina sp. nov.

(Figs 3, 4A–D, H–I, M–O, 5A)

Tryonia sp.—Williams *et al*. 1985: 50 (reference to Yepomera populations).
Tryonia n. sp. 1.—Hershler *et al*. 2005: 1757 (COI sequences).

Types. Holotype, USNM 874032, Ojo Vareleño, 2.4 km northwest of Casas Grandes, Chihuahua, 30º24'1.95" N, 107º59'7.8" W, leg. J.J.L. and P. Hines, 16/ix/1990. Paratypes (from same lot), USNM 1153677.

Etymology. The species name is derived from the Latin adjective *peregrinus*, meaning wandering, and refers to the distribution of this species in the Río Casas Grandes (interior) and Río Papigochic (Pacific) drainages.

Referred material. CHIHUAHUA. USNM 892114, topotypes, leg. R.H and J.J.L., 6/xii/1998. USNM 873288, USNM 873299, spring on east side of Yepomera, 29º3'19.55" N, 107º50'33.82" W, leg. J.J.L., 15/iv/1973. USNM 1138233, *ibid.*, leg. J.J.L., 11/iii/2010. USNM 873197, spring on west side of creek in northwest part of Yepomera, 29º3'55" N, 107º51'29" W (estimated), leg. J.J.L., 10/xi/1980. USNM 873269, spring run at Rancho El Ojito, 29º3'58" N, 107º51'13" W (estimated), leg. J.J.L., 16/iv/1973.

Diagnosis. Shell medium-sized, conic; penis having two distal papillae on the inner edge and a basal papilla both on the inner and outer edges. Differs from *T. zaragozae* (described next), which is the only other congener that is distributed in the Río Casas Grandes or Río Papigochic drainages, in its more convex and weaker sculptured teleoconch whorls, more rounded adapical end of the shell aperture, umbilicate shell, and smooth inner side of operculum. Differs from *T. hertleini* (Drake, 1956), an apparently extinct species (Hershler 2001) which was distributed near the terminus of the Río Casas Grandes drainage (Fig. 1, locality 1), in its larger size (4.08 vs. 3.08 mm mean shell height, t-test, t=-5.916, df = 8.3, $P<0.01$; n=5 for *T. hertleini*), larger size and number of cusps on the inner marginal radular teeth, smaller basal papilla on the inner edge of the penis, and in having a papilla on the outer edge of the penis.

Description. Shell (Fig. 4A–D) up to 5.9 mm tall, large females having 4.75–7.5 whorls, spire height 150–200% width of shell, male shells smaller than those of females. Teleoconch whorls medium to highly convex, evenly rounded with impressed sutures. Aperture usually rounded, sometimes weakly angled adapically. Parietal lip complete, adnate or slightly disjunct, umbilicus narrow. Outer lip usually orthocline, sometimes weakly opisthocline, sometimes weakly sinuate. Sculpture of strong growth lines and weak spiral threads. Periostracum dark brown.

Shell measurements (mean in parentheses): height 3.45–4.80 mm (4.08), width 1.56–1.90 mm (1.71), body whorl height 1.83–2.29 mm (2.06), body whorl width 1.46–1.82 mm (1.64), aperture height 1.06–1.29 mm (1.18), aperture width 0.86–1.06 mm (0.94), total number of whorls 5.75–6.50 (6.12) (USNM 1153677, $n = 13$).

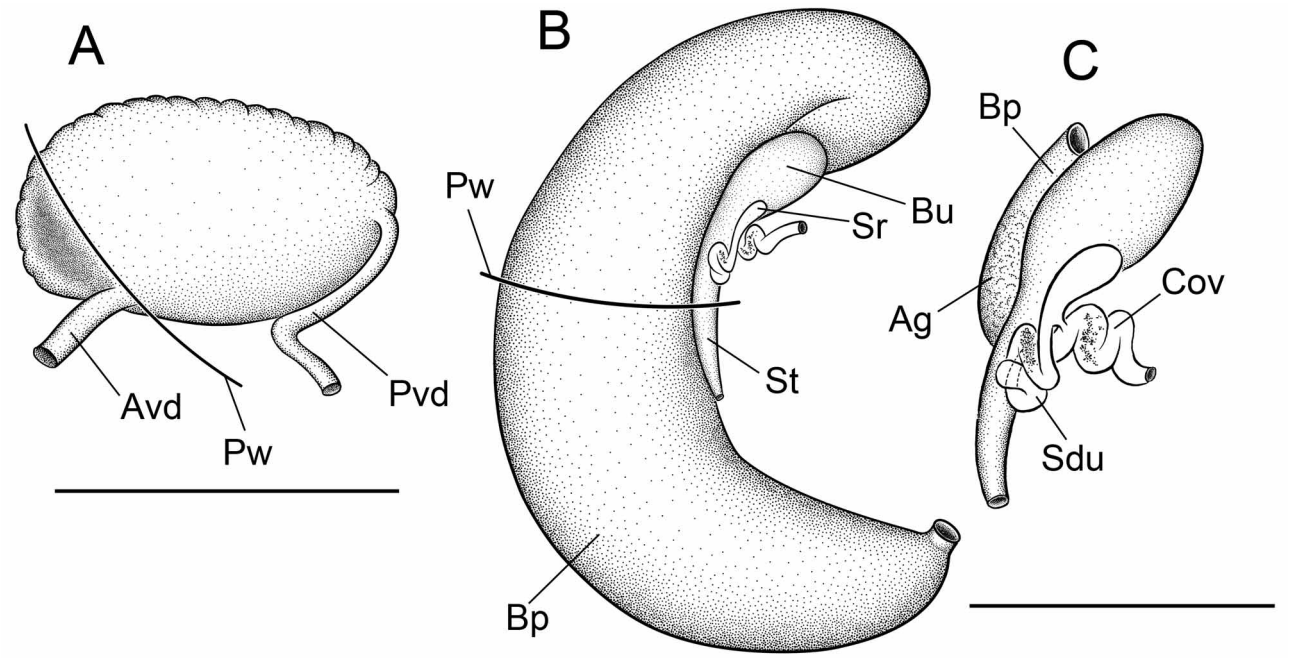

FIGURE 3. *Tryonia peregrina* **sp. nov**. A. Prostate gland (viewed from left side), USNM 1153677. B–C. Female brood pouch and associated structures (B, viewed from left side, embryos not shown; C, close-up of sperm pouches and associated ducts), USNM 1153677. Scale bars A = 250 µm, B–C = 500 µm. Ag = albumen gland, Avd = anterior section of vas deferens, Bp = brood pouch, Bu = bursa copulatrix, Cov = coiled oviduct, Pvd = posterior section of vas deferens, Pw = posterior wall of pallial cavity; Sdu, sperm duct; Sr, seminal receptacle; St, sperm tube.

Measurements of holotype: height 3.94 mm, width 1.57 mm, body whorl height 1.96 mm, body whorl width1.51 mm, aperture height 0.92 mm, aperture width 0.40 mm, 6.25 whorls.

Inner and outer sides of operculum smooth (Fig. 4H-I). Radula (Fig. 4M-O): dorsal edge of central teeth concave, basal tongue rounded or V-shaped, median cusps elongate, distally pointed, parallel-sided proximally, lateral cusps four–six, basal cusps one–three, usually two (innermost larger; Fig. 4N). Lateral teeth having two–three cusps on inner and four–five cusps on outer side, length of outer wing about 200% width of cutting edge, central cusp pointed or hoe-shaped (Fig. 4O). Inner marginal teeth with 21–33 cusps, outer marginal teeth with 29–42 cusps. Radula data are from USNM 873288, USNM 1153677.

Animal darkly pigmented. Penis (Fig. 5A) having two distal and one basal papillae on inner edge and a slightly enlarged basal papilla on outer edge (40 of 46 specimens from two samples); one specimen differed in having a single distal papilla on inner edge, one specimen had three distal papillae along the inner edge, and three specimens lacked a papilla on the outer edge. Basal papilla along inner edge often small. Distal bulb of penis expanded laterally on inner side, black; stylet small. Penial duct undulating along most of length. Penial data are from USNM 873299, USNM 1153677.

Distribution and habitat. *Tryonia peregrina* is distributed in a single locality in both the Río Casas Grandes and Río Papigochic drainages (Fig. 1, localities 2–3). The type locality, Ojo Vareleño, consists of numerous small springs that form a large cienega (Fig. 6A). Some of these springs have been developed for domestic water usage while others have been diverted into an earthen canal that courses southwest towards Casas Grandes. *Tryonia peregrina* was found in intermediate elevation springs within the cienega (in detritus) and in the canal; snails were especially abundant in the latter at a small ranch, Chulavista, about 1.0 km downflow from the spring sources. A *Tryonia*-like species, *Eremopyrgus elegans* Hershler *et al*., 2002b is distributed in the upper portion of this cienega (Hershler *et al*. 2002b). The water temperature of these habitats is about 27°C. *Tryonia peregrina* is also distributed in a large spring on the east side of Yepomera (Fig. 6B) that is referred to locally as El Ojo de Yepomera (Miller *et al*. 2005). In 1973 this snail was found in both the walled headspring (on rocks) and in the outflow (on rocks and on the bases of aquatic vegetation). The site was re-visited in 1998, when the headspring was being developed into a new domestic water system, and *T. peregrina* was not found. However, in 2010 it was abundant (in sand and aquatic vegetation) in the (19°C) outflow; the status of the population in the headspring, which has been transformed into a large pond, is uncertain. In 1973 *T. peregrina* was also found in a small (17°C) spring brook at Ran-

cho El Ojito on the north side of Yepomera, and in an oxbow cienega on the northwest side of the village. Snails were not found at these sites during several subsequent visits to the area; the spring at Rancho El Ojito was dry or capped when visited in 1998.

Remarks. *Tryonia peregrina* was delineated in the Bayesian analysis as a well supported lineage (Fig. 2). The two populations of this species are closely similar in all morphological details; their haplotypes differed by 0.17–0.5%.

***Tryonia zaragozae* sp. nov.**
(Figs 4E–G, J–L, P–R, 5B)

Tryonia n. sp. 2.—Hershler *et al*. 2005: 1757 (COI sequence).

Types. Holotype, USNM 873286, springs ca. 4.8 km north-east of Ignacio Zaragoza along the south side of Highway 5, Chihuahua, 29º39'47.9" N, 107º44'25.8" W, leg. J.J.L. *et al*., 25/viii/1971. Paratypes (from same lot), USNM 873260, USNM 873289, USNM 874120, USNM 1153679.

Etymology. The species name is a geographic epithet referring to the nearby town of Ignacio Zaragoza.

Referred material. CHIHUAHUA. USNM 854942, topotypes, leg. R.H. and J.J.L., 8/xii/1998.

Diagnosis. Shell medium-sized, conic or turriform, apex usually eroded; penis having two distal papillae on inner edge and a basal papilla both on the inner and outer edges. Contrasted with *T. peregrina* above.

Description. Shell (Fig. 4E–G) up to 6.7 mm tall, whorls 6.5–8.75, spire height 150–200% width of shell, sexual dimorphism of shells not obvious. Teleoconch whorls weakly convex to almost flat, evenly rounded or, less frequently, narrowly shouldered, with adpressed sutures. Aperture sharply angled adapically, parietal lip usually incomplete, usually adnate when complete, rarely slightly disjunct, umbilicus absent. Outer lip thin, orthocline or weakly prosocline. Sculpture of strong growth lines and well developed spiral threads (Fig. 4L). Periostracum tan.

Shell measurements (mean in parentheses): height 3.85–4.65 mm (4.20), width 1.60–1.78 mm (1.69), body whorl height 2.10–2.41 mm (2.21), body whorl width 1.53–1.67 mm (1.60), aperture height 1.23–1.41 mm (1.31), aperture width 0.91–1.08 mm (0.99), total number of whorls 6.50–7.25 (6.78) (USNM 1153679, n = 15).

Measurements of holotype: height 4.39 mm, width 1.68 mm, body whorl height 2.30 mm, body whorl width 1.60 mm, aperture height 1.35 mm, aperture width 1.01 mm, 7.25 whorls.

Edges of last operculum whorl strongly frilled on outer side (Fig. 4J); muscle attachment scar margins somewhat thickened on inner side of operculum (Fig. 4K). Radula (Fig. 4P-R): dorsal edge of central radular teeth concave, basal tongue rounded or V-shaped, median cusps elongate, distally pointed, parallel-sided proximally, lateral cusps five–six, basal cusps two–three (innermost larger) (Fig. 4Q). Lateral teeth having two–three cusps on inner and four–six cusps on outer side, length of outer wing 175–200% width of cutting edge, central cusp pointed (Fig. 4R). Inner marginal teeth with 24–35 cusps, outer marginal teeth with 30–40 cusps. Radula data are from USNM 1153679.

Animal darkly pigmented. Penis (Fig. 5B) having two distal papillae on inner edge and a basal papilla both on the inner and outer edges (30 of 30 specimens). Papilla on outer edge sometimes very small. Distal bulb of penis expanded laterally on inner side, lightly pigmented; stylet small. Penial duct undulating for most of length. Penial data are from USNM 1153679.

Distribution and habitat. *Tryonia zaragozae* is known only from its type locality, a large (ca. 0.01 km^2) cienega and spring system (Fig. 6C) in the upper Río Casas Grandes drainage (Fig. 1, locality 4). Snails were collected (on gravel and on soft substrates) from several springs and bogs (29–30°C) within this cienega. This habit has been severely degraded by overgrazing in recent years, although one of the larger head springs is now fenced (first noted in 1998).

***Tryonia ovata* sp. nov.**
(Figs 5C, 7A–B, F–G, J–L)

Types. Holotype, USNM 873264, Ojos de Arrey, western-most head spring, south of Galeana, Chihuahua, 30º3'28.3" N, 107º35'26.3" W, leg. J.J.L. *et al*., 25/viii/1971. Paratypes (from same lot), USNM 1153676.

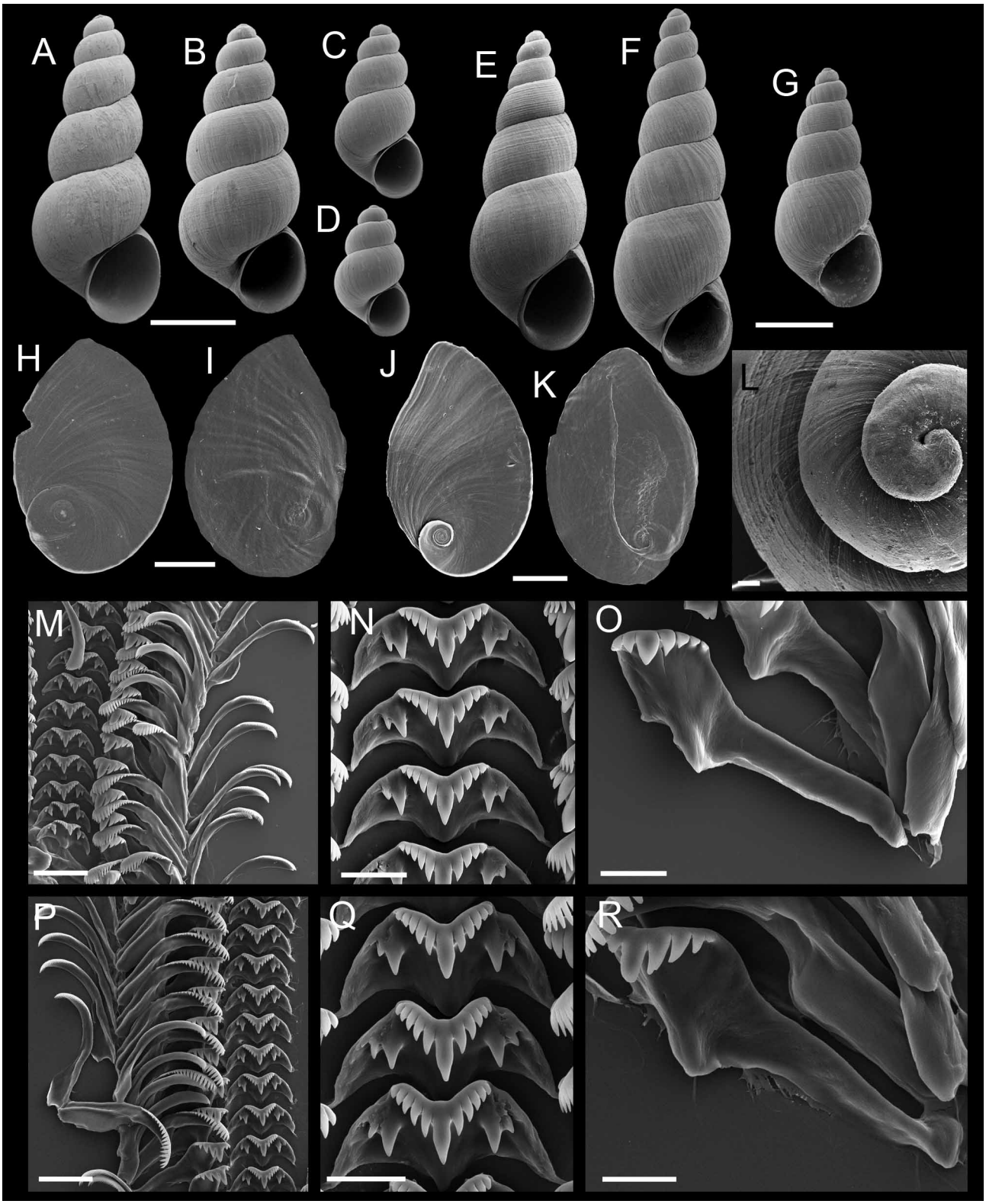

FIGURE 4. *Tryonia peregrina* **sp. nov**. and *Tryonia zaragozae* **sp. nov**. A. Holotype, *T. peregrina*, USNM 874032. B–D. Shells, *T. peregrina*, USNM 873288 (C and D are males). E. Holotype, *T. zaragozae*, USNM 873286. F–G. Male shells, *T. zaragozae*, USNM 874120. H–I. Operculum (outer, inner sides), *T. peregrina*, USNM 1153677. J–K. Operculum (outer, inner sides), *T. zaragozae*, USNM 1153679. L. Apical view of shell showing spiral sculpture on teleoconch, *T. zaragozae*, USNM 1153679. M. Portion of radular ribbon, *T. peregrina*, USNM 1153677. N. Central radular teeth, *T. peregrina*, USNM 1153677. O. Lateral tooth, *T. peregrina*, USNM 1153677. P. Portion of radular ribbon, *T. zaragozae*, USNM 1153679. Q. Central radular teeth, *T. zaragozae*, USNM 1153679. R. Lateral tooth, *T. zaragozae*, USNM 1153679. Scale bars A–G = 1.0 mm, H–L = 250 µm, M, P = 25 µm, N–O, Q–R = 10 µm.

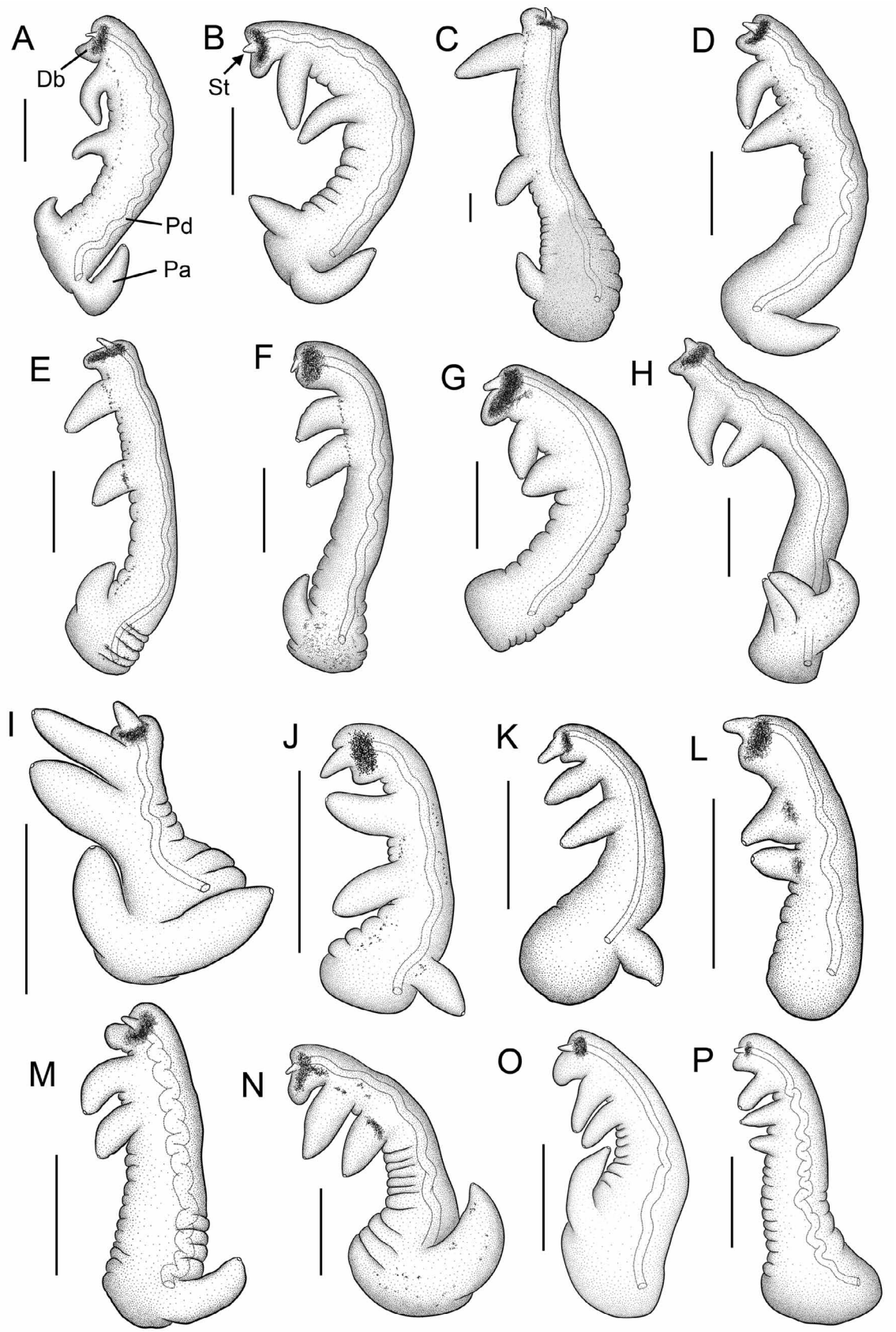

FIGURE 5. Penes. A. *T. peregrina* **sp. nov.**, USNM 1153677. B. *T. zaragozae* **sp. nov.**, USNM 1153679. C. *T. ovata* **sp. nov.**, USNM 1153676. D. T. *angosturae* **sp. nov.**, USNM 874174. E. *T. molinae* **sp. nov.**, USNM 1153674. F. *T. contrerasi* **sp. nov.**, USNM 1153670. G. *T. taylori* **sp. nov.**, USNM 874047. H. *T. taylori* **sp. nov.**, USNM 873252. I. *T. metcalfi* **sp. nov.**, USNM 1153672. J. *T. chuviscarae* **sp. nov.**, USNM 1001756. K. *T. minckleyi* **sp. nov.**, USNM 1153673. L. *T. julimesensis* **sp. nov.**, USNM 1153671. M. *T. allendae* **sp. nov.**, USNM 1153667. N. *T. oasiensis* **sp. nov.**, USNM 1153675. O. *T. seemani*, USNM 874125. P. *T. seemani*, USNM 874123. Scale bars = 250 µm. Db = distal bulb, Pa = papilla, Pd = penial duct, St = stylet.

FIGURE 6. Photographs of habitats of species treated in this paper. A. Ojo Vareleño, Chihuahua, type locality of *T. peregrina* **sp. nov**. (photograph taken on 16/ix/1990). B. Main spring in Yepomera, Chihuahua, *T. peregrina* habitat (18/ix/1990). C. Springs northeast of Ignacio Zaragoza, Chihuaua, type locality of *T. zaragozae* **sp. nov**. (8/xii/1998). D. Western-most head spring, Ojos de Arrey, Chihuahua, type locality of *T. angosturae* **sp. nov**. and *T. ovata* **sp. nov**. (7/xii/1998). E. Spring in northern part of El Molino, Chihuahua, type locality of *T. molinae* **sp. nov**. (26/iv/2010). F. Ojo del Apache, Chihuahua, type locality of *T. contrerasi* **sp. nov**. (14/xii/1998). G. Ojo Carbonero, Chihuahua, *T. contrerasi* habitat (2/iv/1991). H. Outflow of Ojo Caliente, Chihuahua, type locality of *T. taylori* **sp. nov**. (7/xii/1998). I–J. El Ojo de Servin, Chihuahua, *T.taylori* habitat (27-viii-1971, 7/xii/1998, respectively). K. Seeps in La Cienega, Texas, type locality of *T. metcalfi* **sp. nov**. (6/xii/2001). L–M. Balneario de San Diego de Alcala, Chihuahua, type locality of *T. chuviscarae* **sp. nov**. and *T. minckleyi* **sp. nov**. (4/xii/2001). N. Springs southeast of Julimes, Chihuahua, type locality of *T. julimesensis* **sp. nov**. (5/iv/1991). O. El Ojito (outflow), southwest of Talamantes, Chihuahua, type locality of *T. allendae* **sp. nov**. (10/xii/1998). P. Caroline Spring, Oasis Ranch, Texas, type locality of *T. oasiensis* **sp. nov**. (30/iii/2009). Q. Spring in Nombre de Dios, Durango, *T. seemani* habitat (2/ix/1971). R. Spring in Amado Nervo, Durango, *T. seemani* habitat (7/iv/1991).

Referred material. CHIHUAHUA. USNM 854944, topotypes, leg. R.H. and J.J.L., 7/xii/1998. UTEP 977, Ojos de Arrey, ca. 6.4 km south of Galeana, opposite road to Ejido Horcon, leg. A. Metcalf and D.W. Taylor, 3/ix/1969.

Etymology. The species name is an adjective referring to the broad shell of this snail.

Diagnosis. Shell medium-sized, ovate-conic, apex usually eroded; penis having two distal and one basal papillae on the inner edge. Distinguished from sympatric *T. angosturae* by its more convex teleoconch whorls, presence of a basal papilla on the inner edge of the penis and absence of a basal papilla on the outer edge of the penis.

Description. Shell (Fig. 7A–B) up to 3.9 mm tall, whorls 4.0–5.0, spire height 85–110% width of shell, sexual dimorphism of shells not obvious. Teleoconch whorls medium to highly convex, evenly rounded or narrowly shouldered, sutures deeply impressed. Aperture sometimes weakly angled adapically, parietal lip complete, usually adnate, rarely slightly disjunct, umbilicus narrow. Outer lip thin, orthocline or weakly prosocline. Sculpture of strong growth lines. Periostracum tan.

Shell measurements (mean in parentheses): height 2.71–3.06 mm (2.87), width 1.64–1.94 mm (1.74), body whorl height 1.83–2.11 mm (1.92), body whorl width 1.55–1.70 mm (1.61), aperture height 1.04–1.15 mm (1.10), aperture width 0.90–1.08 mm (0.96), total number of whorls 4.00–5.00 (4.45) (USNM 1153676, $n = 5$).

Measurements of holotype: height 2.89 mm, width 1.68 mm, body whorl height 1.92 mm, body whorl width 1.57 mm, aperture height 1.11 mm, aperture width 0.95 mm, 5.0 whorls.

Inner and outer sides of operculum smooth (Fig. 7F–G). Radula (Fig. 7J–L): dorsal edge of central radular teeth concave, basal tongue V-shaped, median cusps elongate, distally pointed, parallel-sided proximally, lateral cusps four–six, basal cusps two–three (innermost larger) (Fig. 7K). Lateral teeth having two–three cusps on inner and three–five cusps on outer side, length of outer wing about 200% width of cutting edge, central cusp pointed (Fig. 7L). Inner marginal teeth with 14–26 cusps, outer marginal teeth with 29–42 cusps. Radula data are from USNM 1153676.

Animal darkly pigmented. Penis (Fig. 5C) having two distal and one basal papillae on inner edge (29/30 specimens); one specimen differed in having a single distal papilla. Distal bulb of penis only slightly expanded laterally on inner side, lightly pigmented; stylet small. Penial duct near straight or undulating basally. Penial data are from USNM 1153676.

Distribution and habitat. *Tryonia ovata* is endemic to Ojos de Arrey, a large spring complex in the Río Santa Maria basin (interior drainage) (Fig. 1, locality 5) that is situated along the northern edge of a hill (Cerro Angostura). These springs have also been referred to as La Angostura and Ojo de los Reyes. *Tryonia ovata* and *T. angosturae* (described next) snail were collected in the (southwestern) portion of the spring complex that has been developed for recreational purposes; there are several additional springs to the northeast that have not been sampled. Both species are found below the main headspring (Fig. 6D; also see Miller *et al*. 2005: plate 68) on *Chara* and *Potamogeton* and in soft sediments under submerged vegetation (26–27°C water temperature).

***Tryonia angosturae* sp. nov.**

(Figs 5D, 7C–E, H–I, M–O)

Tryonia n. sp. 3.—Hershler *et al*. 2005: 1757 (COI sequence).

Types. Holotype, USNM 873259, Ojos de Arrey, western-most head spring, south of Galeana, Chihuahua, 30º3'28.3" N, 107º35'26.3" W, leg. J.J.L. *et al*., 25/viii/1971. Paratypes (from same lot), USNM 873261, USNM 873285, USNM 905267, USNM 1153668.

Etymology. The species name is a geographic epithet referring to a nearby village, La Angostura.

Referred material. CHIHUAHUA. USNM 873268, topotypes, leg. J.J.L., 14/iv/1973. USNM 874250, USNM 874174, *ibid*., leg. J.J.L. and P. Hines, 16/ix/1990. USNM 854943, *ibid*., leg. R.H. and J.J.L., 7/xii/1998. USNM 873293, canal outflow from Ojos de Arrey at Hwy 10, 30º4'11" N, 107º36'15" W, leg. J.J.L., 25/viii/1971. BellMNH 21128, Oja del Rey (sic), leg. D.W. Taylor, 3/ix/1969. BellMNH 21175, east Ojo del Rey (sic), northwest end of Cerro Angostura, leg. D.W. Taylor and A. Metcalf, 3/ix/1969. BellMNH 21174, Ojo del Torreon, northwest end of Cerro Angostura, leg. D.W. Taylor and A. Metcalf, 3/ix/1969.

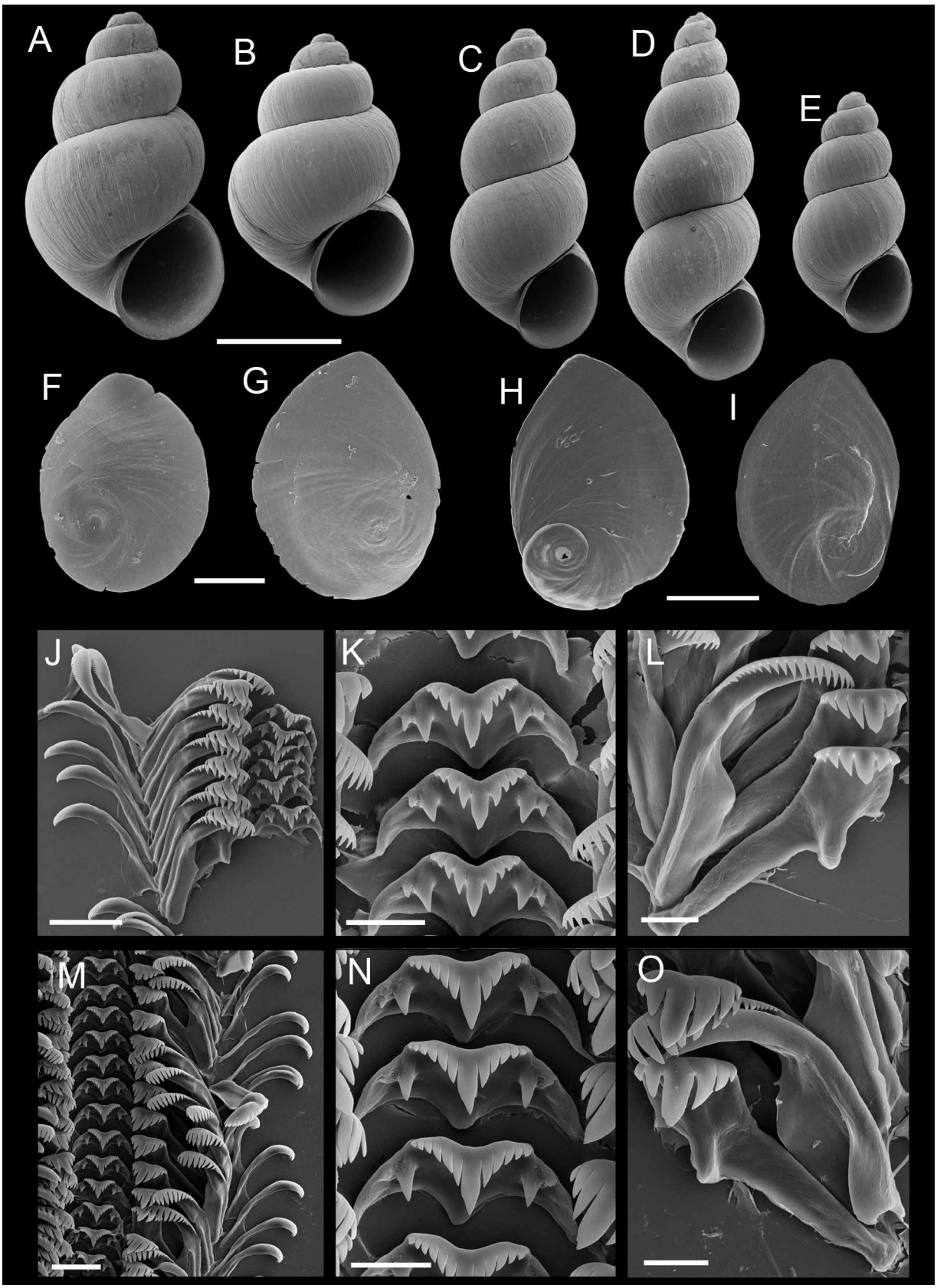

FIGURE 7. *Tryonia ovata* **sp. nov**. and *Tryonia angosturae* **sp. nov**. A. Holotype, *T. ovata*, USNM 873264. B. Male shell, *T. ovata*, UTEP 977. C. Holotype, *T. angosturae*, USNM 873259. D–E. Shells, *T. ovata*, USNM 1153668 (E is a male). F–G. Operculum (outer, inner sides), *T. ovata*, USNM 1153676. H–I. Operculum (outer, inner sides), *T. angosturae*, USNM 1153688. J. Portion of radular ribbon, *T. ovata*, USNM 1153676. K. Central radular teeth, *T. ovata*, USNM 1153676. L. Lateral and inner marginal teeth, *T. ovata*, USNM 1153676. M. Portion of radular ribbon, *T. angosturae*, USNM 1153688. N. Central radular teeth, *T. angosturae*, USNM 1153688. O. Lateral and inner marginal teeth, *T. angosturae*, USNM 115368. Scale bars A–E = 1.0 mm, F–I = 250 µm, J, M = 25 µm, K–L, M–O = 10 µm.

Diagnosis. Shell medium-sized, conic; penis having two distal papillae on the inner edge and a basal papilla on the outer edge. Contrasted with *T. ovata* above. Differentiated from other Río Santa Maria basin congeners by having a basal papilla on the outer edge of the penis.

Description. Shell (Fig. 7C–E) up to 4.9 mm tall, large females having 5.0–8.0 whorls, spire height 85–110% width of shell, male shells smaller than those of females. Teleoconch whorls weak to medium convex, evenly rounded, sutures impressed. Aperture weakly angled adapically, parietal lip usually complete, usually adnate, rarely very slightly disjunct, umbilicus absent. Outer lip thin, weakly prosocline. Sculpture of strong growth lines. Periostracum brown or tan.

Shell measurements (mean in parentheses): height 2.69–3.36 mm (3.01), width 1.16–1.38 mm (1.25), body whorl height 1.41–1.68 mm (1.55), body whorl width 1.13–1.45 mm (1.26), aperture height 0.76–0.89 mm (0.82), aperture width 0.65–0.82 mm (0.72), total number of whorls 5.25–6.75 (5.92) (USNM 1153668, *n* = 15).

Measurements of holotype: height 2.76 mm, width 1.25 mm, body whorl height 1.49 mm, body whorl width 1.19 mm, aperture height 0.82 mm, aperture width 0.68 mm, 5.75 whorls.

Edges of last 0.5 operculum whorl sometimes weakly frilled on outer side (Fig. 7H); inner side of operculum smooth (Fig. 7I). Radula (Fig. 7M–O): dorsal edge of central radular teeth weakly convex, basal tongue rounded V-shaped, median cusps distally pointed, parallel-sided proximally, lateral cusps four–six, basal cusps one–three (innermost larger) (Fig. 7N). Lateral teeth having two–three cusps on inner and three–four cusps on outer sides, length of outer wing about 180% width of cutting edge, central cusp pointed (Fig. 7O). Inner marginal teeth having 14–19 cusps, outer marginal teeth having 27–38 cusps. Radula data are from USNM 1153668.

Animal darkly pigmented. Penis (Fig. 5D) having two distal papillae on the inner edge and a basal papilla on the outer edge (all 36 specimens from three samples). Distal bulb of penis expanded laterally on inner side, dark brown; stylet small. Penial duct undulating along most of length. Penial data are from USNM 873293, USNM 874174, USNM 905267.

Distribution and habitat. *Tryonia angostura* is endemic to the type locality area in the Río Santa Maria basin (Fig. 1, locality 5). Habitat as for *T. ovata* (described above). *Tryonia angostura* has also been collected in the main spring canal (from Ojos de Arrey) at the Highway 10 crossing.

Tryonia molinae sp. nov.

(Figs 5E, 8A–C, G–H, K–M)

Types. Holotype, USNM 1139278, unnamed spring in northern part of El Molino, ca. 125 m east of Chihuahua Highway 15, Chihuahua, 29º12'11" N, 107º24'24" W, leg. J.J.L., 26/iv/2010. Paratypes (from same lot), USNM 1153674.

Etymology. A geographical epithet referring to El Molino.

Diagnosis. Shell medium-sized, elongate-conic; penis having two distal and one basal papillae on the inner edge. Differentiated from closely similar *T. taylori* (described below) by having a single basal papilla on the inner edge of the penis.

Description. Shell (Fig. 8A–C) up to 3.9 mm tall, large females having 4.75–6.25 whorls, spire height 133–167% width of shell, male shells smaller than those of females. Teleoconch whorls weak to medium convex, evenly rounded, with impressed sutures. Aperture weakly angled and sometimes slightly thickened adapically, parietal lip complete, sometimes thickened, adnate, umbilicus narrow. Outer lip orthocoline or weakly prosocline. Sculpture of strong growth lines and weak spiral threads. Periostracum tan.

Shell measurements (mean in parentheses): height 2.84–3.92 mm (3.35), width 1.35–1.77 mm (1.54), body whorl height 1.70–2.04 mm (1.85), body whorl width 1.25–1.63 mm (1.44), aperture height 0.96–1.19 mm (1.06), aperture width 0.79–0.96 mm (0.87), total number of whorls 4.75–6.25 (5.73) (USNM 1153674, *n* = 10).

Measurements of holotype: height 3.26 mm, width 1.55 mm, body whorl height 1.90 mm, body whorl width 1.48 mm, aperture height 1.05 mm, aperture width 0.90 mm, 5.75 whorls.

Inner and outer sides of operculum smooth (Fig. 8G–H). Radula (Fig. 8K-M): dorsal edge of central radular teeth concave, basal tongue V-shaped, median cusps elongate, distally pointed or jagged-edged, parallel-sided proximally, lateral cusps four–seven, basal cusps two–three (innermost larger) (Fig. 8L). Lateral teeth having two–six cusps on inner and three–six cusps on outer side, length of outer wing 167–200% width of cutting edge,

central cusp pointed or jagged-edged (Fig. 8M). Inner marginal teeth with 19–31 cusps, outer marginal teeth with 27–35 cusps. Radula data are from USNM 1153674.

Animal darkly pigmented. Penis (Fig. 5E) having two distal and one basal papillae on the inner edge (30 of 30 specimens examined). Basal papilla often small, sometimes positioned ventrally near inner edge. Distal bulb of penis expanded laterally on inner side, lightly pigmented; stylet small. Penial duct nearly straight. Penial data are from USNM 1153674.

Distribution and habitat. *Tryonia molinae* is endemic to a single locality in the Río Santa Maria basin (Fig. 1, locality 6) that is locally known as "El Ojo." The outflow of this thermal (28°C) spring is ponded by a small retention dam and used for recreation (Fig. 6E). Snails were abundant on all substrates (including rocks, rootlets and algae) in the headspring and upper portion of the pool.

Remarks. *Tryonia molinae* was delineated as a well supported lineage in the Bayesian analysis (Fig. 2).

Tryonia contrerasi new species

(Figs. 5F, 8D–F, I–J, N–P)

Types. Holotype, USNM 874121, Ojo del Apache, south of Rancho Nuevo, Chihuahua, 30º34'27" N, 106º54'27" W, leg. J.J.L. and D. Wong, 2/iv/1991. Paratypes (from same lot), USNM 1153670.

Etymology. A patronym honoring Salvador Contreras-Balderas (Professor Emeritus, Department of Biology, Universidad Autonoma de Nuevo Leon, Monterrey, Mexico) for his dedicated efforts over many years to promote the conservation of Chihuahuan Desert aquatic biota.

Referred material. CHIHUAHUA. USNM 854951, topotypes, R.H. and J.J.L., 14/xii/1998. UTEP 881, ca. 4 km southwest of Hacienda Santo Domingo, leg. W. Strain, no date. USNM 854124, USNM 874124, USNM 874128, Ojo Carbonero, southeast of Rancho Nuevo, Chihuahua, 30º34'47.5" N, 106º52'26" W, leg. J.J.L. and D. Wong, 2/iv/1991. USNM 854952, *ibid.*, leg. R.H. and J.J.L., 14/xii/1998.

Diagnosis. Shell medium-to large-sized, conic, rather strongly sculptured; penis having two distal and one basal papillae on the inner edge. Distinguished from other regional congeners by its more strongly sculptured shell. Further differentiated from conchologically similar *T. molinae* by its larger size (t-test for shell height, t = 8.892, df = 8.892, $P<0.01$) and evenly rounded distal bulb of the penis; and from *T. ovata*, which has closely similar penial morphology, by its less convex teleoconch whorls, typically incomplete parietal lip and smaller umbilicus.

Description. Shell (Fig. 8D–F) up to 6.2 mm tall, large females having 5.75–8.75 whorls, spire height 140–200% width of shell, male shells smaller than those of females. Teleoconch whorls weak to medium convex, evenly rounded with impressed sutures. Sculpture of widely spaced collabral riblets or cords and more numerous spiral threads or cords, sometimes resulting in a cancellate appearance. Aperture strongly angled adapically, parietal lip usually incomplete or a thin glaze across the parietal wall, rarely complete and adnate or slightly disjunct, umbilicus narrow or absent. Outer lip slightly orthocline or prosocline. Periostracum brown or tan.

Shell measurements (mean in parentheses): height 4.39–6.13 mm (4.92), width 1.85–2.25 mm (2.02), body whorl height 2.39–2.97 mm (2.62), body whorl width 1.71–2.09 mm (1.89), aperture height 1.42–1.71 mm (1.56), aperture width 1.08–1.26 mm (1.15), total number of whorls 5.75–7.75 (6.54) (USNM 1153670, $n = 13$).

Measurements of holotype: height 5.22 mm, width 2.21 mm, body whorl height 2.90 mm, body whorl width 2.03 mm, aperture height 1.69 mm, aperture width 1.27 mm, 6.5 whorls.

Edges of last 0.5 operculum whorl sometimes frilled on outer side (Fig. 8I), inner side of operculum smooth (Fig. 8J). Radula (Fig. 8N-P): dorsal edge of central radular teeth concave, basal tongue rounded, median cusps elongate, distally pointed, parallel-sided proximally, lateral cusps four–seven, basal cusps one–three (innermost larger) (Fig. 8O). Lateral teeth having two–four cusps on inner and three–five cusps on outer side, length of outer wing about 180% width of cutting edge, central cusp hoe-shaped (Fig. 8P). Inner marginal teeth with 16–25 cusps, outer marginal teeth with 30–40 cusps. Radula data are from USNM 874128, USNM 1153670.

Animal darkly pigmented. Penis (Fig. 5F) having two distal papillae and one basal papilla on inner edge (56 of 57 specimens from two samples); one specimen differed in lacking a basal papilla. Distal bulb of penis evenly rounded; stylet small. Penial duct weakly undulating along most of length. Penial data are from USNM 874128, USNM 1153670.

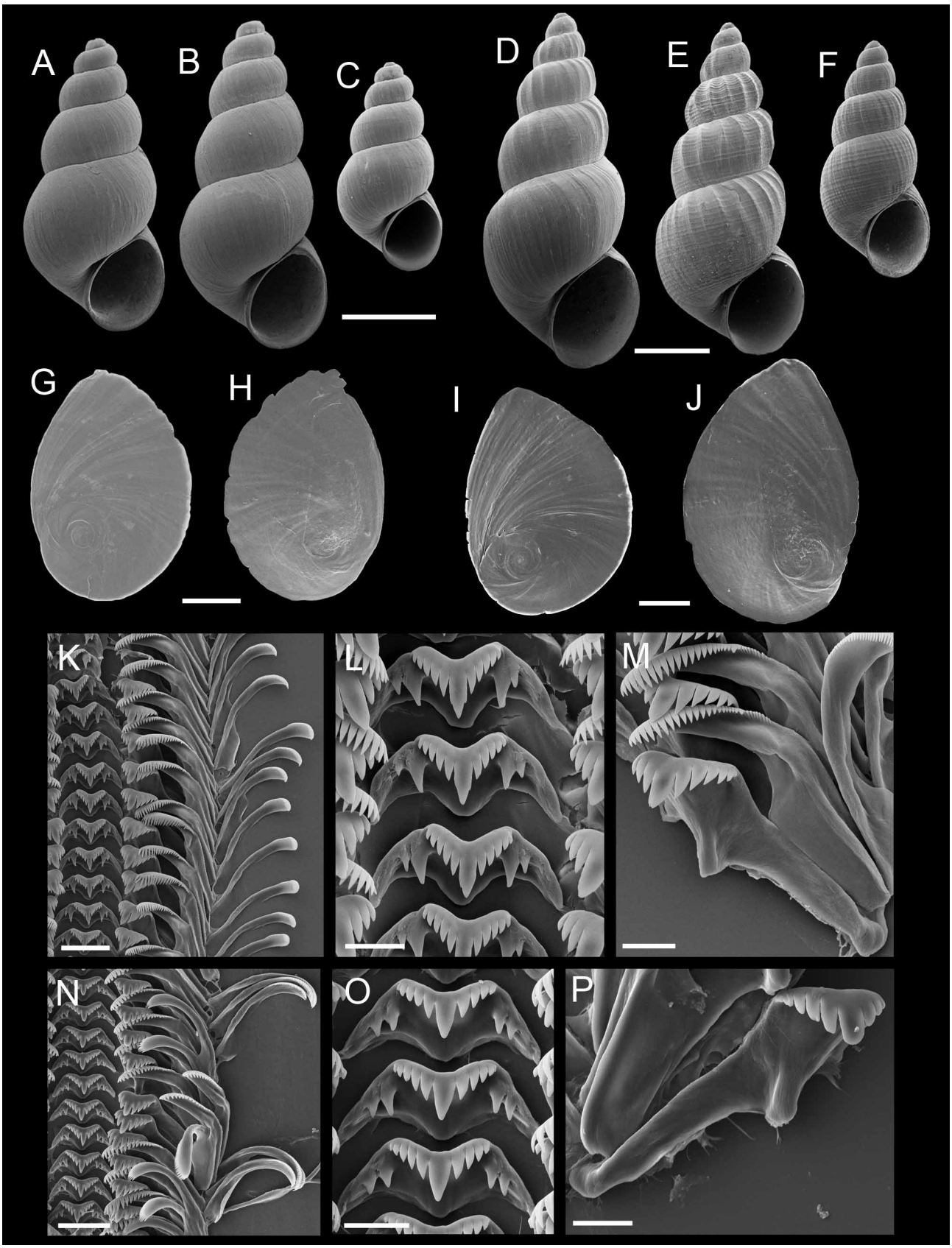

FIGURE 8. *Tryonia molinae* **sp. nov**. and *Tryonia contrerasi* **sp. nov**. A. Holotype, *T. molinae*, USNM 1139278. B–C. Shells, *T. molinae*, USNM 1153674 (C is a male). D. Holotype, *T. contrerasi*, USNM 874121. E–F. Shells, *T. contrerasi*, USNM 874128 (F is a male). G–H. Operculum (outer, inner sides), *T. molinae*, USNM 1153674. I–J. Operculum (outer, inner sides), *T. contrerasi*, USNM 1153670. K. Portion of radular ribbon, *T. molinae*, USNM 1153674. L. Central radular teeth, *T. molinae*, USNM 1153670. M. Lateral and inner marginal teeth, *T. molinae*, USNM 1153670. N. Portion of radular ribbon, *T. contrerasi*, USNM 1153670. Q. Central radular teeth, *T. contrerasi*, USNM 1153670. R. Lateral tooth, *T. contrerasi*, USNM 1153670. Scale bars A–F = 1.0 mm; G–J = 250 µm; K, N = 25 µm, L–M, O–P = 10 µm.

Distribution and habitat. *Tryonia contrerasi* is distributed in two closely proximal (ca. 3 km) springs in the (endorheic) Bolson de los Muertos (Fig. 1, locality 8). These springs are part of a complex to the west of Villa Ahumada near Rancho Nuevo. All of these springs with the exception of Ojo Carbonero (referred to as Ojo Carbonera by Miller *et al*. 2005) have been highly modified. The type locality, Ojo del Apache, is a thermal spring (27°C) that has been severely degraded (trampled) by horses (Fig. 6F). Snails were found in this spring on aquatic vegetation. Ojo Carbonero contains at least eight discrete sources that coalesce into a spring run for about 100 m (Fig. 6G) before flowing into a canal. Snails were common in this thermal (26–27°C) spring both in detritus and on sand. UTEP 881, which consists of old, worn shells, may have been collected from a playa lake (Laguna Colorada) along the highway southwest of Hacienda Santo Domingo.

Remarks. *Tryonia contrerasi* was delineated in the Bayesian analysis as a well supported lineage (Fig. 2). Snails from Ojo Carbonero (Fig. 8E–F) are slightly smaller and have more highly sculptured shells than those from the type locality (Fig. 8D); these two populations differed by 0.6% COI divergence.

***Tryonia taylori* sp. nov.**
(Figs 5G–H, 9A–D, G–I, L–N)

Types: Holotype, USNM 873254, ouflow of Ojo Caliente at Rancho Ojo Caliente, south of Highway 10, Chihuahua, 29º54'10.2" N, 107º15'27.1" W, leg. J.J.L. *et al*., 27/viii/1971. Paratypes (from same lot), USNM 1153678.

Etymology. A patronym honoring the late Dwight W. Taylor for his pioneering taxonomic studies of *Tryonia* (Taylor 1987).

Referred material. CHIHUAHUA. USNM 873251, topotypes, leg. J.J.L. *et al*., 27/viii/1971. USNM 874047, topotypes, leg. J.J.L. and P. Hines, 18/ix/1990. USNM 1135493, topotypes, R.H. and J.J.L., 7/xii/1998. USNM 873283, El Ojo de Servin, 5.6 km west of Rancho Ojo Caliente, 0.2 km north of Highway 10, 29º54'17.2" N, 107º18'27.2" W, leg. J.J.L., 14/iv/1973. USNM 873252, USNM 873297, *ibid*, leg. J.J.L. *et al*., 27/viii/1971. USNM 874050, *ibid.*, leg. J.J.L., 18/ix/1990. USNM 892118, *ibid.*, leg. R.H. and J.J.L., 7/xii/1998. UTEP 978, *ibid.*, leg. A. Metcalf and D.W. Taylor, 4/ix/1969. BellMNH 21172, BellMNH 21173, *ibid.*, leg. D.W. Taylor and A. Metcalf, 4/ix/1969.

Diagnosis. Shell medium- to large-sized, conic or elongate-conic; penis having two distal papillae on inner edge and sometimes two–four basal papillae on inner edge and/or dorsal surface. Differentiated from closely similar *T. molinae* above.

Description. Shell (Fig. 9A–D) up to 6.7 mm tall, whorls ca. 5.50–8.75, spire height 135–220% width of shell, male shells smaller than those of females. Teleoconch whorls usually weak to medium convex, rarely high convex, evenly rounded or weakly shouldered with impressed or adpressed sutures. Aperture weakly or sharply angled adapically, parietal lip usually complete, usually adnate, rarely slightly disjunct, umbilicus narrow or absent. Outer lip sometimes slightly thickened adapically, orthocline or weakly prosocline. Sculpture of strong growth lines and weak spiral threads. Periostracum tan.

Shell measurements (mean in parentheses): height 3.42–4.25 mm (3.74), width 1.54–1.84 mm (1.67), body whorl height 1.93–2.22 mm (2.09), body whorl width 1.46–1.73 mm (1.59), aperture height 1.03–1.33 mm (1.22), aperture width 0.89–1.09 mm (1.00), total number of whorls 5.50–6.50 (6.00) (USNM 1153678, n = 15).

Measurements of holotype: height 3.74 mm, width 1.59 mm, body whorl height 2.16 mm, body whorl width 1.55 mm, aperture height 1.24 mm, aperture width 1.01 mm, 6.0 whorls.

Outer side of operculum smooth (Fig. 9G) or with edges of last 0.5 whorl frilled; inner side of operculum nearly smooth (Fig 10H) or with edges of muscle attachment scar thickened (Fig. 9I). Radula (Fig. 9L-N): dorsal edge of central radular teeth concave, basal tongue rounded, median cusps elongate, distally pointed, lateral cusps four–seven, basal cusps one–three (innermost larger) (Fig. 9M). Lateral teeth having two–five cusps on inner and three–seven cusps on outer side, length of outer wing 160–200% width of cutting edge, central cusp pointed (Fig. 9N) or jagged-edged. Inner marginal teeth with 19–32 cusps, outer marginal teeth with 25–49 cusps. Radula data are from USNM 873283, USNM 1153678.

Animal darkly pigmented. Penis (Fig. 5G–H) usually having two distal papillae on inner edge (46 of 56 specimens from two samples), eight specimens differed in having three distal papillae and two differed in having a single distal papilla. Ojo Caliente specimens usually lacking basal penial papillae (25 of 27 specimens), one specimen

differed in having a basal papilla both on the inner and outer edges, one specimen differed in having two dorsally positioned basal papillae. Ojo de Servin specimens usually having two–three dorsally positioned basal penial papillae (27 of 29 specimens) and sometimes also having a basal papilla on the inner edge (12 of 29 specimens); one specimen had four dorsally positioned papillae and one specimen lacked basal papillae. Distal bulb of penis evenly rounded or expanded laterally on inner side, black; stylet small. Penial duct nearly straight to strongly undulating along most of length. Penial data are from USNM 873251, USNM 873252.

Distribution and habitat. Narrowly endemic in the Río Santa Maria drainage (Fig. 1, locality 7). The type locality (Ojo Caliente) is a thermal spring (36–39°C) that is enclosed in a bath house (Fig. 6H). *Tryonia taylori* was found on mud, rocks and aquatic vegetation in the outflow 5–6 meters below the bath house. We did not discern a marked change in this spring from 1971–1998. The second locality, El Ojo de Servin, is a warm spring complex (23–26°C) about 5 km west of Ojo Caliente. *Tryonia taylori* is extremely abundant on algae and *Chara* in the headspring area and somewhat less common in shallow portions of the spring runs on mud. This formerly lush cienega (as observed in 1971, Fig. 6I) is now severely overgrazed (Fig. 6J).

Remarks. The two populations of *T. taylori* formed a strongly supported clade in the Bayesian tree (Fig. 2). These populations differ in shell size (3.7 vs. 5.8 mm mean shell height, t-test, t = -13.811, df = 18.6, $P<0.01$, n=13 for the El Ojo de Servin sample), teleoconch whorl convexity, number of cusps on the outer marginal teeth, and the number and arrangement of basal papillae on the penis. However, they do not form reciprocally monophyletic clades in the Bayesian tree and their sequence divergence ranged from 0.3 to 1.7% (Table 2). We treat these morphologically distinctive populations as conspecific based on the evolutionary lineage concept used herein.

TABLE 2. Divergence of haplotypes detected in the Ojo Caliente (Try7) and Ojo de Servin (Try8) populations of *T. taylori*.

	Try7A	Try7B	Try7C	Try7D	Try7E	Try8A	Try8B	Try8C	Try8D	Try8F	Try8G
Try7A											
Try7B	0.000										
Try7C	0.003	0.003									
Try7D	0.000	0.000	0.003								
Try7E	0.000	0.000	0.003	0.000							
Try8A	0.003	0.003	0.006	0.003	0.003						
Try8B	0.003	0.003	0.006	0.003	0.003	0.000					
Try8C	0.017	0.017	0.017	0.017	0.017	0.020	0.020				
Try8D	0.002	0.002	0.005	0.002	0.002	0.005	0.005	0.018			
Try8F	0.014	0.014	0.014	0.014	0.014	0.017	0.017	0.003	0.015		
Try8G	0.002	0.002	0.005	0.005	0.002	0.005	0.005	0.018	0.000	0.015	
Try8H	0.015	0.015	0.015	0.015	0.015	0.018	0.018	0.002	0.017	0.002	0.017

***Tryonia metcalfi* sp. nov.**
(Figs 5I, 9E–F, J–K, O–Q)

Types. Holotype, USNM 1001931, unnamed seeps in La Cienega, ca. 0.8 km east of cemetery, Presidio County, Texas, 30º6'38.9" N, 104º40'21.1" W, leg. R.H. and J.J.L., 6/xii/2001. Paratypes (from same lot), USNM 1153672.

Etymology. A patronym honoring Art Metcalf (University of Texas at El Paso, now retired) for his many years of study of regional mollusks and for the unfailing encouragement and support that he provided to other such researchers.

Referred material. TEXAS. Presidio County. USNM 1151243, topotypes, J.J.L., 15/ii/2011.

Diagnosis. Shell medium-sized, ovate-conic; penis having two distal and two basal papillae on the inner edge. Distinguished from Chihuahuan Desert congeners by the greatly enlarged size of the penial papillae relative to the penis. Further differentiated from lower Río Conchos basin congeners by having a basal papilla on the inner edge of the penis, and from Pecos River basin congeners by its larger penial stylet.

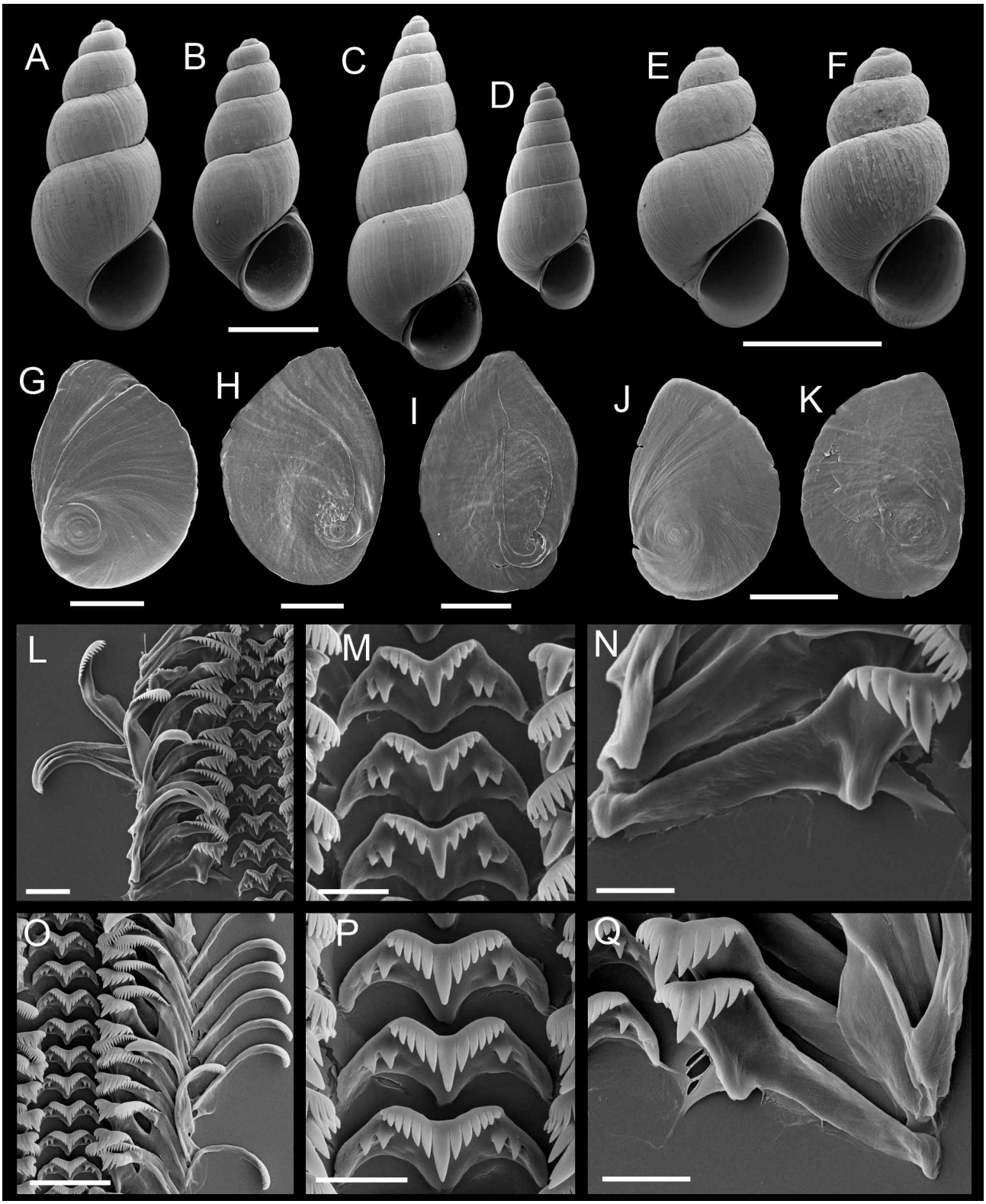

FIGURE 9. *Tryonia taylori* **sp. nov** and *T. metcalfi* **sp. nov**. A. Holotype, *T. taylori*, USNM 873254. B. Male shell, *T. taylori*, USNM 1153678. C–D. Shells, *T. taylori*, USNM 873283 (D is a male). E. Holotype, *T. metcalfi*, USNM 1001931. F. Shell, *T. metcalfi*, USNM 1153672. G–I. Operculum (outer, inner, inner sides), *T. taylori*, USNM 1153678. J–K. Operculum (outer, inner sides), *T. metcalfi*, USNM 1153672. L. Portion of radular ribbon, *T. taylori*, USNM 1153678. M. Central radular teeth, *T. taylori*, USNM 1153678. N. Lateral tooth, *T. taylori*, USNM 1153678. O. Portion of radular ribbon, *T. metcalfi*, USNM 1153672. P. Central radular teeth, *T. metcalfi*, USNM 1153672. Q. Lateral teeth, *T. metcalfi*, USNM 1153672. Scale bars A–F = 1.0 mm; G–K = 250 µm; L, O = 25 µm, M–N, P–Q = 10 µm.

Description. Shell (Fig. 9E–F) up to 2.6 mm tall, large females having 4.5–5.0 whorls, spire height 100–130% width of shell, sexual dimorphism of shells not obvious. Teleoconch whorls medium convex, shouldered, sutures impressed. Aperture ovate, inner lip complete, slightly thickened, adnate or disjunct, umbilicus narrow or absent. Outer lip thin, orthocline. Sculpture of strong growth lines. Periostracum tan, usually absent owing to erosion of shell surface.

Shell measurements (mean in parentheses): height 1.99–2.62 mm (2.24), width 1.08–1.34 mm (1.19), body whorl height 1.34–1.66 mm (1.51), body whorl width 0.99–1.27 mm (1.12), aperture height 0.77–0.97 mm (0.87), aperture width 0.67–0.80 mm (0.73), total number of whorls 4.50–5.00 (4.78) (USNM 1153672, *n* = 10).

Measurements of holotype: height 2.27 mm, width 1.17 mm, body whorl height 1.52 mm, body whorl width 1.12 mm, aperture height 0.89 mm, aperture width 0.73 mm, 4.75 whorls.

Inner and outer sides of operculum smooth (Fig. 9J–K). Radula (Fig. 9O–Q): dorsal edge of central radular teeth strongly concave, basal tongue V-shaped, median cusps distally pointed, parallel-sided proximally, lateral cusps five–seven, basal cusps one–two (innermost larger) (Fig. 9P). Lateral teeth having four–six cusps both on the inner and outer sides, length of outer wing about 160% width of cutting edge, central cusp pointed (Fig. 9Q). Inner marginal teeth having 24–28 cusps, outer marginal teeth having 26–32 cusps. Radula data are from USNM 1153672.

Animal darkly pigmented. Penis (Fig. 5I) having two distal and two basal papillae on the inner edge (30/30 specimens), the basal-most papilla is sometimes positioned partly on the dorsal surface. Distal bulb of penis expanded laterally on inner side, black; stylet large. Penial duct weakly undulating in medial section. Penial data are from USNM 1151243.

Distribution and habitat. Endemic to a single locality along the east side of the Rio Grande above the mouth of the Río Conchos (Figure 1, locality 12). This locality is a complex of small seeps that discharges into a broad arroyo (Fig 6K). *Tryonia metcalfi* was found on mud, decaying vegetation and on the undersides of rocks in 19°C water. This habitat has been heavily degraded by livestock.

Remarks. *Tryonia metcalfi* was delineated as a well supported lineage in the Bayesian tree (Fig. 2). This species was discovered coincidentally while searching for additional localities for *Pyrgulopsis metcalfi* (Taylor, 1987), which is distributed a little to the south of La Cienega (Taylor 1987).

Tryonia chuviscarae sp. nov.

(Figs 5J, 10A–C, F–G, J–L)

Types. Holotype, USNM 873270, Balneario de San Diego de Alcala, Chihuahua, 28º35'17.6" N, 105º32'50.8" W, leg. J.J.L. *et al*., 29/viii/1971. Paratypes (from same lot), USNM 873294, USNM 905265, 1153669.

Etymology. Epithet refers to the Río Chuviscar, which is close to the type locality of this species.

Referred material. CHIHUAHUA. USNM 854941, topotypes, leg. R.H. and J.J.L., 9/xii/1998. USNM 1001750, USNM 1001756, *ibid.*, leg. R.H. and J.J.L., 4/xii/2001.

Diagnosis. Shell small, broadly- or ovate-conic; penis having two distal papillae on the inner edge and one–two basal papillae on the outer edge. Differentiated from sympatric *T. minckleyi* (described next) in its smaller shells (t-test for shell height, t = -10.699, df = 24.7, $P<0.01$), thickened inner lip of shell, larger umbilicus, more convex dorsal edge of central radular teeth, V-shaped basal tongue of central radular teeth, narrower central radular teeth, and square-shaped face of lateral teeth; and from conchologically similar and closely related *T. julimesensis* (described below) in its larger shells (t-test for shell height, t = -6.666, df = 23.8, $P<0.01$), in having basal papillae on the penis, and in having a larger number of cusps on the outer marginal radular teeth.

Description. Shell (Fig. 10A–C) up to 2.5 mm tall, large females having 3.75–5.00 whorls, spire height 75–95% width of shell, male shells smaller than those of females. Teleoconch whorls high convex, frequently shouldered, sutures impressed, last 0.5 whorl sometimes loosened. Aperture usually rounded adapically, rarely weakly angled, inner lip complete, usually thickened, adnate or disjunct, umbilicus narrow or open. Outer lip thin, orthocline or prosocline, weakly sinuate. Sculpture of strong growth lines, weak spiral threads also sometimes present. Periostracum light tan or absent.

Shell measurements (mean in parentheses): height 1.80–2.17 mm (1.98), width 1.21–1.43 mm (1.31), body whorl height 1.36–1.61 mm (1.48), body whorl width 1.06–1.24 mm (1.15), aperture height 0.79–0.99 mm (0.88), aperture width 0.71–0.85 mm (0.77), total number of whorls 3.75–4.25 (4.13) (USNM 1001750, *n* = 12).

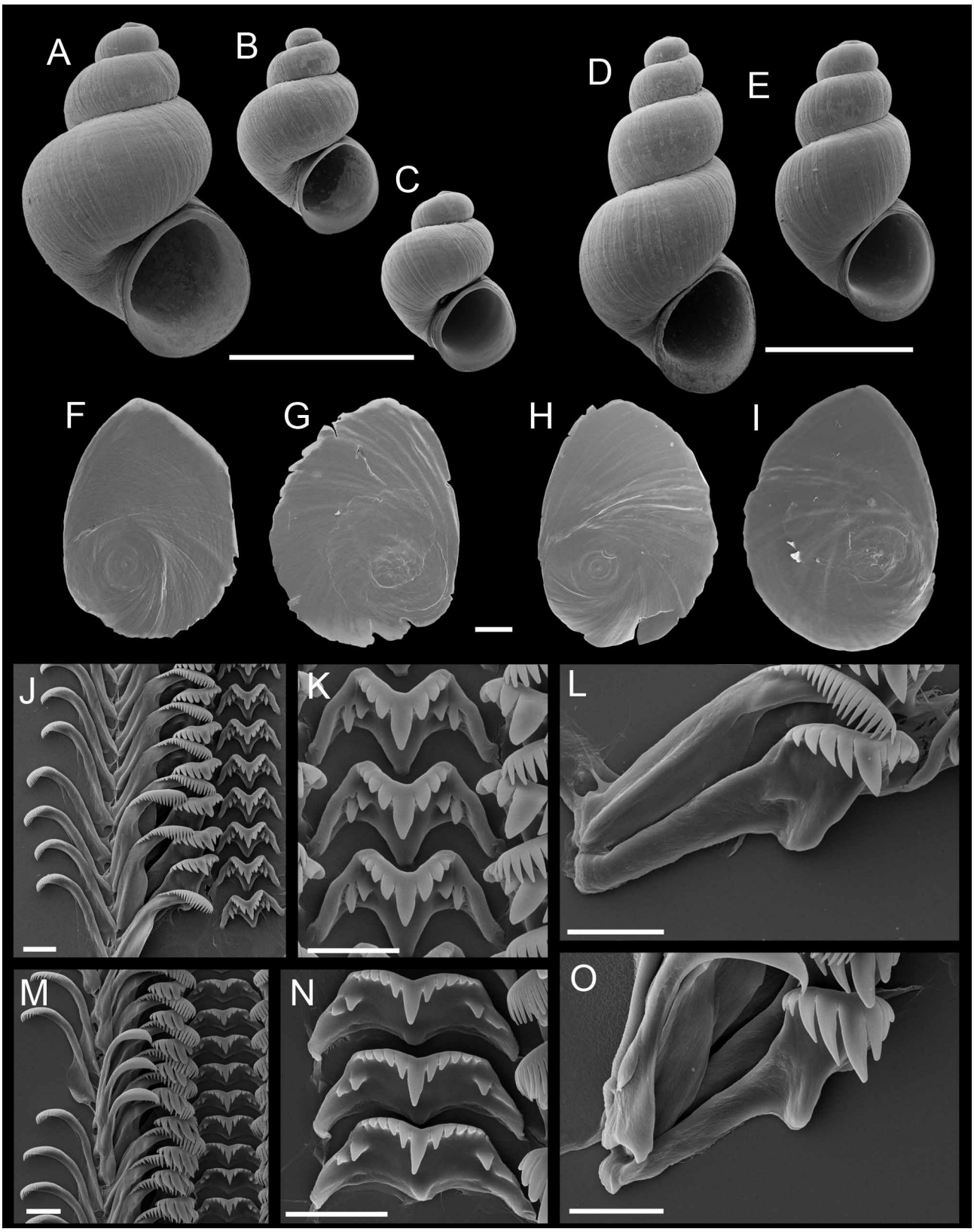

FIGURE 10. *Tryonia chuviscarae* **sp. nov**. and *Tryonia minckleyi* **sp. nov**. A. Holotype, *T. chuviscarae*, USNM 873270. B. Male shell, *T. chuviscarae*, USNM 1153669. C. Male shell, *T. chuviscarae*, USNM 1001750. D. Holotype, *T. minckleyi*, USNM 1001751. E. Male shell, *T. minckleyi*, USNM 1153673. F–G. Operculum (outer, inner sides), *T. chuviscarae*, USNM 1001750. H–I. Operculum (outer, inner sides), *T. minckleyi*, USNM 1153673. J. Portion of radular ribbon, *T. chuviscarae*, USNM 001750. K. Central radular teeth, *T. chuviscarae*, USNM 1001750. L. Lateral and inner marginal teeth, *T. chuviscarae*, USNM 1001750. M. Portion of radular ribbon, *T. minckleyi*, USNM 1153673. N. Central radular teeth, *T. minckleyi*, USNM 1153673. O. Lateral tooth, *T. minckleyi*, USNM 1153673. Scale bars A–E = 1.0 mm, F–I = 100 µm, J–O = 10 µm.

Measurements of holotype: height 2.28 mm, width 1.45 mm, body whorl height 1.66 mm, body whorl width 1.31 mm, aperture height 0.98 mm, aperture width 0.79 mm, 4.5 whorls.

Outer side of operculum smooth (Fig. 10F), portion of attachment scar margin slightly thickened on inner side (Fig. 10G). Radula (Fig. 10J-L): dorsal edge of central radular teeth strongly concave, basal tongue V-shaped, median cusps distally pointed, parallel-sided proximally, lateral cusps four–six, basal cusps two–three (outermost larger) (Fig. 10K). Lateral teeth having two–four cusps on inner and three–six cusps on outer sides, length of outer wing about 140% width of cutting edge, central cusp pointed (Fig. 10L). Inner marginal teeth having 18–24 cusps, outer marginal teeth having 20–28 cusps. Radula data are from USNM 1001750.

Animal darkly pigmented. Penis (Fig. 5J) having two distal papillae on the inner edge and one–two basal papillae on the outer edge (27 of 30 specimens), two specimens differed in also having a basal papilla on the inner edge. Distal bulb of penis expanded laterally on inner side, black; stylet large. Penial duct straight or weakly undulating along most of length. Penial data are from USNM 1001756.

Distribution and habitat. Endemic to the type locality in the Río Conchos basin (Fig. 1, locality 9). This site, which is also known as Baños de San Diego de Alcala, is a warm spring complex (headspring temperatures ca. 42–45°C) that has long been used for recreation. Numerous springs discharge from a travertine mound (where a large bathhouse is situated) on the western edge of the complex (Fig. 6L–M). *Tryonia chuviscarae* and *T. minckleyi* were found throughout the spring complex (except in the headspring vents) on mud and gravel; the highest temperature recorded for this snail habitat was 41°C.

Remarks. The occurrence of undescribed *Tryonia* in the Balneario de San Diego de Alcala was noted by Minckley & Minckley (1986), however it is not clear whether they were referring to *T. chuviscarae*, *T. minckleyi*, or both. *Tryonia chuviscarae* was delineated as a well supported lineage in the Bayesian tree (Fig. 2).

***Tryonia minckleyi* new species**
(Figs 5K, 10D–E, H–I, M–O)

Types. Holotype, USNM 1001751, Balneario de San Diego de Alcala, Chihuahua, 28º35'17.6" N, 105º32'50.8" W, leg. R.H. and J.J.L., 4/xii/2001. Paratypes (from same lot), USNM 1001755, USNM 1153673.

Etymology. A patronym honoring the late Wendell L. Minckley for his remarkable record of research on aquatic biota of the Chihuahuan Desert (Collins *et al*. 2002) and for leading the collecting expeditions that resulted in the discovery of this (and many other) species.

Referred material. CHIHUAHUA. USNM 873200, USNM 905268, USNM 905269, topotypes, J.J.L. *et al.*, 29/viii/1971.

Diagnosis. Shell small, ovate-conic or conic; penis having two distal papillae on the inner edge and one–two basal papillae on the outer edge. Contrasted with syntopic *T. chuviscarae* above. Differs from *T. julimesensis* (described next), which is also distributed in the Río Conchos basin, in having basal penial papillae. Readily distinguished from conchologically similar *T. allendae* (described below), which is also distributed in the Río Conchos basin, by its more rounded shell whorls, more elongate cusps on the lateral radular teeth, larger penial stylet, weakly undulating penial duct, and smaller lateral expansion of the terminal bulb of the penis.

Description. Shell (Fig. 10D–E) up to 2.8 mm tall, large females having 4.75–5.50 whorls, spire height 120–140% width of shell, male shells smaller than those of females. Teleoconch whorls high convex, shouldered, sutures impressed. Aperture rounded adapically, parietal lip complete, usually adnate, rarely slightly disjunct, umbilicus narrow or absent. Outer lip thin, orthocline. Sculpture of strong growth lines, weak spiral thread also sometimes present. Periostracum light tan.

Shell measurements (mean in parentheses): height 2.25–2.70 mm (2.48), width 1.17–1.31 mm (1.24), body whorl height 1.44–1.62 mm (1.53), body whorl width 1.06–1.24 mm (1.16), aperture height 0.81–0.95 mm (0.87), aperture width 0.70–0.78 mm (0.74), total number of whorls 4.75–5.25 (4.93) (USNM 1153673, n = 15).

Measurements of holotype: height 2.69 mm, width 1.28 mm, body whorl height 1.62 mm, body whorl width 1.19 mm, aperture height 0.94 mm, aperture width 0.74 mm, 5.0 whorls.

Inner and outer sides of operculum smooth (Fig. 10H–I). Radula (Fig. 10M-O): dorsal edge of central radular teeth weakly concave, basal tongue rounded, median cusps distally pointed, parallel-sided proximally, lateral cusps four–five, basal cusps two (equal-sized or innermost larger), small (Fig. 10N). Lateral teeth having two–three cusps

on inner and four–five cusps on outer sides, length of outer wing about 180% width of cutting edge, central cusp pointed, curved (Fig. 10O). Inner marginal teeth having 19–30 cusps, outer marginal teeth having 25–31 cusps. Radula data are from USNM 1153673.

Animal darkly pigmented. Penis (Fig. 5K) usually having two distal papillae on the inner edge and one–two basal papillae on the outer edge (19 of 30 specimens). Two specimens differed in having a single distal papilla on the inner edge, one specimen differed in having three distal papillae on the inner edge, two specimens lacked a papilla on the outer edge, two specimens had three basal papillae on the outer edge, one specimen had five basal papillae on the outer edge, and one specimen had two distal and four basal papillae on the outer edge. Distal bulb of penis weakly expanded laterally on inner side, black; stylet large. Penial duct straight or weakly undulating along most of length. Penial data are from USNM 1153673.

Distribution and habitat. Endemic to the type locality in the Río Conchos basin (Fig. 1, locality 9). Habitat as for *T. chuviscarae* (see above).

Remarks. *Tryonia minckleyi* was delineated as a well supported lineage in the Bayesian tree (Fig. 2).

Tryonia julimesensis new species

(Figs 5L, 11A–C, F–G, J–L)

Types. Holotype, USNM 874130, unnamed springs along east side of Río Conchos, south-southeast of Julimes, Chihuahua, 28º24'37.2" N, 105º25'21.6 " W, leg. J.J.L. *et al*., 5/v/1991. Paratypes (from same lot), USNM 1153671.

Etymology. A geographic epithet referring to the distribution of this species near the town of Julimes, Chihuahua.

Referred material. CHIHUAHUA. USNM 854940, topotype, R.H. and J.J.L., 9/xii/1998.

Diagnosis. Shell small, broad- or ovate-conic; penis having two distal papillae on the inner edge. Contrasted with *T. chuviscarae* and *T. minckleyi* above.

Description. Shell (Fig. 11A–C) up to 2.0 mm tall, large females having 4.00–4.50 whorls, spire height 80–99% width of shell, male shells smaller than those of females. Teleoconch whorls high convex, frequently shouldered, sutures impressed, last 0.25 whorl sometimes loosened. Aperture usually rounded adapically, rarely weakly angled, inner lip complete, slightly thickened, adnate or disjunct, umbilicus narrow or open. Outer lip thin, orthocline or prosocline, weakly sinuate. Sculpture of strong growth lines, weak spiral thread also sometimes present. Periostracum light tan.

Shell measurements (mean in parentheses): height 1.54–1.98 mm (1.69), width 1.03–1.21 mm (1.09), body whorl height 1.15–1.34 mm (1.21), body whorl width 0.92–1.07 mm (0.97), aperture height 0.66–0.79 mm (0.71), aperture width 0.61–0.71 mm (0.65), total number of whorls 4.00–4.50 (4.18) (USNM 1153671, $n = 15$).

Measurements of holotype: height 1.90 mm, width 1.24 mm, body whorl height 1.34 mm, body whorl width 1.07 mm, aperture height 0.81 mm, aperture width 0.69 mm, 4.25 whorls.

Inner and outer sides of operculum smooth (Fig. 11F–G). Radula (Fig. 11J-L): dorsal edge of central radular teeth strongly concave, basal tongue rounded or V-shaped, median cusps distally pointed, parallel-sided proximally, lateral cusps four–five, basal cusps one–three (roughly equal-sized) (Fig. 11K). Lateral teeth having three–four cusps on inner and four–five cusps on outer sides, length of outer wing about 160% width of cutting edge, central cusp pointed (Fig. 11L). Inner marginal teeth having 16–21 cusps, outer marginal teeth having 15–20 cusps. Radula data are from USNM 1153671.

Animal darkly pigmented. Penis (Fig. 5L) having two distal papillae on the inner edge (26 of 30 specimens), four specimens differed in having a single distal papilla. Distal bulb of penis expanded laterally on inner side, black; stylet large. Penial duct weakly undulating in medial section. Penial data are from USNM 1153671.

Distribution and habitat. Endemic to the type locality, a warm spring complex along the east side of the Río Conchos (Fig. 1, locality 10). *Tryonia julimesensis* was abundant (on hard substrate and in detritus) in the main spring runs (44°C) (Fig. 6N) when first discovered in 1991. It was also found in a small rheocrene just to the west of the main spring pools (44°C) as well as in semi-aquatic habitats on exposed rootlets and stones. When visited in 2001 the springs had been draglined (excavated) and *T. julimensis* could not be found. We presume that this species is now extinct.

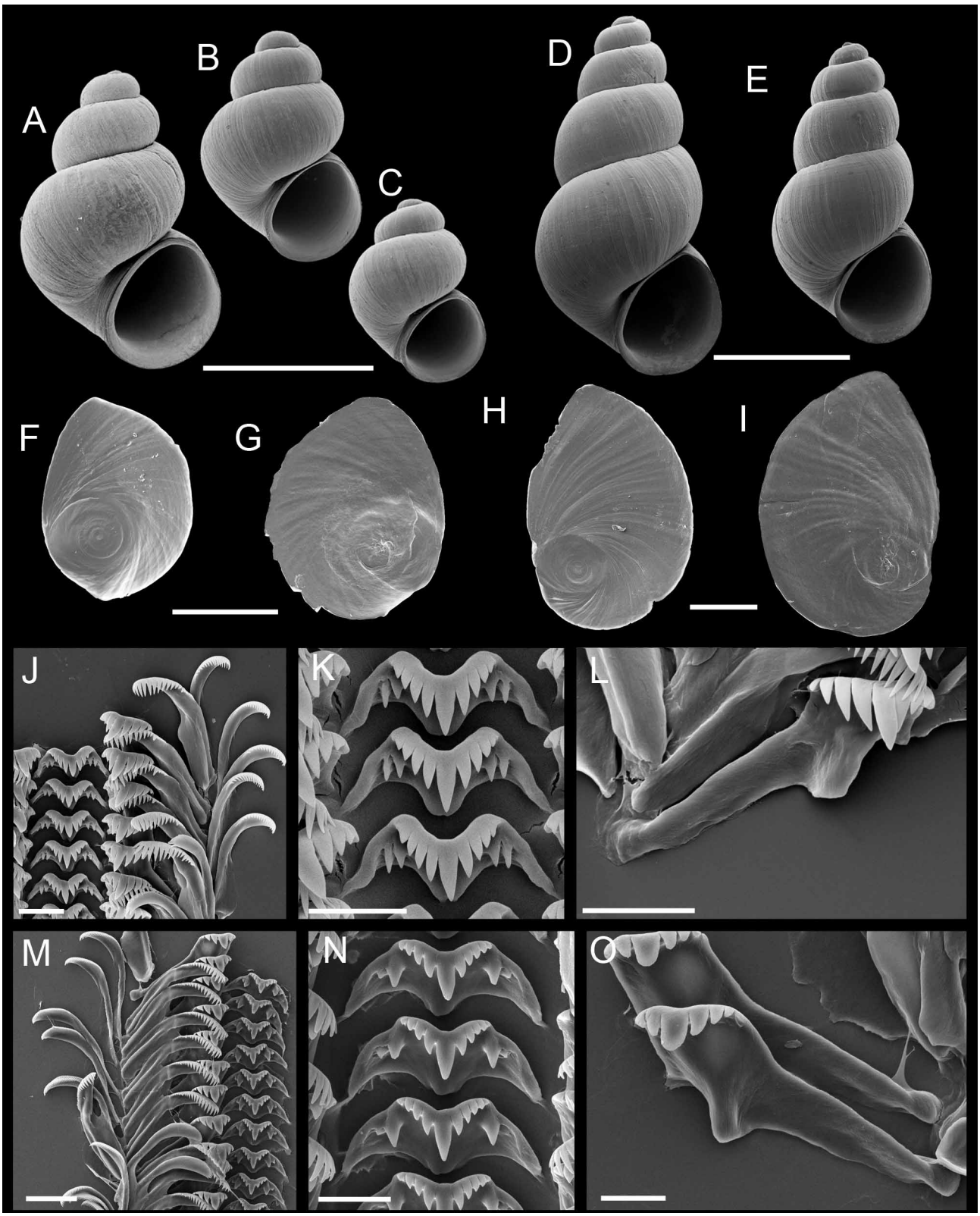

FIGURE 11. *Tryonia julimesensis* **sp. nov**. and *Tryonia allendae* **sp. nov**. A. Holotype, *T. julimesensis*, USNM 874130. B–C. Male shells, *T. julimesensis*, USNM 1153671. D. Holotype, *T. allendae*, USNM 892115. E. Shell, *T. allendae*, USNM 1153667. F–G. Operculum (outer, inner sides), *T. julimesensis*, USNM 1153671. H–I. Operculum (outer, inner sides), *T. allendae*, USNM 1153671. J. Portion of radular ribbon, *T. julimesensis*, USNM 1153671. K. Central radular teeth, *T. julimesensis*, USNM 1153671. L. Lateral tooth, *T. julimesensis*, USNM 1153671. M. Portion of radular ribbon, *T. allendae*, USNM 1153667. N. Central radular teeth, *T. allendae*, USNM 1153667. R. Lateral teeth, *T. allendae*, USNM 1153667. Scale bars A–E = 1.0 mm; F–I = 250 µm; J, K–L, N–O = 10 µm; M = 25 µm.

***Tryonia allendae* sp. nov.**
(Figs 5M, 11D–E, H–I, M–O)

Tryonia n. sp. 4.—Hershler *et al*. 2005: 1757 (COI sequence).

Types. Holotype, USNM 892115, El Ojito, southwest of Talamantes, Chihuahua, 26º54'12.6" N, 105º27'19.8" W, leg. R.H. and J.J.L., 10/xii/1998. Paratypes (from same lot), USNM 1153667.

Etymology. A geographic epithet referring to the municipality of Allende in which this species is distributed.

Diagnosis. Shell medium-sized, ovate-conic or conic; penis having two distal papillae on the inner edge and a basal papilla on the outer edge. Contrasted with conchologically similar *T. minckleyi* above. Differentiated from *T. chuviscarae* and *T. julimesensis*, which are also distributed in the Río Conchos basin, in having a more strongly undulating penial duct.

Description. Shell (Fig. 11D–E) up to 5.8 mm tall, large females having 5.0–5.75 whorls, spire height 110–140% width of shell, male shells smaller than those of females. Teleoconch whorls weak to medium convex, evenly rounded, sutures impressed. Aperture angled adapically, parietal lip complete, usually adnate, rarely slightly disjunct, umbilicus narrow or absent. Outer lip thin, orthocline. Sculpture of strong growth lines, weak spiral thread also sometimes present. Periostracum tan.

Shell measurements (mean in parentheses): height 2.69–3.66 mm (2.92), width 1.40–1.76 mm (1.53), body whorl height 1.64–2.20 mm (1.82), body whorl width 1.23–1.67 mm (1.43), aperture height 0.94–1.22 mm (1.06), aperture width 0.82–1.06 mm (0.89), total number of whorls 5.00–5.75 (5.35) (USNM 1153667, *n* = 15).

Measurements of holotype: height 2.91 mm, width 1.44 mm, body whorl height 1.72 mm, body whorl width 1.35 mm, aperture height 0.97 mm, aperture width 0.83 mm, 5.5 whorls.

Outer side of operculum smooth (Fig. 11H), inner side smooth or with edges of last 0.5 whorl weakly frilled (Fig. 11I). Radula (Fig. 11M-O): dorsal edge of central radular teeth concave, basal tongue rounded, median cusps distally pointed, parallel-sided proximally, lateral cusps four–six, basal cusps one–two (innermost larger) (Fig. 11N). Lateral teeth having two–three cusps on inner and three–four cusps on outer sides, length of outer wing about 150% width of cutting edge, central cusp pointed (Fig. 11O). Inner marginal teeth having 20–26 cusps, outer marginal teeth having 22–40 cusps. Radula data are from USNM 1153677.

Animal lightly pigmented. Penis (Fig. 5M) having two distal papillae on inner edge and a basal papilla on outer edge (30 of 30 specimens). Distal bulb of penis expanded laterally on inner side, black. Penial duct strongly undulating along most of length; stylet small. Penial data are from USNM 1153667.

Distribution and habitat. Endemic to a single site (El Ojito) in an upper reach of the Río Conchos watershed (Fig. 1, locality 11). The springs at this locality have been impounded with a concrete dam for recreational purposes (Edwards *et al*. 2003). *Tryonia allendae* was abundant (on rootlets and dead leaves) in the outflow (25°C) of the impoundment (Fig. 6O).

***Tryonia oasiensis* sp. nov.**
(Figs 5N, 12A–B, F–G, J–L)

Types. Holotype, USNM 1123759, Caroline Spring, upper reach of outflow of lower-most pond, Terrell County, Texas, 30º28'2.2" N, 101º48'6.6" W, leg. R.H. and J.J.L., 30/iii/2009. Paratypes (from same lot; 12 dry shells and 15 alcohol-preserved animals), USNM 1153675.

Etymology. The specific epithet refers to the distribution of this snail on the Oasis Ranch.

Diagnosis. Shell medium-sized, conic; penis having two distal papillae on the inner edge and a basal papilla on the outer edge. Distinguished from its two Pecos River basin congeners by its less convex teleoconch whorls and smooth inner side of the operculum. Further differentiated from *T. cheatumi* (Pilsbry, 1935) in having a basal papilla on the inner edge of the penis, broader central radular teeth, and longer outer wing of the lateral radular teeth; and from *T. circumstriata* (Leonard & Ho, 1960) in having weaker spiral sculpture on the teleoconch whorls and lacking a basal papilla on the inner edge of the penis.

Description. Shell (Fig. 12A–B) up to 3.4 mm tall, large females having 6.25–6.50 whorls, spire height about 180% width of shell, male shells smaller than those of females. Teleoconch whorls weak convex, evenly rounded,

sutures adpressed. Aperture ovate, adapically angled, inner lip complete, thin, adnate, umbilicus narrow or absent. Outer lip thin, orthocline or weakly prosocline. Sculpture of strong growth lines and, in some specimens, weak spiral threads. Periostracum tan.

Measurements of holotype: height 3.52 mm, width 1.40 mm, body whorl height 1.89 mm, body whorl width 1.36 mm, aperture height 0.97 mm, aperture width 0.81 mm, 6.25 whorls.

Outer side of operculum smooth or having edges of last 0.25 operculum whorl weakly frilled (Fig. 12F); inner side of operculum smooth (Fig. 12G). Radula (Fig. 12J-L): dorsal edge of central radular teeth weakly concave, basal tongue rounded, median cusps pointed, lateral cusps four–six, basal cusps two–four (innermost larger) (Fig. 12K). Lateral teeth having three–five cusps on both inner and outer sides, length of outer wing about 200% width of cutting edge, central cusp pointed (Fig. 12L). Inner marginal teeth having 15–25 cusps, outer marginal teeth having 24–36 cusps. Radula data are from USNM 1153675.

Animal darkly pigmented. Penis (Fig. 5N) having two distal papillae on inner edge and a basal papilla on outer edge (15 of 18 specimens), one specimen differed in having three distal papilla on inner edge, one specimen differed in having a (very small) basal papilla on the inner edge, and one specimen differed in lacking a papilla on the outer edge. Distal bulb of penis expanded laterally on inner side, black; stylet small. Penial duct weakly undulating along most of length. Penial data are from USNM 1153675.

Distribution and habitat. Endemic to a single site in the lower Pecos River basin (Fig. 1, locality 13). This complex of large springs, which is also known as T5 Springs (Brune 1981), discharges into two large ponds which have been used for recreational purposes (Karges 2003). *Tryonia oasiensis* was found in low abundance (in silt) along the edges of a short (ca. 5 m) reach of the outflow of the lower pond (Fig. 6P); the water temperature was 20°C. This species could not be found during two subsequent visits to the site in 2011. The status of *T. oasiensis* is uncertain because we have not carefully searched for it in the two ponds; there is no suitable habitat further downflow from the type locality. The ranch, on which these springs are situated, was purchased by The Nature Conservancy in 2000 (Karges 2003).

Remarks. *Tryonia oasiensis* was delineated as a well supported lineage in the Bayesian tree (Fig. 2). This species was discovered coincidentally during a visit to Oasis Ranch to collect other freshwater snails (Hershler *et al*. 2010). We did not obtain shell measurements for *T. oasiensis* (aside from the holotype) because our single sample was very small and most of the specimens were highly eroded.

***Tryonia seemani* (Frauenfeld, 1863)**
(Figs 5O–P, 12C–E, H–I, M–O)

Hydrobia seemani Frauenfeld, 1863: 1025. Frauenfeld, 1865: 525, plate 8.

Types. Syntypes (5 dry shells), BMNH 20001099.

Type locality. N. W. Mexico, Durango.

Referred material. DURANGO. USNM 874125, unnamed spring on west side of Nombre de Dios, 23º51'1.2" N, 104º14'54" W, leg. J.J.L. *et al.*, 7/v/1991. USNM 854937, *ibid.*, leg. R.H. and J.J.L., 11/xii/1998. USNM 873242, unnamed spring in Amado Nervo, southwest of Villa Union, 23º50'34.2" N, 104º11'18" W, leg. J.J.L. *et al.*, 2/xi/1971. USNM 874123, *ibid.*, leg. J.J.L. *et al*., 7/v/1991. USNM 854936, *ibid.*, leg. R.H. and J.J.L., 11/xii/1998.

Diagnosis. Shell medium-sized, conic or turriform, weakly sculptured; penis having two distal and sometimes one basal papillae on the inner edge.

Description (of referred material). Shell (Fig. 12C–E) up to 4.3 mm tall, large females having 5.25–7.25 whorls, spire height 130–200% width of shell, male shells smaller than those of females. Teleoconch whorls medium to highly convex, evenly rounded with impressed sutures. Sculpture of strong growth lines, weak spiral threads rarely present. Aperture pyriform, parietal lip complete in larger shells, usually adnate, rarely slightly disjunct, umbilicus narrow or absent. Outer lip slightly orthocline or prosocline. Periostracum olive or tan.

Shell measurements (mean in parentheses): height 3.01–4.26 mm (3.52), width 1.27–1.59 mm (1.40), body whorl height 1.55–1.89 mm (1.69), body whorl width 1.24–1.52 mm (1.35), aperture height 0.85–1.03 mm (0.94), aperture width 0.72–0.93 mm (0.81), total number of whorls 6.00–7.25 mm (6.44) (USNM 874123, n = 12).

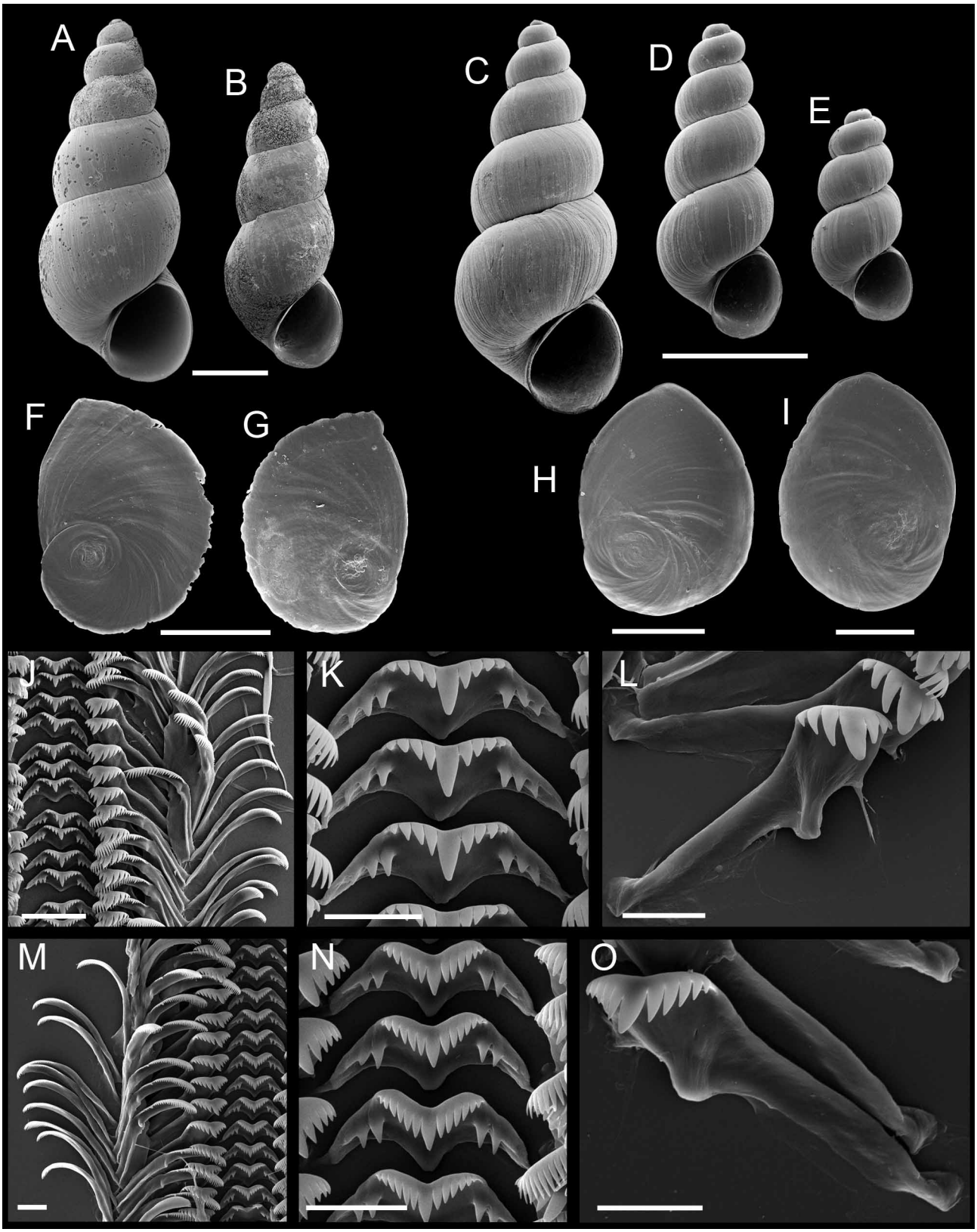

FIGURE 12. *Tryonia oasiensis* **sp. nov**. and *Tryonia seemani* (Frauenfeld). A. Holotype, *T. oasiensis*, USNM 1123759. B. Male shell, *T. oasiensis*, USNM 1153675. C. Shell, *T. seemani*, USNM 874123. D–E. Shells, *T. seemani*, USNM 874125 (D is a male). F–G. Operculum (outer, inner sides), *T. oasiensis*, USNM 1153675. H–I. Operculum (outer, inner sides), *T. seemani*, USNM 874123. J. Portion of radular ribbon, *T. oasiensis*, USNM 1153675. K. Central radular teeth, *T. oasiensis*, USNM 1153675. L. Lateral teeth, *T. oasiensis*, USNM 1153675. M. Portion of radular ribbon, *T. seemani*, USNM 874123. N. Central radular teeth, *T. seemani*, USNM 874123. O. Lateral tooth, *T. seemani*, USNM 874123. Scale bars A–E = 1.0 mm, F–I = 250 µm, J = 25 µm. K–O = 10 µm.

Inner and outer sides of operculum smooth (Fig. 12H–I). Radula (Fig. 12M-O): dorsal edge of central radular teeth concave, basal tongue rounded, median cusps elongate, distally pointed, parallel-sided proximally, lateral cusps five–eight, basal cusps one–two (innermost larger) (Fig. 12N). Lateral teeth having four–seven cusps on inner and five–eight cusps on outer side, length of outer wing 145–185% width of cutting edge, central cusp pointed (Fig. 12O). Inner marginal teeth with 26–37 cusps, outer marginal teeth with 24–34 cusps. Radula data are from USNM 874123, USNM 874125.

Animal lightly pigmented. Penis (Fig. 5O–P) having two (39 of 47 specimens from two samples) or three (5 of 47) distal papillae and sometimes a basal papilla (19 of 47) on inner edge; one specimen differed in having a single distal papilla. Distal bulb of penis expanded laterally on inner side; stylet small. Penial duct nearly straight. Penial data are from USNM 874123, USNM 874125.

Distribution and habitat. Distributed in the upper Río Mezquital drainage (Fig. 1, localities 16–18). The springs at Nombre de Dios are at the western edge of the village on the south side of Highway 45. The first collections (in 1971) of *T. seemani* from this area were from a spring (adjacent to the highway) that flowed south into a canal. Snails were also found in a nearby cienega (Fig. 6Q) which discharged toward the Río Durango. When visited again in 1991 the spring adjacent to the highway was dry and the cienega had been developed for a school. However, *T. seemani* was found abundantly (on vegetation and detritus) in small spring runs (19°C) within the cienega. *Tryonia seemani* has also been collected from springs to the east of Nombre de Dios that are locally referred to as Ojitos de Amado Nervo. The first collections at this site (1971) were made at a highly degraded spring (23°C) by the highway (Fig. 6R) where snails were found at the bases of *Chara* mats. By 1998 this spring had dried, but *T. seemani* was abundant (on aquatic vegetation and soft substrates) in other spring vents and brooks (22°C) about 50 m to the north. The only specimens that had been previously referred to this species (aside from the syntypes) were collected near the end of the 19th century from the spring that served as the domestic water source for Durango City (USNM 251826; Morrison 1945). This site was almost certainly the Ojo de Agua del Obispo (in El Parque Guadiana) (Fig. 1, locality 16) based on historical accounts (e.g., Cigarroa 1990). One of us (J.J.L.) recently (2011) visited this spring, which has been impounded and otherwise extensively modified, and did not find *T. seemani*, which has likely been extirpated from the site.

Remarks. The type locality of *T. seemani* has not been further restricted subsequent to its original description (Hershler *et al*. 2002a); thus it is not known if Frauenfeld was referring to Durango City or, more generally, Durango State (Thompson 2008). Hershler *et al*. (2002a) transferred *Hydrobia seemani* to *Tryonia* based on the glandular penial papillae and short (female) sperm tube that was observed in resuscitated specimens (USNM 251826) whose shells closely conformed to the syntypes of this species. We have further studied these specimens and determined that they also have the diagnostic male reproductive anatomy of *Tryonia*. Hershler *et al*.'s (2002a, fig. 2) illustration of the penis of these snails is incorrect as the basal papilla is actually positioned on the inner (not outer) edge.

The Amado Nervo and Nombre de Dios snails are assigned to *T. seemani* based on the close similarity between their shells and the high spired, convex whorled syntypes of this species (Hershler *et al*. 2002a, fig. 1B). These two populations, which are separated by about 6.0 km, were delineated as a poorly supported (46% posterior probability) clade in the Bayesian analysis (Fig. 2). They differ in shell size (3.52 vs. 2.39 mm shell height, t-test, t = 8.118, df = 18.0, P<0.01, n = 8 for Nombre de Dios sample) and number of shell whorls relative to shell height (1.84 vs. 2.34, t-test, t = -9.275, df = 11.0, P<0.01) (Fig. 12D–F), and are further differentiated in that specimens from Nombre de Dios consistently have a basal penial papilla (all 17 specimens) while those from Adamo Nervo rarely do (2 of 30 specimens). However, our COI data suggests limited (0.8%) genetic divergence between these populations, thus we treat them as conspecific.

Discussion

The novelties described herein increase the diversity of *Tryonia* from 18 to 31 species and partly fill the large (>500 km) gap that previously existed between congeners distributed in the northern (*T. cheatumi*, *T. circumstriata*, *T. hertleini*) and southern (*T. seemani*) portions of the Chihuahuan Desert. Most of the previously described western North American species of *Tryonia* are narrowly distributed within single drainage basins consistent with the apparently tight linkage between these snails and their aquatic habitats. The only exceptions are *T. imitator* (Pils-

bry, 1899), an estuarine species which is distributed along the southern California Pacific Coast (Taylor 1981); and widely ranging *T. porrecta* (Mighels, 1845), which is the only parthenogenetic member of the genus (Hershler *et al*. 2005). All of the new species described herein conform to the typical distribution pattern for the genus except *T. peregrina*, which ranges among the Río Casas Grandes and Río Papigochic basins (Fig. 1, localities 2–3). We speculate that the disjunct distribution of this snail, which is paralleled by several freshwater fishes, is a product of stream capture (Miller 1959, Hendrickson *et al*. 1980, Schönhuth *et al*. 2011) or (inadvertent) translocation. The propensity for local differentiation of *Tryonia* is further evidenced by the morphological and/or genetic divergence among closely proximal populations that was documented for three of species treated herein (*T. contrerasi*, *T. seemani*, *T. taylori*). The most interesting example is provided by *T. taylori*, whose phylogeographic structure (Fig. 2, Table 2) suggests that its morphologically distinctive populations have not yet diverged to the point of reciprocal monophyly or are undergoing secondary contact at Ojo de Servin. The only previously reported occurrence of sympatric *Tryonia* species was from Ash Meadows, southern Nevada (Hershler & Sada 1987). Herein we have documented additional instances of sympatric species pairs in both the Río Conchos (*T. chuviscarae*, *T. minckleyi*) and Río Santa Maria (*T. angosturae*, *T. ovata*) basins. Interestingly, in both cases the congeners involved do not appear to be sister species (Fig. 2).

Although the phylogenetic relationships of *Tryonia* generally were not well resolved using COI data, our Bayesian analysis nonetheless delineated two strongly supported lineages composed of species described herein (Fig. 2). One of these (clade A) contains species from several drainage basins in Chihuahua while the other (clade B) is a local species flock (in the Río Conchos basin) whose members live in the warmest waters yet recorded for *Tryonia*. The long branches associated with this lineage suggest that it is relatively old or has evolved at an especially rapid rate.

Although some of the new species described herein are distributed in habitats that contain previously recognized endemic taxa, e.g., Balneario de San Diego de Alcala (Bowman 1981, Minckley & Minckley 1986, Meyer *et al*. 2010), Ojo Vareleño (Schotte 2000, Hershler *et al*. 2002b), springs near Ejido Rancho Nuevo (Smith & Miller 1980); others such as *T. metcalfi* and *T. molinae* are from "new" localities and thus may help delineate additional areas of endemism within the Chihuahuan Desert. One of these novelties (*T. julimesensis*) became extinct sometime between 1991 and 2001 and another (*T. oasiensis*) disappeared from its single known locality shortly after it was first discovered in 2009 and also may be extinct. All of the other species treated herein are at risk of extirpation because of the declining extent and quality of their unprotected habitats as described above.

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