Systematics of the North and Central American Aquatic Snail Genus *Tryonia* (Rissooidea: Hydrobiidae)

ROBERT HERSHLER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 612

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Folklife Studies
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Lawrence M. Small
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 612

Systematics of the North and Central American Aquatic Snail Genus *Tryonia* (Rissooidea: Hydrobiidae)

Robert Hershler

Smithsonian Institution Press
Washington, D.C.
2001

ABSTRACT

Hershler, Robert. Systematics of the North and Central American Aquatic Snail Genus *Tryonia* (Rissooidea: Hydrobiidae). *Smithsonian Contributions to Zoology*, number 612, 53 pages, 29 figures, 2 maps, 2001.—Morphological variation among members of the genus *Tryonia* (and its subgenus *Paupertryonia*) is congruent with a recently published phylogenetic analysis based on mtDNA sequences that showed that these taxa are polyphyletic assemblages of ecologically similar snails. *Tryonia* is reconstituted as a North and Central American monophyletic subunit of the subfamily Cochliopinae based on a synapomorphy of posterodorsal insertion of the vas deferens into the prostate gland. Presumably derived modifications of the shell, radular teeth, and genitalia unite groups of species within this genus.

Tryonia is redefined and 18 species are recognized in the genus. Congeners are *T. aequicostata* (Pilsbry, 1890a), distributed in the Florida peninsula; *T. cheatumi* (Pilsbry, 1935) and *T. circumstriata* (Leonard and Ho, 1960), Rio Grande basin; *T. hertleini* (Drake, 1956), interior drainage of northeast Mexico; *T. clathrata* Stimpson, 1865, and *T. gilae* Taylor, 1987, lower Colorado River basin; *T. angulata* Hershler and Sada, 1987, *T. elata* Hershler and Sada, 1987, *T. ericae* Hershler and Sada, 1987, *T. margae* Hershler, 1989, *T. monitorae* Hershler, 1999, *T. rowlandsi* Hershler, 1989, *T. salina* Hershler, 1989, and *T. variegata* Hershler and Sada, 1987, southern Great Basin; *T. porrecta* (Mighels, 1845), lower Colorado River basin, Great Basin, Hawaii; *T. quitobaquitae* Hershler in Hershler and Landye, 1988, Rio Sonoyta basin; *T. imitator* (Pilsbry, 1899), southern California coast; and *T. exigua* (Morelet, 1851), Lake Petén Itza, Guatemala. *Tryonia protea* (Gould, 1855) is found to be a junior synonym of *Paludina porrecta* Mighels, 1845.

Tryonia kosteri Taylor, 1987, from the Pecos River basin, is found to be a member of the genus *Durangonella* Morrison, 1945, which was previously known only from the Mexican Plateau. A new North American genus, *Pseudotryonia* Hershler, is erected for three species previously placed in *Tryonia*. *Pseudotryonia* is diagnosed by a combination of genitalic characters. Its congeners are *P. brevissima* (Pilsbry, 1890b), Florida panhandle; *P. adamantina* Taylor, 1987, and *P. alamosae* Taylor, 1987, Rio Grande basin; and an undescribed species from the Tombigbee River basin. A new monotypic genus, *Ipnobius* Hershler, is erected for *Tryonia robusta* Hershler, 1989, from Death Valley, California. *Ipnobius* is diagnosed by genitalic autapomorphies. Lectotypes are designated for *Melania exigua* Morelet, and *Amnicola protea* Gould.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Annals of the Smithsonian Institution.* SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging-in-Publication Data
Hershler, Robert
Systematics of the North and Central American aquatic snail genus Tryonia
(Rissooidea: Hydrobiidae) / Robert Hershler.
p. cm. — (Smithsonian contributions to zoology ; no. 612)
Includes bibliographical references (p.)
1. Tryonia–Classification. I. Title. II. Series.
QL1.S54 no. 612 [QL430.5.H9] 590 s–dc21 [594'.32] 2001020792

♾ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

Contents

Systematics of the North and Central American Aquatic Snail Genus *Tryonia* (Rissooidea: Hydrobiidae)

Robert Hershler

Introduction

The gastropod subfamily Cochliopinae (family Hydrobiidae), composed of 31 genera and more than 260 Recent species, is one of the largest groups of aquatic mollusks in the New World (Hershler and Thompson, 1992). As is the case for hydrobiids generally, the systematics of cochliopine snails is in an early stage of refinement. Monophyly of the Cochliopinae has not been rigorously established, although diagnostic features include several possible synapomorphies within the context of the Hydrobiidae, notably the posterior folding of the female glandular oviduct (Hershler and Thompson, 1992). Phylogenetic structure of the Cochliopinae has not been evaluated, and most of its species are still known only by their shells. In what was intended as a first step toward revising the Cochliopinae, Hershler and Thompson (1992) redefined its genera based on shell and anatomical characters, but this study focused largely on type species only.

Tryonia Stimpson, 1865, is the fourth largest cochliopine genus, with 23 Recent species currently placed in the group (Hershler and Thompson, 1992; Hershler, 1999). *Tryonia* ranges across southern North America, with most congeners concentrated in the major drainages of the American Southwest. Although present in the Rio Grande basin and Gulf Coastal and Atlantic drainages in Florida, *Tryonia* is absent from the intervening southern Great Plains and Mississippi River basin. Although most *Tryonia* species are restricted to springs, which often are thermal and highly mineralized, some congeners also live in lakes (Thompson, 1968, as *Hyalopyrgus*), and one species is restricted to brackish, coastal waters (Kellogg, 1985). When present, these tiny snails are typically among the more abundant members of the invertebrate benthos (e.g., Meffe and Marsh, 1983). The genus also is of interest in terms of reproductive biology because one species is parthenogenetic (Mulvey and Hershler, ms), and many congeners have skewed sex ratios and marked sexual dimorphism in body size (Thompson, 1968 (as *Hyalopyrgus*); Taylor, 1987). Owing to their typical narrow distributions and small habitats, western congeners are especially vulnerable to perturbations relating to water development: one species (*T. alamosae*) is currently listed as endangered by the United States Fish and Wildlife Service (USDI, 1991), and three others (*T. adamantina, T. kosteri, T. stocktonensis* (=*T. circumstriata*)) are candidates for addition to this list (USDI, 1997).

Most species of *Tryonia* are readily distinguished by shell and penial characters, and their taxonomy has been little confused at the specific level; however, the scope and content of the genus has been unstable and continues to rest on a shaky foundation. *Tryonia* was established as a monotypic genus by Stimpson (1865) for his new species, *T. clathrata*, which was described from material that probably originated from the White River trough in southeast Nevada (Stearns, 1893, 1901; Morrison, 1940; Taylor, 1966b). Although *Tryonia* is considered exclusively North American in the most recent literature (Taylor, 1987; Hershler and Thompson, 1992), Central and South American taxa previously have been placed in the genus, beginning with Tate (1870) and especially by Taylor (1966b). Allocations of Neogene fossils from tropical America to *Tryonia* remain controversial (Nuttall, 1990; Wesselingh, 1996). Whereas Hershler and Thompson (1987) and Thompson (1999) allocated snails from the southeast United States to *Tryonia*, Taylor (1987) treated the genus as exclusively western.

Robert Hershler, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560.

Review Chairman: Kristian Fauchald, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560.

Reviewers: Terrence J. Frest, Deixis Consultants, 2517 NE 65th Street, Seattle, Washington, 98115; and one anonymous reviewer.

Stimpson (1865) originally diagnosed *Tryonia* by the narrow, ribbed shell of its type species. A simple conchological definition of *Tryonia* remained in place for more than 100 years until a limited anatomical context was provided by Taylor (1966b), who placed the genus in the subfamily Littoridininae (= Cochliopinae), which he characterized in part by penial ornament of bulbous or elongate lateral lobes. In a subsequent publication, Taylor (1987) diagnosed *Tryonia* by features that included a penis ornamented with a small number of glandular papillae and having a bulbous, pigmented distal portion, with a terminal stylet (Figure 1); however, neither these nor the additional female genitalic features used by Hershler and Thompson (1992) to diagnose *Tryonia* are unique to the group. The concept of *Tryonia* also is vague because the anatomy of only five congeners has been described in detail (*T. angulata*, Hershler and Sada, 1987; *T. clathrata*, Hershler and Thompson, 1987, 1992; *T. gilae*, *T. quitobaquitae*, Hershler and Landye, 1988; *T. monitorae*, Hershler, 1999). Most other congeners are known only in terms of shell and external morphology (e.g., species described by Taylor, 1987) or only by their shells (e.g., *T. hertleini*, *T. imitator*).

During the past decade alcohol-preserved material was acquired for 22 of the 23 extant species assigned to *Tryonia* in recent treatments. A survey of morphological variation has revealed that only 17 of these congeners conform to the anatomical groundplan of the type species, and it suggested a basis for recognizing this subset of taxa as a monophyletic unit. The purposes of the present study are to (1) redefine and revise the content of *Tryonia,* (2) briefly describe the Recent species of *Tryonia* s.s., and (3) transfer five species incorrectly identified as *Tryonia* in the recent literature to three other genera, two of which are newly described herein. This revision of *Tryonia*-like snails is completely congruent with a phylogenetic analysis based on mtDNA sequences, which revealed this genus as composed of four distinct lineages that together do not form a monophyletic group (Hershler, Liu, and Mulvey, 1999, fig. 3). This paper is the third and final part of a series reviewing the larger genera of western North American hydrobiid snails (Hershler, 1994; Hershler and Frest, 1996).

Material and Methods

Tryonia brunei Taylor, 1987, was the only extant species of *Tryonia* s.l. for which anatomical material could not be obtained, because this snail could not be found at its only known locality in west Texas. In the wake of the present study, available data (Taylor, 1987) are not sufficient to confidently assign this species to a genus. For the same reason, the various fossil and subfossil species that have been assigned to *Tryonia* are not treated in this study.

Snails used for anatomical study were fixed in dilute formalin (10% of stock solution) and were preserved in 70% ethanol. Unless otherwise specified, dissected specimens were relaxed with menthol crystals (prior to fixation) so that the head-foot and penis were extended. Prior to dissection of snails, shells were removed by immersion in dilute hydrochloric acid. Sections were cut at 4 μm and stained with hematoxylin and eosin. Methods of preparation of material for scanning electron microscopy follow Hershler (1998). All drawings were made with a camera lucida. Penial drawings were of whole-mounted preparations that were stained in hematoxylin and then cleared.

In referring to size of shells, the following states were recognized: small (shell height<2.0 mm), medium (2.0–5.0 mm), and large (>5.0 mm). Other character states are either keyed to an illustration or follow those described and illustrated by Hershler and Ponder (1998). Length of the outer wing of the lateral radular tooth was measured along its long axis, rather than parallel to the dorsal edge of the tooth face (fide Hershler and Ponder, 1998, fig. 9a), so that this feature could be described independently of wing flexure (e.g., angling of the wing relative to the tooth face).

Inasmuch as most congeners have been well described in terms of traditional characters (Thompson, 1968; Hershler and Sada, 1987; Taylor, 1987; Hershler, 1989, 1999), all of this information is not reiterated herein, but instead capsule summaries are provided that focus on diagnostic and newly acquired data. Owing to the limited alcohol-preserved material available for most species, sexual dimorphism in body size was not analyzed within the context of this study. Note that shape of the wings on the marginal radular teeth may provide useful information for discriminating among species of *Tryonia*-like taxa, but it was not studied in sufficient detail for utilization herein.

All type specimens cited have been examined. Holotypes for species described by Taylor (1987) are alcohol-preserved specimens whose shells are now softened. Paratype shells are instead figured for these taxa. This study is largely based on material reposited at the National Museum of Natural History (NMNH) (which houses the collections of the former United States National Museum (USNM), Smithsonian Institution), although type specimens and additional material from the Academy of Natural Sciences of Philadelphia (ANSP), Bernice P. Bishop Museum (BPBM), California Academy of Sciences (CAS), Florida Museum of Natural History (UF), Los Angeles County Museum of Natural History (LACM), The [British] Natural History Museum (BMNH), Santa Barbara Museum of Natural History (SBMNH), and University of Michigan Museum of Zoology (UMMZ) also were examined. In the "Material Examined" section of each species account, reference is only made to material figured in this paper and to alcohol-preserved material used for dissection.

Acknowledgments

The following individuals and institutions loaned specimens: G. Rosenberg (ANSP), R. Cowie (BPBM), T. Gosliner and E. Kools (CAS), F.G. Thompson (UF), L. Groves and J.H. McLean (LACM), P. Mordan (BMNH), P.V. Scott (SBMNH),

and J.B. Burch (UMMZ). Art Metcalf (University of Texas, El Paso) greatly facilitated the study of species described by Taylor (1987) by distributing paratypes of these taxa to the NMNH. Fred G. Thompson and J.J. Landye generously provided live or freshly preserved material for various species. Yolanda Villacampa (NMNH) gathered radular data, prepared scanning electron micrographs, and prepared photographic prints. Kary Darrow (NMNH) inked anatomical drawings and Molly Ryan (NMNH) prepared shell drawings and assisted with the preparation of plates. Dan Cole (NMNH) generated the base map of North and Central America. This study was partly supported by awards from the Bureau of Land Management (United States Department of the Interior), Biological Resources Division of the United States Geological Survey, and the Smithsonian Institution's Scholarly Studies Program. Terrence J. Frest and an anonymous reviewer are thanked for their constructive comments on a draft version of this paper.

Family HYDROBIIDAE Troschel, 1857

The name is preoccupied in Coleoptera (Newton and Thayer, 1990); see Giusti et al. (1998) for a proposal to remove the homonymy.

Subfamily COCHLIOPINAE Tryon, 1866

Genus *Tryonia* Stimpson, 1865

Tryonia Stimpson, 1865:54 [type species: *Tryonia clathrata* Stimpson, 1865, by original designation].—[Not *Tryonia* Stephenson, 1941:331; Mollusca: Buccinidae?]

Calipyrgula Pilsbry, 1934:15 [type species: *Calipyrgula carinifer* Pilsbry, 1934, by original designation].—Hershler and Thompson, 1992:107 [synonymized with *Tryonia*.]

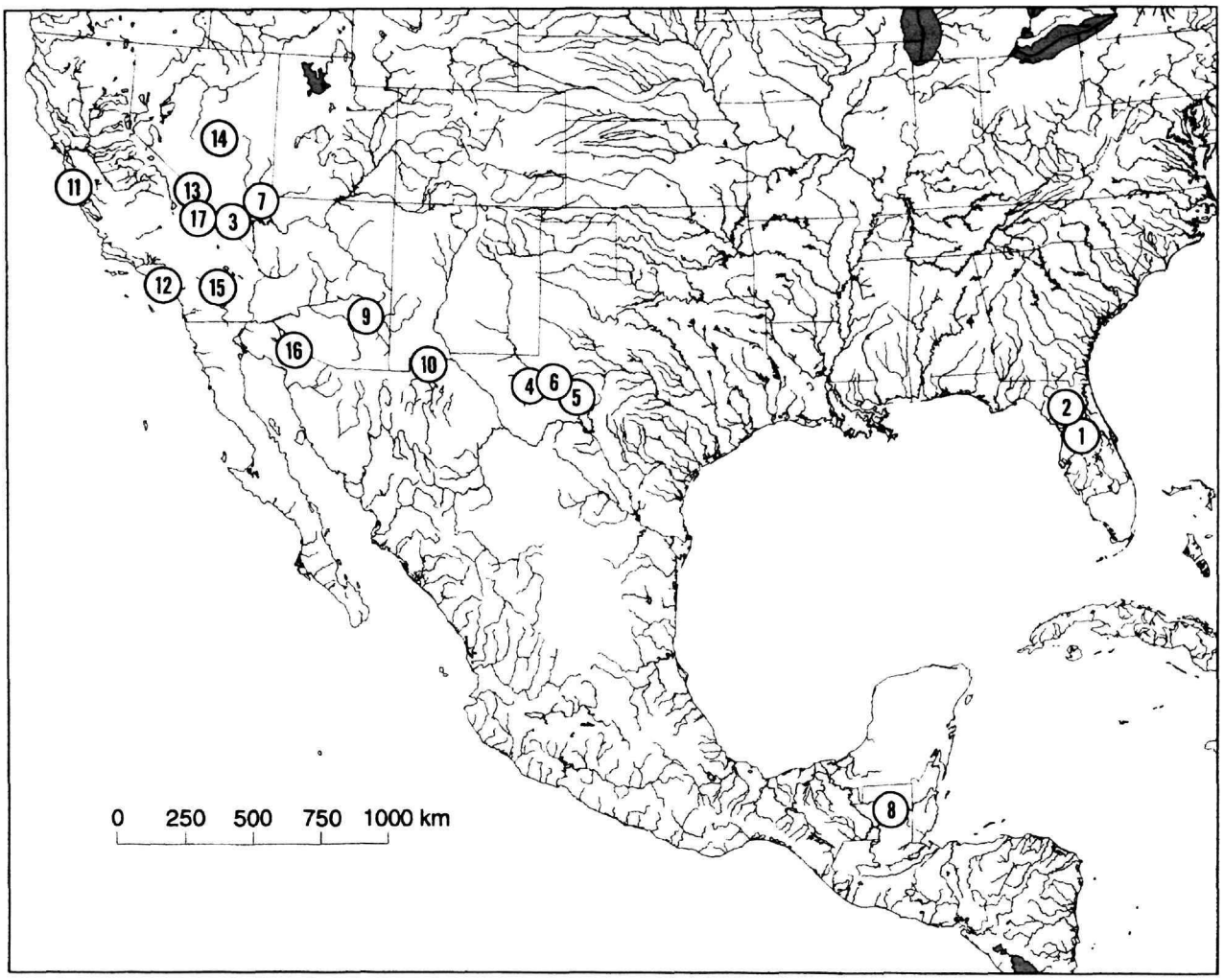
Hyalopyrgus Thompson, 1968:43 [type species: *Bythinella aequicostata* Pilsbry, 1890a; by original designation].—Hershler and Thompson, 1987:26 [synonymized with *Tryonia*].

Paupertryonia Taylor, 1987:38 [type species: *Potamopyrgus cheatumi* Pilsbry, 1935, by original designation; proposed as subgenus of *Tryonia*].—Hershler and Thompson, 1992:107 [synonymized with *Tryonia*.]

DIAGNOSIS.—Shell ovate-conic to turriform, smooth or variously sculptured. Penis ornamented with 2–6 glandular papillae borne singly along edges; distal penis often swollen along inner edge. Females ovoviviparous. Bursa copulatrix and seminal receptacle present; renal oviduct a large coil, usually pigmented; sperm duct coiled, opening to bursal duct behind pallial wall; sperm tube variable in length.

DESCRIPTION.—Shell (Figure 4) gray or clear, 1.2–7.5 mm tall, ovate-conic to turriform, whorls 3.75–9.75. Periostracum thin. Protoconch (Figure 5) small (<1.0 whorl), blunt, typically smooth; teleoconch smooth or variably sculptured. Aperture usually small, inner lip usually complete across parietal wall, umbilicus variable. Operculum (Figure 6) thin, ovate or ellipsoidal, multispiral, nucleus eccentric, inner side usually without pronounced muscle scar. Ctenidium well developed, connected to pericardium by short efferent vein (Figure 2B); lateral surfaces of ctenidial filaments often bearing low ridges (pleats). Osphradium small (Hershler and Landye, 1988, fig. 42), narrow, usually centrally positioned along ctenidial axis. Kidney having small pallial portion (Hershler and Landye, 1988, fig. 44a), opening slightly muscularized. Pericardium bulging slightly into pallial cavity (Hershler and Landye, 1988, fig. 44a). Style sac about as long as remainder of stomach, posterior caecum of stomach absent or small (Figure 2C). Rectum straight, anus near mantle edge. Radula with 35–55 tooth rows, cusps generally narrowly pointed. Central teeth trapezoidal, with 1–3 pairs of basal cusps (Figure 7). Lateral teeth with enlarged central cusp; basal tongue usually well developed; outer wing longer than width of tooth face (Figure 8). Inner (Figure 9) and outer (Figure 10) marginal teeth with numerous (15 to 37) cusps borne largely or entirely on outer side; teeth with well-developed wings on outer edge and narrow, raised area extending from face to base. Large testis of numerous (>10) stalked lobes; seminal vesicle exiting from and tightly coiled against left side of anterior portion of testis (Figure 2D). Prostate gland usually small, largely or entirely visceral (Hershler and Landye, 1988, fig. 44a). Visceral vas deferens opening to posterodorsal edge of prostate gland, pallial vas deferens exiting from anterior edge of prostate gland. Penis medium to large (Taylor, 1987, fig. 17d), narrow, base slightly expanded; terminal portion densely ciliated (Hershler and Landye, 1988, fig. 45), usually bulbous, often with swelling along inner edge (Figure 1). Penial-duct opening through well-developed stylet. Edges of penis ornamented with 2–6 glandular papillae borne singly. Penis usually darkly pigmented with melanin distally, variably pigmented elsewhere. Females ovoviviparous, brooded young few to many (2–30), of different sizes (having up to 2.5 shell whorls). Ovary a small, simple sac. Glandular oviduct large, mostly consisting of thin-walled brood pouch, usually with a single posterior fold, anterior opening muscular (Figure 3). Albumen gland very small relative to brood pouch (Figure 3C), positioned partly or entirely on right side of bursa copulatrix. Bursa copulatrix small relative to brood pouch (Figure 3A–C), duct exiting anterior edge. Seminal receptacle usually smaller than bursa copulatrix, positioned along anteroventral portion of bursa copulatrix, duct usually short (Figure 3D). Sperm duct entirely visceral, of two overlapping loops, opening to bursal duct. Oviduct issuing small gonopericardial duct proximal to coiled section. Renal oviduct a single, large, almost vertical loop; epithelium of loop usually invested with pigment. Distal to loop, oviduct connecting to seminal receptacle duct by a very short duct and opening to posterior edge of albumen gland. Sperm tube narrow, opening either in posterior or anterior portion of pallial cavity (opening fused with that of brood pouch in one species).

DISTRIBUTION.—*Tryonia* is disjunctly distributed in southern North America, with congeners living in the Florida Panhandle and in a western region extending from the Rio Grande basin to the Pacific Coast (Map 1). With the reallocation of *Melania exigua* Morelet to *Tryonia* herein, the range of the genus is ex-



MAP 1.—Type locality areas of *Tryonia* species and junior synonyms thereof: 1, Lake Panasoffkee, Florida (*T. aequicostata*); 2, Oklawaha River drainage, Florida (*Fontigens oxybeles=T. aequicostata*); 3, upper Amargosa River drainage, Nevada (*T. angulata, T. elata, T. ericae, T. variegata*); 4, Phantom Lake, Texas (*T. cheatumi*); 5, late Pleistocene deposits, Pecos River drainage, Texas (*T. circumstriata*); 6, Pecos River drainage, Texas (*T. stocktonensis=T. circumstriata*); 7, White River drainage, Nevada (*T. clathrata*); 8, Lake Petén Itza, Péten, Guatemala (*T. exigua*); 9, Gila River drainage, Arizona (*T. gilae*); 10, interior drainage, Chihuahua, Mexico (*T. hertleini*); 11, coastal drainage, Santa Cruz, California (*T. imitator*); 12, Pleistocene deposits, San Pedro, California (*Paludestrina curta=T. imitator*); 13, lower Amargosa River drainage, California (*T. margae, T. rowlandsi*); 14, Monitor Valley, Nevada (*T. monitorae*); 15, Salton Sea basin (*Amnicola protea, Pyrgulopsis imminens, Pyrgulopsis blakeana, Pyrgulopsis cahuillarum*, all synonyms of *T. porrecta*); Rio Sonoyta drainage, Arizona (*T. quitobaquitae*); 17, lower Amargosa River drainage, California (*T. salina*). The Hawaiian type locality for *T. porrecta* is not shown.

tended into northern Central America. This Guatemalan species is broadly disjunct from northern congeners, although this gap may be narrowed upon completion of ongoing taxonomic study of undescribed *Tryonia*-like snails (e.g., Williams et al., 1985; Minckley and Minckley, 1986) of northern Mexico. A clearer indication of the southern extent of the range of *Tryonia* must await further study of the poorly known hydrobiid fauna of Tropical America, which includes two Recent Brazilian species (described by Haas, 1938, 1949) that were allocated to the genus by Taylor (1966b). The allocation of a European fossil to *Tryonia* by Sandberger (1875:672) is disregarded herein following Fischer and Crosse (1891:256).

REMARKS.—Live animals of three species (*T. aequicostata, T. clathrata, T. gilae*) were examined for details of head-foot

morphology, which are as follows: snout rectangular, slightly expanded distally; cephalic tentacles slightly longer to about 150% length of snout, slender, tapering but little distally; snout and tentacles variably pigmented with melanin and scattered white or yellow granules, granules concentrated around eyespot and along edges of "neck." Ciliation of penis, head, and floor of pallial cavity was not studied in detail, but it is a possible source of additional characters. Previous work on four species has shown that the cephalic tentacles bear several longitudinal ciliary tracts, and the left tentacle has a few transverse bands of cilia along the outer edge basally (Hershler and Thompson, 1987, figs. 13–17; Hershler and Landye, 1988, fig. 41a–e). Note that in *Tryonia* (and the other genera reviewed below) the small protoconch is well demarcated only in uneroded embryonic shells (Figure 5E), and the transition between the end of growth in the brood pouch and the remainder of the teleoconch is usually indistinct.

In all members of *Tryonia* s.s. (except parthenogenetic *T. porrecta*), the visceral portion of the vas deferens inserts into the posterodorsal edge of the prostate gland (Figure 2A). The generalized condition in hydrobiid snails is for the visceral vas deferens to instead open to the ventral edge of the prostate gland. This condition apparently is unique to *Tryonia* within the Cochliopinae (and perhaps the Hydrobiidae generally) and therefore is hypothesized to be synapomorphic for the genus. A phylogenetic analysis of mtDNA sequences (Hershler, Liu, and Mulvey, 1999) also indicated monophyly (with high bootstrap support) of this group (minus *T. exigua* and *T. hertleini*, which were not included in the study). *Tryonia* is further distinguished from *Mexipyrgus*, which is closely similar morphologically (Hershler and Thompson, 1992) and has been identifed as the sister taxon to this genus based on mtDNA sequences (Hershler, Liu, and Mulvey, 1999), by the combination of a simple pattern of posterior looping of the glandular oviduct, and the small size of the bursa copulatrix relative to the brood pouch (compare Figure 3 with Hershler, 1985, figs. 41–43).

Although variation within *Tryonia* is not marked, several subunits of the genus are recognizable on the basis of morphology (and variously supported by mtDNA sequences; Hershler, Liu, and Mulvey, 1999). In two California congeners (*T. imitator*, *T. salina*), the basal tongue of the central radular teeth is weakly convex (Figure 7B), whereas in all other congeners, and in cochliopines generally, the basal tongue is V- or U-shaped (Figure 7A,D–F). These two species are further united by their relatively squat shells and broad central cusps of the central radular teeth. In 12 *Tryonia* species the terminal, bulbous portion of the penis has a pronounced swelling along the inner edge (e.g., Figure 1), whereas in the remaining six congeners, all from the Amargosa River and Gila River drainages (*T. angulata*, *T. elata*, *T. ericae*, *T. gilae*, *T. rowlandsi*, *T. variegata*), the bulb is evenly rounded (e.g., Figure 25F) as in other cochliopines. Therefore the distal swelling of the terminal bulb is hypothesized as a synapomorphy for this large group of congeners. In two congeners from the Amargosa River basin (*T. elata*, *T. ericae*), the long sperm tube abuts or is fused with (e.g., Figure 3A) the opening of the brood pouch. In all other congeners, the sperm tube opens in the posterior half of the pallial cavity (Figure 3B,C). Although both conditions occur among other cochliopines (Hershler and Thompson, 1992), *Mexipyrgus*, the presumed sister taxon to *Tryonia* (fide Hershler, Liu, and Mulvey, 1999) has a short tube; thus, the elongate condition is interpreted as a derived feature uniting these two congeners. Two congeners from the Great Basin (*T. margae*, *T. monitorae*) share a narrow, generally turriform shell (Figure 23G,H), whereas other congeners, *Mexipyrgus*, and cochliopine snails generally have a broader shell.

As pointed out by Kabat and Hershler (1993), early treatments of *Tryonia* as synonymous with one or more genera of Lake Baikal (Asia) hydrobioids (Dall, 1877; Tryon, 1883) were erroneous, as there are no anatomical features suggesting a close phylogenetic relationship between these broadly disjunct groups. Instead, *Tryonia* is related most closely to North American snails (Hershler, Liu, and Mulvey, 1999). Taylor (1966b) placed three genera of Neogene fossils from the Amazon basin of South America (*Liris* Conrad, 1871; *Dyris* Conrad, 1871; *Conradia* Wenz, 1925) in synonymy with *Tryonia*. These synonomies were rejected by Parodiz (1969), who instead compared the South American fossil taxa to *Calipyrgula* (which is now considered a synonym of *Tryonia*). Nuttall (1990) also maintained that *Tryonia* is distinct from these Neogene taxa, given the differences in their shells and their broadly disjunct temporal and geographic distributions. Wesselingh (1996), however, identified putative fossil *Tryonia* in intervening portions of central and northernmost South America. Given that *Tryonia* is diagnosed by an anatomical character and Recent *Tryonia*-like snails represent a phylogenetic mosaic (Hershler, Liu, and Mulvey, 1999), generic placement of these fossils probably will remain controversial until a stronger phylogenetic signal can be extracted from the shells of hydrobioid snails.

Taylor (1987) erected the subgenus *Paupertryonia* for five species from the Rio Grande basin, which he diagnosed by the absence of basal papillae on the penis. Based on the results of the current study, only the type species of this subgenus (*T. cheatumi*) is retained in *Tryonia,* whereas other members are allocated to *Durangonella* and a new genus described below. MtDNA sequences (Hershler, Liu, and Mulvey, 1999) congruently indicated that *Paupertryonia* consists of three distinct lineages (which together do not form a monophyletic group).

Tryonia aequicostata (Pilsbry, 1890)

Bythinella aequicostata Pilsbry, 1890a:86, pl. III: fig. 16 [type locality, Sumter County, Florida].—Baker, 1964:171 [lectotype selection].

Fontigens oxybeles Pilsbry, 1950:37–38, pl. 3: figs. 1,1a,1b [type locality, Silver Spring Run, Lake George, Marion County, Florida].—Thompson, 1968:46 [synonymized with *Hyalopyrgus aequicostatus*].

Hyalopyrgus aequicostatus.—Thompson, 1968:46–52, figs. 5, 25C,D, 29F, 32B, 39A–F, 49A–E, 59D–F, tables 2, 3 [reassignment; suggested type lot probably from Lake Panasoffkee, Florida].

plete but very thin across parietal wall; shell imperforate or narrowly umbilicate. Operculum (Figure 6B) ovate, border of attachment area slightly thickened. Ctenidial filaments about 27, pleated. Stomach with very small posterior caecum. Radula with about 51 rows of teeth, length/width of ribbon 550%. Dorsal edge of central radular teeth slightly convex to indented, basal tongue U-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4–6; basal cusps 1 or 2, outer cusps weakly to well developed. Lateral teeth (Figure 8B) with 3 cusps on inner side and 3 or 4 cusps on outer side; outer wing broad, well flexed, length 167% width of tooth face. Inner marginal teeth with 18–26 cusps, outer marginal teeth with 31–41 cusps.

Prostate gland small, ovate, pallial section 33% of total length. Distal penis blunt, pigmented, swelling along inner edge small, penial duct nearly straight (Figure 25C). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening subterminal, slightly thickened; brooded embryos about 13. Albumen gland on right side of bursa copulatrix. Bursa copulatrix medium to large for genus, narrowly ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior 33%–50% of pallial cavity.

DISTRIBUTION.—Drainage of Toyah Creek, Pecos River basin, Texas.

REMARKS.—*Tryonia cheatumi* is distinguished from other congeners by the absence of basal papillae on the penis (Figure 25C).

MATERIAL EXAMINED.—UNITED STATES. *Texas:* Phantom Lake, Reeves County, ANSP 16388 (lectotype); Phantom Lake spring, Reeves County, USNM 883952, USNM 883955, USNM 883957.

Tryonia circumstriata (Leonard and Ho, 1960)

Calipyrgula circumstriata Leonard and Ho, 1960:125–127, pl. 12: figs. 1–3 [type locality, late Pleistocene terrace deposits in right bank of Pecos River, one-fourth mile [0.4 km] above mouth of Independence Creek, on Chandler Ranch, Terrell County, Texas].

Tryonia circumstriata.—Taylor, 1966b:196–197 [reassignment].

Tryonia stocktonensis Taylor, 1987:37–38, fig. 18, table 42 [type locality, Diamond Y Draw, nine miles [14.4 km] north of Fort Stockton and 0.5 mile [0.8 km] west of State Highway 18, Pecos County, Texas].—Hershler and Thompson, 1992:110 [synonymized with *Tryonia circumstriata*].

DIAGNOSIS.—Shell medium- to large-sized, conical. Penial ornament of 2 distal papillae along inner edge and single, large, basal papillae on inner and outer edges.

DESCRIPTION.—Shell (Figures 4H, 22E,F) 3.0–5.5 mm tall. Shell apex shown in Figure 5A,C. Whorls, 5.0–7.0, medium convexity; teleoconch almost smooth or sculptured with 10–15 regularly spaced spiral lirae, sometimes crossed by weak collabral ribs. Aperture ovate-pyriform, lip complete, thin, adnate; shell imperforate or narrowly umbilicate. Operculum ovate, border of attachment area weakly thickened (Figure 6D). Ctenidial filaments about 25, pleated. Stomach without posterior caecum. Radula with about 36 rows of teeth; length/width of ribbon 450%. Dorsal edge of central teeth (Figure 7F) weakly indented, basal tongue broadly V-shaped, central cusps broadly triangular, lateral cusps 4–6; basal cusps 2 or 3, outer cusps sometimes weakly developed. Lateral teeth with broad central cusp, 3–5 cusps on inner side and 5–7 cusps on outer side; outer wing strongly flexed, length 170% width of tooth face. Inner marginal teeth (Figure 9D) with 23–31 cusps, outer marginal teeth with 28–39 cusps.

Prostate gland large, bean-shaped, pallial section 33%–50% of total length. Terminal portion of penis blunt, pigmented, pronounced swelling along inner edge, penial duct undulating (Figure 25D). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, slightly muscularized, brooded embryos 7–10. Albumen gland on right side of bursa copulatrix. Bursa copulatrix large for genus, narrowly ovate; seminal receptacle much smaller than bursa copulatrix, globular. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior one-third of pallial cavity.

DISTRIBUTION.—Pecos River drainage, Texas.

REMARKS.—This species is distinguished from *T. cheatumi* (the only other congener present in the Pecos River drainage) by its narrower, more strongly sculptured shell and by its more numerous penial papillae. Extant populations are variable in sculpture and include weakly lirate and nearly smooth-shelled individuals (Figure 22F), but nonetheless they intergrade completely with Pleistocene material, which was the basis for earlier placement of *T. stocktonensis* in synonymy with *T. circumstriata* (Hershler and Thompson, 1992).

MATERIAL EXAMINED.—UNITED STATES. *Texas:* Diamond Y Draw, Pecos County, LACM 2090 (holotype, *Tryonia stocktonensis*), USNM 854092 (paratypes, *Tryonia stocktonensis*), USNM 883406, USNM 883958; Diamond Y Spring, Pecos County, USNM 892020; late Pleistocene deposits along Pecos River, Terrell County (holotype, *Calipyrgula circumstriata*), USNM 440734.

Tryonia clathrata Stimpson, 1865

Tryonia clathrata Stimpson, 1865:54, pl. 8: fig. 1 [type locality, basin of the Colorado Desert].—Baker, 1964:172 [lectotype selection].—Hershler and Thompson, 1987, figs. 1, 2, 11–15, 19, 21–23; 1992, figs. 71a,c–e, 72.—Hershler, 1999:331–332, fig. 14 [distribution map].

DIAGNOSIS.—Shell medium- to large-sized, conical. Penial ornament of 4 medial to proximal and 1 basal papillae along inner edge, and occasional basal papilla arising from near midline (rather than from penis edge).

DESCRIPTION.—Shell (Figures 4E, 22G) 2.9–7.0 mm tall. Whorls, 5.75–8.75, weakly convex; collabral sculpture varying from low ribs to almost spinose projections, beginning at about 1.5 whorls, becoming strong at whorl 3.0; sculptural elements about 15 on body whorl. Aperture ovate-pyriform, lip complete in larger specimens, thin, adnate; shell imperforate or narrowly umbilicate. Operculum (Figure 6C,F) ellipsoidal, nucleus

highly eccentric, inner side smooth. Ctenidial filaments about 42, pleated. Stomach with small posterior caecum. Radula with about 56 rows of teeth; length/width of ribbon 550%. Dorsal edge of central radular teeth (Figure 7D) weakly indented, basal tongue U-shaped, central cusps narrowly pointed, lateral cusps 6–8, basal cusps 2 or 3. Lateral teeth (Figure 8A) with 3 or 4 cusps on inner side and 4–6 cusps on outer side; outer wing strongly flexed, length 150% width of tooth face. Inner marginal teeth with 22–29 cusps, outer marginal teeth with 28– 32 cusps.

Prostate gland large, bean-shaped, pallial section 33% of total length. Distal penis pigmented, well-developed swelling on inner edge, penial duct gently undulating (Figure 25E). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, slightly muscular; brooded embryos about 15. Albumen gland on right side of and partly dorsal to bursa copulatrix. Bursa copulatrix large for genus, ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to proximal portion of bursal duct. Sperm-tube opening in posterior 33%–50% of pallial cavity.

DISTRIBUTION.—White River trough, southern Nevada.

REMARKS.—*Tryonia clathrata* is distinguished from other congeners by its strong collabral shell sculpture (Figure 4E), ellipsoidal operculum (Figure 6C,F), and more numerous papillae on the inner edge of the penis (Figure 25E). Hershler (1999) reviewed the literature concerning the type locality of this species, which should be attributed to the White River drainage of southern Nevada.

MATERIAL EXAMINED.—UNITED STATES. *Nevada:* White River drainage, ANSP 27969 (lectotype); spring west of Oasis Spring, Moapa Valley, Clark County, USNM 850291, USNM 873192; six miles [9.6 km] northwest of Moapa, USNM 791488.

Tryonia elata Hershler and Sada, 1987

Tryonia elata Hershler and Sada, 1987:831, figs. 39b, 42c, 44, 53e–h, 56, table 2 [type locality, Point of Rocks Springs, Ash Meadows, Nye County, Nevada].—Hershler, 1989, table 2.

DIAGNOSIS.—Shell small- to medium-sized, narrow-conic. Penial ornament of 2 distal and 1 basal papillae along inner edge.

DESCRIPTION.—Shell (Figures 4I, 22H) 1.8–2.9 mm tall. Whorls, 5.25–6.75, medium convexity, sutures impressed. Aperture ovate, lip complete, slightly thickened, often separated from body whorl; umbilicus rimate. Operculum ovate, inner side smooth. Ctenidial filaments about 17, without pleats. Stomach without posterior caecum. Radula with about 34 rows of teeth; length/width of ribbon 510%. Dorsal edge of central radular teeth weakly indented, basal tongue U-shaped, central cusps narrowly pointed, lateral cusps 5 or 6; basal cusps 1 or 2, outer cusps weakly developed. Lateral teeth (Figure 8D) with 3 or 4 cusps on inner side and 4 or 5 cusps on outer side; outer wing weakly flexed, length 150% width of tooth face. Inner marginal teeth (Figure 9C) with 19–22 cusps, outer marginal teeth with 23–28 cusps.

Prostate gland very small, subglobose, pallial section very short. Distal penis pigmented, without swelling along inner edge, penial duct nearly straight (Figure 25F). Oviduct loop posterior-oblique, pigmented. Brood pouch not extending into posteriorly folded section of glandular oviduct; opening of brood-pouch terminal, slightly thickened; brooded embryos about 4. Albumen gland extending posterior to bursa copulatrix. Bursa copulatrix large for genus, ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to proximal portion of bursal duct. Sperm tube long, opening alongside brood-pouch opening.

DISTRIBUTION.—Endemic to Ash Meadows, Amargosa River basin, Nevada.

REMARKS.—*Tryonia elata* is distinguished from other congeners by the combination of small size and narrow-conic shell (Figures 4I, 22H). This species also is unique within the genus in lacking a posteriorly folded component of the brood pouch.

MATERIAL EXAMINED.—UNITED STATES. *Nevada:* Point of Rocks spring, Nye County, USNM 859159 (holotype), USNM 850309.

Tryonia ericae Hershler and Sada, 1987

Tryonia ericae Hershler and Sada, 1987:826–831, figs. 39c,d, 42f,i, 44, 53a–d, 54, 55, table 2 [type locality, North Scruggs Spring, Ash Meadows, Nye County, Nevada].—Hershler, 1989, table 2.

DIAGNOSIS.—Shell small, conical. Penial ornament of 2 distal and 1 basal to medial papillae along inner edge.

DESCRIPTION.—Shell (Figure 22I) 1.2–1.9 mm tall. Shell apex shown in Figure 5F. Whorls, 3.75–6.0, medium convexity, sutures impressed. Aperture ovate, lip complete, often slightly thickened all around, often separated from body whorl; umbilicus rimate to broadly open. Operculum ovate, whorl edges slightly flared on outer side. Ctenidial filaments about 14, without pleats. Stomach without posterior caecum. Radula with about 42 rows, posteriormost 12 rows weakly developed; length/width of ribbon 410%. Dorsal edge of central radular teeth weakly indented, basal tongue V-shaped, central cusps narrowly pointed, lateral cusps 5 or 6, basal cusps 2. Lateral teeth having 3 cusps on inner side and 4 or 5 cusps on outer side; outer wing weakly flexed, length 175% width of tooth face. Inner marginal teeth with 14–25 cusps, outer marginal teeth with 21–28 cusps.

Prostate gland very small, bean-shaped, pallial section 33% of total length. Distal penis pigmented, weak swelling along inner edge, penial duct with several weak undulations (Figure 26A). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, slightly raised (Figure 3A); brooded embryos 1 or 2. Albumen gland on right side of bursa copulatrix. Bursa copulatrix large for genus, ovate; seminal receptacle much smaller than bursa copulatrix, globular. Sperm-duct opening to

base of bursal duct. Sperm tube long, fused with brood-pouch opening.

DISTRIBUTION.—Endemic to Ash Meadows, Amargosa River basin, Nevada.

REMARKS.—This snail is distinguished from other congeners by its small size and conical shell with impressed sutures and frequently thickened aperture (Figure 22I). *Tryonia ericae* also is unique in the genus in that the female sperm tube and brood pouch are fused (Figure 3A) instead of opening separately.

MATERIAL EXAMINED.—UNITED STATES. *Nevada:* North Scruggs Spring, Nye County, USNM 859162 (holotype), USNM 850312.

Tryonia exigua (Morelet, 1851)

Melania exigua Morelet, 1851:23 [type locality, Lake Petén Itza (=Laguna de Flores), Petén Department, Guatemala] [not *Melania exigua* Conrad, 1855].

Melania minuta Brot, 1862:43 [unnecessary replacement name for *Melania exigua* Morelet, 1851].

Tryonia exigua.—Fischer and Crosse, 1891:275–276, pl. L: fig. 2,2a,2b [reassignment].—Taylor, 1966b:197.

Paludestrina exigua.—Goodrich and van der Schalie, 1937:36 [reassignment].

Pyrgophorus exiguus.—Hershler and Thompson, 1992:93 [reassignment].

DIAGNOSIS.—Shell medium- to large-sized, conic to elongate-conic. Penial ornament of 2 or 3 distal and 1 basal papillae on inner edge.

DESCRIPTION.—Shell (Figures 4J, 23A) 4.2–7.3 mm tall. Whorls, 6.5–7.5, weakly convex; teleoconch sculptured with narrow costae (about 13 per whorl); sculpture beginning at 2.5 whorls, weakening on body whorl. Aperture narrowly ovate, lip complete, usually thickened all around, broadly adnate; shell imperforate or narrowly umbilicate. Operculum ovate, border of attachment area often thickened. Ctenidial filaments about 30, pleated. Posterior caecum of stomach large for genus. Radula with about 50 rows of teeth, the posteriormost 14 incompletely developed; length/width of ribbon 525%. Dorsal edge of central radular teeth straight or weakly indented. Basal tongue broadly V-shaped, central cusps elongate, narrowly pointed, lateral cusps 3 or 4, basal cusps 2 or 3. Lateral teeth having 3–5 cusps on inner side and 4–6 cusps on outer side; outer wing weakly flexed, length 180% width of tooth face. Inner marginal teeth with 19–26 cusps, outer marginal teeth with 19–29 cusps.

Prostate gland small, ovate, entirely visceral. Distal penis without pigment, well-developed swelling along inner edge, penial duct undulating (Figure 26B). Oviduct loop anterior-oblique, pigment not evident. Brood-pouch opening terminal, forming well-developed sphincter; brooded embryos about 17, mostly packed into posteriorly folded section of duct. Albumen gland protruding slightly posterior to bursa copulatrix. Sperm pouches minute, ovate; seminal receptacle slightly smaller than bursa copulatrix. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior 33%–50% of pallial cavity.

DISTRIBUTION.—Lake Petén Itza, interior drainage, Guatemala.

REMARKS.—*Tryonia exigua* is distinguished from other congeners by the combination of its large size, collabral shell sculpture (Figure 4J), and very small penial papillae (Figure 26B).

An adult syntype with complete aperture and well-developed collabral shell sculpture is designated as the lectotype for *Melania exigua* (BMNH 1893.2.4.1769). This species has been sparsely treated in the literature, which, along with its varied generic placement, is indicative of it only having been studied previously as empty shells. USNM 874034 (from the northeast corner of Lake Petén Itza), however, includes live-collected specimens of a narrow-shelled snail consistently sculptured with collabral costae that closely corresponds to the type series of *Melania exigua* and to the figures of Morelet's material provided by Fischer and Crosse (1891). The anatomy of this snail clearly conforms to *Tryonia*. (Body pigment has probably faded in this 1978 sample.) Note that the broad-shelled specimen figured by Reeve (1861, pl. LVIII, species 460) more closely resembles the species of *Pyrgophorus* that also lives in this lake.

MATERIAL EXAMINED.—GUATEMALA. *Petén:* Lake Petén Itza, BMNH 1893.2.4.1769 (lectotype), BMNH 1893.2.4.1770–1773 (paralectotypes); northeast corner of Lake Petén Itza, USNM 874034.

Tryonia gilae Taylor, 1987

Tryonia gilae Taylor, 1987:36–37, fig. 17, tables 40, 41 [type locality, unnamed spring on north side of Gila River about two miles [3.2 km] north of Bylas, in T 3S, R 22E, 25,000 feet [7750 m] west and 15,500 feet [4800 m] north of the township line, Graham County, Arizona].

Tryonia gilae Hershler in Hershler and Landye, 1988:43, 47–49, 58 [synonymized with *T. gilae* Taylor noted], figs. 14c,f, 39a–e, 40, 41a–c, 42, 43d–i, 44, 45, 46a, 47b, table 2 [type locality, small spring near Bylas, Graham County, Arizona].

DIAGNOSIS.—Shell small- to medium-sized, conical. Penial ornament of 2 small distal papillae on inner edge and 1 basal papilla on outer edge.

DESCRIPTION.—Shell (Figures 4C, 23B,C) 1.6–3.4 mm tall. Males smaller than females (Taylor, 1987, table 40). Shell apex shown in Figure 5E. Whorls, 4.0–6.0, low to medium convexity; teleoconch often sculptured with weak spiral striae. Aperture ovate, lip complete, thin, adnate or slightly disjunct; shell imperforate or narrowly umbilicate. Operculum ovate, inner side smooth. Ctenidial filaments about 21, pleated. Stomach with very small posterior caecum. Radula with about 42 rows of teeth; length/width of ribbon 470%. Dorsal edge of central radular teeth slightly indented, basal tongue broadly V-shaped, central cusps narrowly pointed, lateral cusps 4–6, basal cusps 2. Lateral teeth having 4 or 5 cusps on inner side and 4–6 cusps on outer side; outer wing well flexed, length 200% width of tooth face. Inner marginal teeth with 21–26 cusps, outer marginal teeth (Figure 10A) with 25–29 cusps.

Prostate gland very small, globose, often entirely visceral. Distal penis pigmented, without swelling along inner edge, pe-

nial duct straight (Figure 26C). Oviduct loop anterior-oblique, pigmented. Brood-pouch opening terminal, forming small papilla; brooded embryos 4 or 5. Albumen gland on right side of bursa copulatrix. Bursa copulatrix small, ovate; seminal receptacle a little smaller than bursa copulatrix, ovate. Sperm-duct opening to proximal portion of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Upper Gila River basin, Arizona.

REMARKS.—This snail is distinguished from other congeners by the combination of small size of the penial papillae and the absence of a distal swelling on the inner edge of the penis (Figure 26C).

MATERIAL EXAMINED.—UNITED STATES. *Arizona:* unnamed spring on north side of Gila River about two miles [3.2 km] north of Bylas, Graham County, LACM 2187 (holotype, *Tryonia gilae* Taylor), USNM 854074 (paratypes, *Tryonia gilae* Taylor); small spring near Bylas, Graham County, USNM 859059 (holotype, *Tryonia gilae* Hershler); Cold Springs, Graham County, USNM 847253; spring northwest of Bylas, Graham County, USNM 883956; spring slightly north of above, USNM 883267.

Tryonia hertleini (Drake, 1956)

Lyrodes hertleini Drake, 1956:44–46, pl. 15 [type locality, springs at Las Palomas, Chihuahua, Mexico].
Fontelicella hertleini.–Taylor, 1975:95 [reassignment].
Tryonia hertleini.—Hershler and Thompson, 1992:110 [reassignment].

DIAGNOSIS.—Shell medium-sized, conical. Penial ornament of 2 distal and 1 massive basal papillae on inner edge.

DESCRIPTION.—Shell (Figures 4D, 23D) 2.5–3.2 mm tall. Whorls, 4.75–5.5, medium convexity; teleoconch sculptured with a few spiral lines. Aperture ovate, lip complete, thin, adnate; shell imperforate or narrowly umbilicate. Operculum ovate, inner side smooth. Ctenidial filaments about 33, pleated. Stomach without posterior caecum. Radula with about 36 rows of teeth, the posteriormost 10 weakly developed; length/width of ribbon 460%. Dorsal edge of central radular teeth weakly indented, basal tongue broadly V-shaped, central cusps narrowly pointed, lateral cusps 4 or 5, basal cusps 2. Lateral teeth with 2 cusps on inner side and 4 or 5 cusps on outer side; outer wing strongly flexed, length 260% of tooth-face width. Inner marginal teeth with 15–17 cusps, outer marginal teeth with 26–32 cusps.

Prostate gland large, thick, subglobose, pallial section 33% of total length. Distal penis without pigment, well-developed swelling along inner edge, penial duct undulating (Figure 26D). Oviduct loop anterior-oblique, pigmented. Brood-pouch opening terminal, slightly thickened; brooded embryos about 18, forming 2 rows in posteriorly folded section. Albumen gland on right side of bursa copulatrix. Bursa copulatrix large for genus, ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to distal portion of bursal duct. Sperm-tube opening to posterior 33% of pallial cavity.

DISTRIBUTION.—Las Palomas, interior drainage of northeast Mexico. This species may be extinct because its only known locality dried more than 25 years ago (Landye in Hershler, 1994).

REMARKS.—*Tryonia hertleini* is distinguished from other congeners by the massive basal papilla on the inner side of the penis (Figure 26D). The highly elongate outer wing of the lateral radular teeth of this species also is unique in the genus.

The holotype of this species has a broken aperture, so a paratype was figured instead (Figure 23D). Note that the UMMZ alcohol-preserved material studied was collected during an ichthyological survey and was not relaxed.

MATERIAL EXAMINED. MEXICO. *Chihuahua:* springs at Las Palomas, CAS 64918 (holotype), CAS 64919 (paratypes), USNM 600498 (paratypes); spring-fed pond 3.6 miles [5.8 km] south of Las Palomas, UMMZ uncataloged.

Tryonia imitator (Pilsbry, 1899)

Paludestrina imitator Pilsbry, 1899:124 [type locality, Santa Cruz, California].—Taylor, 1966b:197.
Paludestrina curta Arnold, 1903:305 [type locality, San Pedro bluffs (California), Upper San Pedro Series (Pleistocene)].—Woodring et al., 1946:66 [synonymized with *Hydrobia protea=Tryonia protea*].—Taylor, 1966b:197 [synonymized with *T. imitator*].
Hydrobia imitator.—Berry, 1948:59 [reassignment].
Amnicola imitator.—Baily and Baily, 1952:51 [reassignment].
Tryonia imitator.—Taylor, 1966b:197 [reassignment]; 1981:153 [distribution].

DIAGNOSIS.—Shell medium- to large-sized, ovate-conic. Penial ornament of 2 distal and 1 basal papillae on inner edge.

DESCRIPTION.—Shell (Figure 23E,F) 2.5–5.5 mm tall. Shell apex shown in Figure 5B. Whorls, 4.25–6.0, medium convexity, teleoconch sculptured with 10–15 strong spiral lines interspersed between weaker threads. Aperture ovate, lip complete, thin, adnate; umbilicus rimate. Operculum ovate, inner side with weak rim along border. Ctenidial filaments about 35, pleated. Stomach with small posterior caecum. Radula with about 45 rows of teeth, length/width of ribbon 580%. Lateral margins of central radular teeth weakly flared (teeth almost square), dorsal edge medium indented, basal tongue slightly convex to V-shaped, central cusp broad, spoon-like, lateral cusps, 6–9, basal cusps 1 or 2, weakly developed. Lateral teeth (Figure 8C) having 3 or 4 cusps on inner side and 5–7 cusps on outer side; outer wing well flexed, length 150% of tooth-face width. Inner marginal teeth with 21–25 cusps, outer marginal teeth with 26–33 cusps.

Prostate gland small, ovate, pallial section 33% of total length, pallial vas deferens broad. Distal penis pigmented, well-developed swelling along inner edge, penial duct weakly undulating (Figure 26E). Oviduct loop anterior-oblique, pigmented. Brood-pouch opening subterminal, raised (Figure 3C); brooded embryos 25 to 30. Albumen gland largely posterior to bursa copulatrix. Bursa copulatrix small, ovate, pigmented; seminal receptacle a little smaller than bursa copulatrix, ovate or elongate (Figure 3D). Sperm-duct opening to distal portion

of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Southern California coast.

REMARKS.—This species is distinguished from closely similar *T. salina* by its typically larger, broader shell and weaker spiral sculpture. *Tryonia imitator* also is unique in the genus in having a pigmented bursa copulatrix (Figure 3D).

MATERIAL EXAMINED.—UNITED STATES. *California:* Pleistocene deposits, San Pedro Bluffs, USNM 162542 (holotype, *Paludestrina curta*); Santa Cruz, Santa Cruz County, ANSP 62670 (lectotype, *Paludestrina imitator*); Morro Bay, San Luis Obispo County, USNM 892057.

Tryonia margae Hershler, 1989

Tryonia margae Hershler, 1989:202–205, figs. 48–50, 51a, 52, table 2 [type locality, (upper) warm spring on limestone bench, Grapevine Springs, Death Valley, Inyo County, California].

DIAGNOSIS.—Shell small- to medium-sized, conic to turriform. Penial ornament of 2 distal and 1 basal papillae on inner edge and an occasional basal papilla on outer edge.

DESCRIPTION.—Shell (Figures 4L, 23G) 1.5–3.5 mm tall. Whorls, 4.5–8.5, weakly convex, sutures impressed. Aperture ovate, lip complete, thin, adnate or slightly disjunct; shell imperforate or narrowly umbilicate. Operculum ovate, inner side smooth. Ctenidial filaments about 28, without pleats. Stomach without posterior caecum. Radula with about 37 rows of teeth, length/width of ribbon 390%. Dorsal edge of central radular teeth weakly indented, basal tongue U-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4 or 5, basal cusps 1 or 2. Lateral teeth having 3 cusps on inner side and 4 or 5 cusps on outer side; outer wing strongly flexed, length 167% tooth-face width. Inner marginal teeth with 20–25 cusps, outer marginal teeth (Figure 10C) with 25–31 cusps.

Prostate gland small, thick, bean-shaped, pallial section about 33% of total length. Distal penis pigmented, narrow swelling along inner edge, penial duct weakly undulating (Figure 27A). Oviduct loop posterior-oblique. Brood-pouch opening terminal, slightly thickened; brooded embryos 3 or 4. Albumen gland on right side of bursa copulatrix. Bursa copulatrix large, narrowly ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to proximal portion of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Endemic to type locality area, Amargosa River basin, California.

REMARKS.—*Tryonia margae* is distinguished from other congeners by the combination of small size and narrow shell.

MATERIAL EXAMINED.—UNITED STATES. *California:* (upper) warm spring on limestone bench, Grapevine Springs, Inyo County, USNM 860408 (holotype), USNM 857952 (paratypes); Grapevine Springs, Inyo County, USNM 854599, USNM 883308.

Tryonia monitorae Hershler, 1999

Tryonia monitorae Hershler, 1999:332, 334, figs. 3D, 13D–G, 14, 15, table 1 [type locality, Hot Springs, Potts Ranch, Monitor Valley, Nye County, Nevada].

DIAGNOSIS.—Shell medium-sized, elongate-conic. Penial ornament of 2 distal and 1 basal papillae on inner edge and 1 basal papilla arising between midline and outer edge.

DESCRIPTION.—Shell (Figure 23H) 3.0–4.6 mm tall. Whorls, 6.25–7.5, weakly to moderately convex; spiral threads sometimes prominent on shells retaining periostracum. Aperture ovate, lip usually complete, thin, adnate; shell imperforate. Operculum ovate, inner side smooth. Ctenidial filaments about 35, pleated. Stomach without posterior caecum. Radula with about 47 rows of teeth; length/width of ribbon 590%. Dorsal edge of central teeth slightly indented, basal tongue V-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 5–7, basal cusps 1 or 2. Lateral teeth with 4 cusps on the inner side and 5 or 6 cusps on the outer side; outer wing well flexed, length 175% width of tooth face. Inner marginal teeth with 19–25 cusps, outer marginal teeth with 22–27 cusps.

Prostate gland small, ovate, pallial section slightly less than 33% of total length. Distal penis pigmented, well-developed swelling on inner edge, penial duct undulating for most of length (Figure 27B). Oviduct loop anterior-oblique, pigmented. Brood-pouch opening terminal, slightly muscularized; brooded embryos about 12. Albumen gland on right side of bursa copulatrix. Bursa copulatrix large, ovate; seminal receptacle much smaller than bursa copulatrix, ovate. Sperm-duct opening to distal portion of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Endemic to Monitor Valley, Great Basin, Nevada.

REMARKS.—This snail is distinguished from closely similar *T. margae* by its larger size and more rounded shell whorls.

MATERIAL EXAMINED.—UNITED STATES. *Nevada:* Hot Springs, Potts Ranch, USNM 892046 (holotype), USNM 860760 (paratypes).

Tryonia porrecta (Mighels, 1845), new combination

Paludina porrecta Mighels, 1845:22 [type locality, Oahu (Hawaii)].—Küster, 1852:34–35, pl. 7: figs. 25, 26.

Amnicola protea Gould, 1855:129–130 [type locality, Colorado Desert (Gran Jornado)].—Gould, 1857:332, pl. XI: figs. 6–9.

Melania exigua Conrad, 1855:269 [type locality, Colorado desert, California].—Binney, 1865:72, fig. 141 [synonymized with *T. protea*].—Baker, 1964:172 [lectotype selection; transferred to *Tryonia*].

Hydrobia porrecta.—Frauenfeld, 1863:1024 [reassignment].

Tryonia protea.—Binney, 1865:71–72, figs. 140, 142.—Bequaert and Miller, 1973:213 [emendation of type locality to near Salton View, Riverside County, California].—Taylor, 1981:153–154 [distribution]; 1985, fig. 35 [distribution map].—Hershler, 1999:334–335, fig. 14 [distribution map], table 2.

Bythinella protea.—Stearns, 1893:278–281 [reassignment].

Paludestrina porrecta.—Sykes, 1900:396 [reassignment].

Paludestrina protea.—Stearns, 1901:277–284, fig. 1, pls. XIX–XXI [reassignment].

Hydrobia protea.—Wenz, 1922:153 [reassignment].

Pyrgulopsis imminens Taylor, 1950:28, figs. 1–3 [type locality, shore of Salton Sea by Fish Springs [=Desert Shores], Imperial County, California].—Hershler and Thompson, 1992:111 [synonymized with *T. protea*].

Pyrgulopsis blakeana Taylor, 1950:30–31, figs. 4–6 [type locality, shore of Salton Sea by Fish Springs, Imperial County, California]; 1966b:196 [synonymized with *T. protea*].

Pyrgulopsis cahuillarum Taylor, 1950:31–32, fig. 7 [type locality, fifty yards [46 m] northeast of the so-called Fish Traps, 7.9 miles [12.6 km] west of Mecca, Riverside County, California]; 1966b:196 [synonymized with *T. protea*].

DIAGNOSIS.—Shell medium- to large-sized, conical. Males absent.

DESCRIPTION.—Shell (Figures 4K, 24A–F) 2.75–7.4 mm tall. Whorls, 5.0–7.5, almost flat to well rounded, sometimes having pronounced subsutural angulations. Teleoconch smooth or sculptured with about 10 regularly spaced spiral ridges (beginning on second whorl) and/or weak collabral ridges (about 10 on last 0.5 whorl), sometimes producing cancellate appearance. Aperture ovate, lip complete, usually thin, adnate or disjunct; shell imperforate or narrowly umbilicate. Operculum ovate, border of attachment area slightly thickened. Ctenidial filaments about 24, without pleats. Posterior caecum of stomach large for genus. Radula with about 45 rows of teeth, length/width of ribbon 500%. Dorsal edge of central radular teeth (Figure 7C) medium indented, basal tongue U-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4 or 5, basal cusps 2 or 3. Lateral teeth with 4 or 5 cusps on inner side and 6 or 7 cusps on outer side, outer wing strongly flexed, length 160% width of tooth face. Inner marginal teeth (Figure 9B) with 32–37 cusps, outer marginal teeth with 30–38 cusps.

Oviduct loop anterior-oblique, weakly pigmented. Brood-pouch opening terminal, slightly thickened; brooded embryos 11–20. Albumen gland extending slightly posterior to bursa copulatrix. Bursa copulatrix small, elongate. Seminal receptacle slightly smaller than bursa copulatrix, elongate, darkly pigmented; duct slightly longer than body of seminal receptacle. Sperm-duct opening to distal portion of bursal duct. Sperm-tube opening in posterior one-third of pallial cavity.

DISTRIBUTION.—Lower Colorado River basin, Great Basin, and Hawaii. Hawaiian populations may have been introduced (Athens and Ward, 1993; Cowie, 1997), but this would have to have occurred prior to 1845.

REMARKS.—In the absence of information on the insertion of the visceral vas deferens into the prostate gland (which is not available for this parthenogenetic snail), this species is assigned to *Tryonia* on the basis of its coiled sperm duct, which further distinguishes this genus from other *Tryonia*-like snails. Note that in the phylogenetic analysis of mtDNA sequences this snail grouped within the "true" *Tryonia* clade (Hershler, Liu, and Mulvey, 1999). *Tryonia porrecta* is distinguished from other congeners by the absence of males. This snail also is unique within the genus in having a darkly pigmented seminal receptacle.

The type material for *Paludina porrecta* has been assumed to be lost (Cowie, 1997). Although most of Mighel's collection, which was reposited at the Portland (Maine) Society of Natural History, was destroyed by fire during the middle part of the 18th century (Norton, 1927), types for some of the species that he described were distributed to other institutions, and some Hawaiian material was sent to private collector Hugh Cuming (Johnson, 1949). The Cuming Collection (now housed in The Natural History Museum, London) contains a six-specimen lot of *Paludina porrecta*, one of which is shown in Figure 24A. The handwriting on the original label of this lot is suggestive of that of Mighels (fide Johnson, 1949:215), and the BMNH label lists this as possible type material, but there is no further indication that these shells represent part of the type series. A lectotype of *Amnicola protea* (Figure 24B) is designated that closely resembles the specimens figured by Gould (1857) and that was in the best condition of the seven syntypes (several of which are highly worn).

The close similarity between *Paludina porrecta* and *Tryonia protea* has been noted previously (Cowie, 1995; Hershler in Cowie, 1997). The possible syntype lot of *P. porrecta* and other samples from the Hawaiian Islands closely conform in all respects to western North American snails referred to *T. protea*. Alcohol-preserved material of the Hawaiian snail (BPMNH uncat.) also conforms closely to *T. protea* in female anatomical details (and in the absence of males), hence these taxa are treated as synonymous.

Two of the three species of *Pyrgulopsis* that Taylor (1950) described from the Salton Trough were subsequently treated by him as synonyms of *T. protea* (e.g., Taylor, 1981). The third species (*P. imminens*) is distinguished by its thicker shell and more angular aperture, which presumably led Taylor (1985, fig. 17) to retain it in the genus *Pyrgulopsis*. Alternatively this feature may be viewed as the endpoint of a continuum of variation within *T. porrecta* (see Figure 24D–F) The impressive shell variation within broadly distributed *T. porrecta* was well described by Stearns (1901). Although Taylor (1966a:53–54) suggested that extant forms referable to *T. protea* may represent several species, recognition of a single species nonetheless is indicated by the invariant anatomy of these animals, and by the genetic uniformity of populations in the American Southwest (Hershler, Liu, and Mulvey, 1999; Hershler, Mulvey, and Liu, 1999; Mulvey and Hershler, Ms).

MATERIAL EXAMINED.—UNITED STATES. *California:* Colorado Desert, ANSP 27965 (lectotype and paralectotypes, *Melania exigua*); shore of Salton Sea by Fish Springs, Imperial County, SBMNH 35497 (holotype, *Pyrgulopsis imminens*), SBMNH 35500 (holotype, *Pyrgulopsis blakeana*); near Salton View, Riverside County, USNM 120174 (lectotype, *Amnicola protea*), USNM 860867 (paralectotypes, *Amnicola protea*); Hunters Spring, Riverside County, USNM 874194; 7.9 miles [12.6 km] west of Mecca, Riverside County, SBMNH 35503 (holotype, *Pyrgulopsis cahuillarum*); Oasis Spring, Riverside

County, USNM 854744, USNM 873441. *Hawaii:* Waiakea, BPMNH uncat., Oahu, BMNH 1995123.

Tryonia quitobaquitae Hershler in Hershler and Landye, 1988

Tryonia quitobaquitae Hershler in Hershler and Landye, 1988:50, figs. 39f–h, 41d–f, 43a–c, 46a, 47a, table 2 [type locality, Quitobaquito Springs, Organ Pipe National Monument, Pima County, Arizona].

DIAGNOSIS.—Shell small, conical. Penial ornament of 1 medial to distal and 1 basal papilla on inner edge.

DESCRIPTION.—Shell (Figures 4B, 24G) 1.4–2.1 mm tall. Shell apex shown in Figure 5D. Whorls, 3.5–4.5, medium convexity, shoulders well developed; teleoconch occasionally sculptured with weak spiral lines. Aperture ovate, lip complete, thin, adnate or disjunct; shell imperforate or narrowly umbilicate. Operculum ovate, inner side smooth. Ctenidial filaments about 22, pleated. Stomach without posterior caecum. Radula with about 46 rows of teeth, length/width of ribbon 540%. Dorsal edge of central radular teeth medium indented, basal sockets V-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4–6, basal cusps 1. Lateral teeth having 3 cusps on inner side and 3–5 cusps on outer side; outer wing well flexed, length 167% width of tooth face. Inner marginal teeth with 20–23 cusps, outer marginal teeth with 26–31 cusps.

Prostate gland small, ovate, almost entirely visceral. Distal penis without pigment, prominent swelling on inner edge, penial duct sometimes undulating proximally (Figure 27C). Distal penial papilla smaller than basal unit. Oviduct loop posterior-oblique, pigment not evident. Brood-pouch opening terminal, slightly muscularized; brooded embryos about 10. Albumen gland on right side of bursa copulatrix. Bursa copulatrix small, narrowly ovate; seminal receptacle slightly smaller than bursa copulatrix, elongate, with rather long duct. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Endemic to the type locality area, Rio Sonoyta basin, interior drainage, Arizona.

REMARKS.—This snail is distinguished from other congeners by its unique pattern of penial ornament, consisting of two papillae along the inner edge (Figure 27C). Note that the body pigment may have faded in the old alcohol material studied.

MATERIAL EXAMINED.—UNITED STATES. *Arizona:* Quitobaquito Springs, Pima County, USNM 859061 (holotype), USNM 847256.

Tryonia rowlandsi Hershler, 1989

Tryonia rowlandsi Hershler, 1989:211–215, figs. 51b, 52, 59, 60, table 2 [type locality, Grapevine Springs, (upper) warm spring on limestone bench, Inyo County, California].

DIAGNOSIS.—Shell small- to medium-sized, conical. Penial ornament of 1 distal and 1 basal papilla on inner edge and 1 medial papilla on outer edge.

DESCRIPTION.—Shell (Figure 24H) 1.7–2.3 mm tall. Whorls, 4.0–4.75, well-rounded, sutures impressed; upper teleoconch whorls sculptured with a few, regularly spaced spiral lines. Aperture ovate, lip complete, usually thin, adnate; shell imperforate. Operculum ovate, inner side smooth. Ctenidial filaments about 18, without pleats. Stomach with very small posterior caecum. Radula with about 44 rows of teeth, length/width of ribbon 580%. Dorsal edge of central radular teeth (Figure 7A) well indented, basal tongue U-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4–7, basal cusps 1. Lateral teeth with 3–5 cusps on inner side and 4 or 5 cusps on outer side; outer wing weakly flexed, length 150% of tooth-face width. Inner marginal teeth with 21–28 cusps, outer marginal teeth (Figure 10B) with 23–31 cusps.

Prostate gland small, subglobular, pallial section up to 33% of total length. Distal penis pigmented, without swelling on inner edge, penial duct nearly straight (Figure 27D). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, muscularized; brooded embryos about 10. Albumen gland extending posterior to bursa copulatrix. Bursa copulatrix very small, ovate; seminal receptacle slightly smaller than bursa copulatrix, ovate. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior 33% of pallial cavity.

DISTRIBUTION.—Endemic to type locality area, Amargosa River basin, California.

REMARKS.—*Tryonia rowlandsi* is distinguished from other congeners by the medial position of the papilla on the outer edge of the penis (Figure 27D).

MATERIAL EXAMINED.—UNITED STATES. *California:* Grapevine Springs, Death Valley, Inyo County, USNM 860409 (holotype), USNM 857953.

Tryonia salina Hershler, 1989

Tryonia salina Hershler, 1989:215–216, figs. 51e, 52, 61, 62, table 2 [type locality, spring in Cottonball Marsh, Inyo County, California].

DIAGNOSIS.—Shell medium-sized, ovate-conic. Penial ornament of 2 distal and 1 basal papillae on inner edge and 1 basal papilla on outer edge.

DESCRIPTION.—Shell (Figures 4A, 24I) 2.4–3.3 mm tall. Whorls, 4.5–5.25, highly convex, sutures impressed, teleoconch sculptured with numerous spiral lirae (about 15–18 on body whorl). Aperture broadly ovate, lip complete, thin, adnate or disjunct; umbilicus perforate. Operculum (Figure 6A) ovate, inner side smooth. Ctenidial filaments 28, pleated. Stomach with very small posterior caecum. Radula with about 44 rows of teeth, length/width of ribbon 550%. Dorsal edge of central radular teeth (Figure 7B) weakly indented, basal tongue weakly convex, central cusp broad, lateral cusps 4–7, basal cusps 2 or 3 (with occasional hint of fourth cusp). Lateral teeth having 3 or 4 cusps on inner side and 5–7 cusps on outer side; central cusp broad; outer wing strongly flexed, length 170% of tooth-face width. Inner marginal teeth with 23–25 cusps, outer marginal teeth with 26–32 cusps.

Prostate gland small, subglobular, pallial section <33% of total length. Distal penis pigmented, well-developed swelling on inner edge, penial duct weakly undulating (Figure 27E). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, muscularized; brooded embryos 8. Albumen gland extending posterior to bursa copulatrix. Bursa copulatrix small, narrowly ovate; seminal receptacle a little smaller than bursa copulatrix, narrowly ovate. Sperm-duct opening to medial portion of bursal duct. Sperm-tube opening in posterior 33%–50% of pallial cavity.

DISTRIBUTION.—Endemic to the type locality area, Amargosa River basin, California.

REMARKS.—This species is distinguished from other congeners by its ovate-conic shell with large aperture and strong spiral sculpture (Figure 4A).

MATERIAL EXAMINED.—UNITED STATES. *California:* Cottonball Marsh, Inyo County, USNM 860410 (holotype), USNM 883326; spring in Cottonball Marsh, Inyo County, USNM 857998.

Tryonia variegata Hershler and Sada, 1987

Tryonia variegata Hershler and Sada, 1987:817, 819, 822–826, figs. 39e–g, 42b,e,g,h, 44–52, table 2 [type locality, Five Springs, Nye County, Nevada].—Hershler, 1989:216–219, 221, 222, figs. 51c, 52, 63, 64, table 2.

DIAGNOSIS.—Shell medium- to large-sized, conic to elongate-conic. Penial ornament of 2 or 3 distal and 1 basal papillae on inner edge and occasional basal papilla on outer edge.

DESCRIPTION.—Shell (Figure 24J) 2.8–7.5 mm tall. Whorls, 5.25–9.75, weakly convex, sometimes narrowly shouldered. Aperture pyriform, lip complete, slightly thickened, adnate; umbilicus rimate. Operculum (Figure 6E) ovate, inner side smooth. Ctenidial filaments 30, pleated. Stomach without posterior caecum. Radula with about 46 rows of teeth, length/width of ribbon 560%. Dorsal edge of central radular teeth medium indented, basal tongue U-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 4–6, basal cusps 2. Lateral teeth with 3 or 4 cusps on inner edge and 4 or 5 cusps on outer edge; outer wing weakly flexed, length 140% width of tooth face. Inner marginal teeth with 21–25 cusps, outer marginal teeth (Figure 10D) with 28–35 cusps.

Prostate gland small, bean-shaped, almost entirely visceral. Distal penis pigmented, swelling along inner edge weak or absent, penial duct weakly undulating (Figure 27F). Oviduct loop posterior-oblique, pigmented. Brood-pouch opening terminal, slightly muscularized; brooded embryos 4–11. Albumen gland extending slightly posterior to bursa copulatrix. Bursa copulatrix large, ovate; seminal receptacle much smaller than bursa copulatrix, globular. Sperm-duct opening to base of bursal duct. Sperm-tube opening in posterior 33%–50% of pallial cavity.

DISTRIBUTION.—Upper Amargosa River basin, California-Nevada.

REMARKS.—This species is distinguished from other congeners by its narrow, smooth, medium to large shell with evenly rounded whorls.

MATERIAL EXAMINED.—UNITED STATES. *Nevada:* Five Springs, Nye County, USNM 859166 (holotype), USNM 850314.

Genus *Durangonella* Morrison, 1945

Durangonella Morrison, 1945:18 [type species, *Hydrobia seemani* Frauenfeld, 1863, by original designation].

DIAGNOSIS.—Shell ovate-conic to turriform, smooth or with weak spiral sculpture. Penis ornamented with single nonglandular lobe; distal penis evenly rounded. Females ovoviviparous. Bursa copulatrix and seminal receptacle present; renal oviduct a small, unpigmented coil; sperm duct straight, opening to sperm tube in pallial cavity; sperm tube elongate.

DESCRIPTION.—Shell 2.3–5.8 mm tall, gray or clear, sexually dimorphic (males smaller; Hershler, 1985, table 33; Taylor, 1987, table 50), whorls 4.25–8.5. Periostracum thin. Protoconch small (<1.0 whorl), surface coarsely roughened; teleoconch smooth or weakly sculptured with spiral lines. Aperture small, inner lip complete across parietal wall, adnate or slightly disjunct, umbilicus rimate to broadly open. Operculum thin, ovate, multispiral, nucleus eccentric. Ctenidium well developed, connected to pericardium by short efferent vein; lateral surfaces of ctenidial filaments often pleated. Osphradium variably sized, narrow, almost centrally positioned along ctenidial axis. Kidney having small pallial portion, opening slightly muscularized. Pericardium bulging slightly into pallial cavity. Style sac about as long as stomach, posterior caecum small or absent (Hershler, 1985, fig. 36A). Rectum straight, anus near mantle edge. Radula with about 45–48 tooth rows, cusps generally narrowly pointed. Central teeth trapezoidal, with 1 or 2 pairs of basal cusps. Lateral teeth with enlarged central cusp, well-developed basal tongue; outer wing longer than width of tooth face. Inner and outer marginal teeth with numerous (19–34) cusps borne largely or entirely on outer side; teeth with well-developed wings on outer edge and narrow, raised area extending from face to base (Figure 12C,D). Large testis of few (~5) stalked lobes; seminal vesicle exiting from and coiled against left side of anterior portion of testis. Prostate gland large, banana-shaped, with about 50% of length in pallial roof. Visceral vas deferens opening to ventral edge of prostate gland slightly behind pallial wall, pallial vas deferens exiting from ventral edge of prostate gland at or just behind anterior edge. Penis medium-sized, rectangular, base slightly expanded; terminal portion densely ciliated, bulbous, without swelling on inner edge. Penial-duct opening through well-developed stylet. Penis ornamented with single, medial or distal, nonglandular lobe along inner edge. Penis pigmented with melanin distally, pigment also sometimes present on penial lobe. Females ovoviviparous, brooded young few to many (1–20), of different sizes (embryos having up to 2.0 shell whorls). Ovary a small sac

(Hershler, 1985, fig. 36A). Glandular oviduct large, mostly consisting of thin-walled brood pouch, with a well-developed posterior fold, anterior opening muscular. Albumen gland very small relative to brood pouch (Hershler, 1985, fig. 36A), positioned entirely on right side of bursa copulatrix. Bursa copulatrix ovate, small relative to brood pouch, positioned well anterior to posterior edge of brood pouch, duct exiting anterior edge. Seminal receptacle ovate or globular, smaller than bursa copulatrix, positioned along anteroventral edge of bursa copulatrix, duct short or medium length. Sperm duct straight, opening to sperm tube in posterior 33% of pallial cavity. Oviduct issuing small gonopericardial duct proximal to coiled section. Renal oviduct a single, small, almost vertical loop; epithelium unpigmented. Distal to loop, oviduct connecting with seminal receptacle duct by a very short duct (Hershler, 1985, fig. 36D) and opening to posterior edge of albumen gland. Sperm tube rather broad, extending near to or abutting brood-pouch opening (Hershler, 1985, fig. 36F,G).

DISTRIBUTION.—The transfer of *Tryonia kosteri* to *Durangonella* extends the range of the latter genus from the Mexican plateau (Hershler and Thompson, 1992, map 5) into the Rio Grande drainage of New Mexico.

REMARKS.—Morrison (1945) erected *Durangonella* for four Mexican species that he distinguished from *Tryonia* by their weaker shell sculpture and different pattern of penial ornament. Taylor (1966b) added a fifth species (*D. coahuilae*), also from Mexico, which was later studied in detail by Hershler (1985) and Hershler and Thompson (1992). *Durangonella coahuilae* and *D. kosteri* are closely similar anatomically and well differentiated from *Tryonia* not only by the absence of penial papillae (e.g., the penial lobe of these species is nonglandular), but also by the smaller coil of the renal oviduct, absence of pigment on this coil, and the elongate sperm duct. More generally, *Durangonella* is distinguished from other cochliopines by the single, nonglandular, medial or distal lobe on the inner curvature of the penis. Because other congeners have not been collected alive (two were described from subfossils), the scope and content of *Durangonella* will require further study as this genus is closely similar in shell to *Tryonia*, which also ranges into northern Mexico.

Durangonella kosteri (Taylor, 1987), new combination

Tryonia (*Paupertryonia*) *kosteri* Taylor, 1987:45–47, fig. 23, tables 50, 51 [type locality, Sago Spring, 900 feet [280 m] west, 2,400 feet [740 m] south, sec. 5, T 10S, R 25E, Chaves County, New Mexico].

DIAGNOSIS.—Shell medium-sized, conical. Penial lobe positioned distally along inner edge.

DESCRIPTION.—Shell (Figures 11A, 28A) 2.5–5.0 mm tall. Males smaller than females (Taylor, 1987, table 50). Whorls, 4.25–5.75, slight to medium convexity, teleoconch sometimes sculptured with weak spiral lines. Protoconch (Figure 11B) about 0.75 whorl. Aperture ovate-pyriform, lip thin, adnate; umbilicus perforate. Operculum shown in Figure 11C,D; border of attachment region thickened. Ctenidial filaments about 27, pleated. Stomach with small posterior caecum. Radula with about 48 rows of teeth, length/width of ribbon 430%. Dorsal edge of central radular teeth (Figure 12A) weakly indented, basal tongue broadly V-shaped, central cusp broadly pointed, lateral cusps 3–6; basal cusps 1, small. Lateral teeth (Figure 12B) having 4 or 5 cusps on inner side and 5 or 6 cusps on outer side; outer wing very narrow, moderately flexed, length 180% width of tooth face. Inner marginal teeth with 24–30 cusps (Figure 12C), outer marginal teeth with 30–34 cusps (Figure 12D).

Pallial section of prostate gland 50% of total length. Pallial vas deferens exiting from ventral edge of prostate gland just behind anterior edge. Penial lobe club-like (Figure 29A). Ovary weakly branched. Oviduct loop sometimes containing sperm. Brood-pouch opening terminal, forming a well-developed, muscular sphincter (Figure 13A); brooded embryos 12–20. Seminal receptacle smaller than bursa copulatrix, duct short (Figure 13A,B). Sperm tube abutting brood-pouch opening.

DISTRIBUTION.—Vicinity of Roswell, Pecos River drainage, New Mexico.

REMARKS.—*Durangonella kosteri* is distinguished from its congeners by its broader shell. This snail further differs from *D. coahuilae* in the more distal position of the penial lobe. Taylor's (1987:45, fig. 23c) observation that this species has a penial papilla apparently was in error as the numerous males that were examined for this study all had a simple, nonglandular lobe.

MATERIAL EXAMINED.—UNITED STATES. *New Mexico:* Sago Spring, Chaves County, LACM 2252 (holotype), USNM 854091 (paratypes), USNM 854957; Lost River, Chaves County, USNM 854727; spring, Roswell Country Club, Chaves County, USNM 883771.

Pseudotryonia Hershler, new genus

TYPE SPECIES.—*Tryonia alamosae* Taylor, 1987.

DIAGNOSIS.—Shell trochoid to conic, smooth. Penis ornamented with 1–3 glandular papillae borne singly along edges; distal penis evenly rounded. Females ovoviviparous. Bursa copulatrix present (except in one species), seminal receptacle present; renal oviduct a small, unpigmented coil; sperm duct straight, opening to sperm tube in pallial cavity; sperm tube elongate.

DESCRIPTION.—Shell (Figure 15A–D) gray or clear, 1.2–5.0 mm tall, trochoid to conic, whorls 3.0–6.5. Periostracum thin. Protoconch (Figure 15E–H) small (<1.0 whorl), blunt, typically smooth; teleoconch smooth, whorls usually well rounded, widest above midpoint. Aperture usually small, inner lip complete across parietal wall, umbilicus variable. Operculum (Figure 16) thin, ovate, multispiral, nucleus eccentric, inner side usually smooth. Ctenidium well developed, connected to pericardium by short efferent vein; lateral surfaces of ctenidial filaments pleated. Osphradium usually small, narrow, centrally posi-

tioned along ctenidial axis. Kidney having small pallial portion, opening slightly muscularized. Pericardium bulging slightly into pallial cavity. Style sac about as long as remainder of stomach, posterior caecum of stomach small or absent. Rectum straight, anus near mantle edge. Radula with about 40–50 tooth rows, cusps generally narrowly pointed. Central teeth trapezoidal, with 1–3 pairs of basal cusps (Figure 17). Lateral teeth with enlarged central cusp, well-developed basal tongue; outer wing longer than width of tooth face (Figure 18A,D,E). Inner (Figure 18B,C) and outer (Figure 18F,G) marginal teeth with numerous (17–30) cusps borne largely or entirely on outer side; teeth with well-developed wings on outer edge and narrow, raised area extending from face to base. Large testis of numerous stalked lobes; seminal vesicle exiting from and tightly coiled against left side of anterior portion of testis. Prostate gland usually small, partly pallial. Visceral vas deferens opening to posteroventral edge of prostate gland, pallial vas deferens exiting from near anterior edge of prostate gland. Penis medium-sized, narrow, base expanded, terminal portion ciliated, blunt, without swelling along inner edge. Penial-duct opening through well-developed stylet. Edges of penis ornamented with 1–3 glandular papillae. Penis usually darkly pigmented with melanin distally, variably pigmented elsewhere. Females ovoviviparous, brooded young few, of different sizes (having up to 2.5 shell whorls). Ovary a small, simple sac. Glandular oviduct large, mostly consisting of thin-walled brood pouch, with a single posterior fold, anterior opening muscular (Figure 14A,C,D). Albumen gland very small, usually positioned entirely on right side of bursa copulatrix. Bursa copulatrix small (absent in one species) relative to brood pouch, positioned near pallial wall, with duct exiting anterior edge. Seminal receptacle usually smaller than bursa copulatrix, positioned along anteroventral portion of bursa copulatrix; duct short. Sperm duct elongate, opening to sperm tube in posterior 33% of pallial cavity. Proximal to coiled section oviduct issuing small gonopericardial duct. Renal oviduct a single, small, posterior-oblique loop; epithelia unpigmented. Distal to loop, oviduct connecting with seminal receptacle duct by a very short duct and opening to posterior edge of albumen gland. Sperm tube variable in width, opening in anterior half of pallial cavity, sometimes abutting or fused with opening of brood pouch.

ETYMOLOGY.—Referring to the similarity between these snails and members of the genus *Tryonia*. Gender feminine.

DISTRIBUTION.—Broadly disjunct in the southern United States, with species living in the Rio Grande basin and coastal drainages of Alabama and Florida (Map 2).

REMARKS.—Live animals of one species (*P. brevissima*) were examined for details of head-foot morphology, which are as follows: snout rectangular, distal lobes well developed; cephalic tentacles about 150% length of snout, slender, tapering distally; snout and tentacles variably pigmented with melanin and scattered yellow granules, granules concentrated around eyspots.

No synapomorphies defining this genus have been identified, and the group is distinguished from other cochliopines instead by a combination of an elongate female sperm duct and penial ornament consisting of one to three glandular papillae borne along the edges of this organ. *Pseudotryonia* is further distinguished from *Tryonia* by the absence of pigment on the renal oviduct, consistent opening of the sperm tube in the anterior portion of the pallial cavity, and the evenly rounded condition of the terminus of the penis in all species. Note that mtDNA evidence revealed *Pseudotryonia* as a well-supported clade (Hershler, Liu, and Mulvey, 1999).

Pseudotryonia adamantina (Taylor, 1987), new combination

Tryonia (*Paupertryonia*) *adamantina* Taylor, 1987:41–42, fig. 20, table 45 [type locality, Diamond Y Spring, Pecos County, Texas].

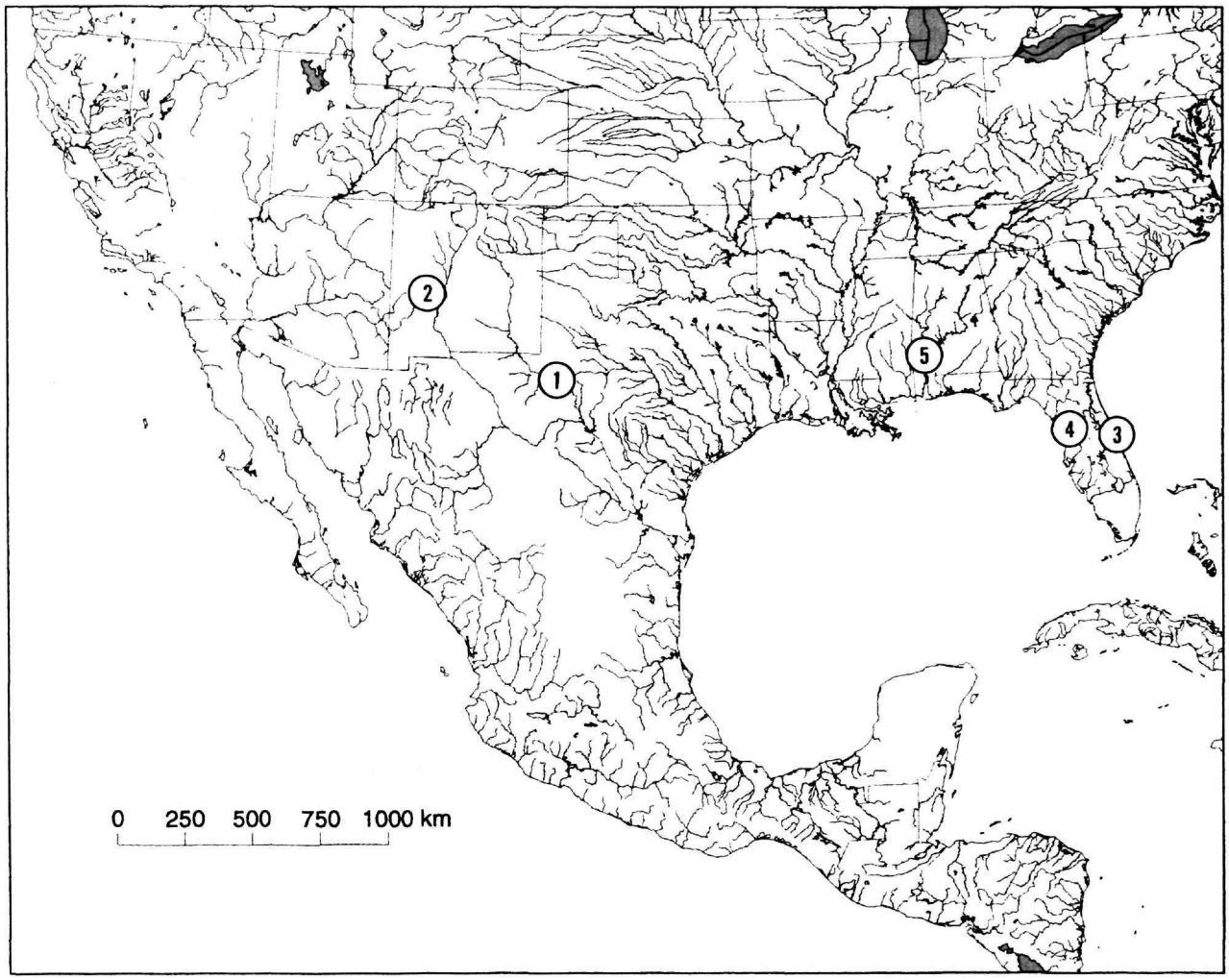
DIAGNOSIS.—Shell small- to medium-sized, conical. Penial ornament of 1 distal papilla on inner edge and 1 medial papilla on outer edge.

DESCRIPTION.—Shell (Figures 15A, 28B) 1.8–3.8 mm tall. Shell apex shown in Figure 15E. Whorls, 4.75–5.75, medium to highly convex, with well-developed shoulders, body whorl sometimes sculptured with weak spiral lines. Aperture ovate, lip complete, usually adnate, columellar lip usually straight, sometimes thickened; umbilicus usually perforate. Operculum shown in Figure 16A,E; whorl edges weakly frilled on outer side, inner side smooth. Ctenidial filaments about 22, black. Stomach with small posterior caecum. Radula with about 47 rows of teeth, length/width of ribbon 525%. Dorsal edge of central radular teeth (Figure 17A) weakly indented, basal tongue broadly V-shaped, central cusps much longer than laterals, narrowly pointed, lateral cusps 5–7, basal cusps 1 or 2. Lateral teeth having 4 or 5 cusps on inner side and 4–6 cusps on outer side; outer wing strongly flexed, length 170% width of tooth face. Inner marginal teeth with 19–24 cusps, outer marginal teeth (Figure 18F) with 23–30 cusps.

Prostate gland very small, bean-shaped, pallial section 50% of total length. Distal penis weakly pigmented, stylet large, penial duct nearly straight (Figure 29B). Oviduct loop posterior-oblique. Brood-pouch opening terminal, slightly muscularized; brooded embryos 7–10. Albumen gland sometimes exposed posterior to bursa copulatrix. Bursa copulatrix very small, ovate, lightly pigmented; seminal receptacle slightly smaller than bursa copulatrix, globular, lightly pigmented. Sperm-tube opening in anterior 50%–66% of pallial cavity.

DISTRIBUTION.—Endemic to type locality area, Pecos River basin, Texas.

REMARKS.—This species is distinguished from other congeners by its penial ornament, consisting of single papillae on the distal inner edge and medial outer edge (Figure 29B). *Pseudotryonia adamantina* also is unique within the genus in having pigmented sperm pouches.



MAP 2.—Type locality areas of *Pseudotryonia* species and junior synonyms thereof: 1, Pecos River drainage, Texas (*P. adamantina*); 2, Rio Grande drainage, New Mexico (*P. alamosae*); 3, coastal drainage, Florida (*P. brevissima*); 4, Lake Panasoffkee, Florida (*Amnicola harperi* = *P. brevissima*); 5, Tombigbee River drainage, Alabama (*Pseudotryonia* sp.).

MATERIAL EXAMINED.—UNITED STATES. *Texas:* Diamond Y Spring, Pecos County, LACM 2089 (holotype), USNM 854075 (paratypes), USNM 873125, USNM 874915, USNM 892120.

Pseudotryonia alamosae (Taylor, 1987), new combination

Tryonia (*Paupertryonia*) *alamosae* Taylor, 1987:42–44, fig. 21, tables 46, 47 [type locality, Ojo Caliente, 700 feet [220 m] west, 1,700 feet [530 m] south, sec. 31, T 8S, R 7W, unsurveyed, Socorro County, New Mexico].

DIAGNOSIS.—Shell medium-sized, ovate-conic to conic. Penial ornament of a single, distal, broadly conical papilla on inner edge.

DESCRIPTION.—Shell (Figures 15B, 28C) 2.1–4.6 mm tall. Males smaller than females (Taylor, 1987, table 46). Shell apex shown in Figure 15F. Whorls, 3.25–5.25, medium convexity, shouldered, teleoconch sometimes sculptured with weak spiral lines. Aperture ovate, lip complete, thin, usually adnate; umbilicus rimate to perforate. Operculum whorls weakly frilled on outer side (Figure 16C), border of attachment region slightly thickened all around (Figure 16G). Ctenidial filaments about 22. Posterior caecum of stomach small or absent. Radula with about 50 rows of teeth, length/width of ribbon 580%. Dorsal edge of central radular teeth (Figure 17B) well indented, basal tongue U-shaped, central cusps narrowly pointed, lateral cusps 4–6, basal cusps 1. Lateral teeth (Figure 18E) having 3 cusps on inner side and 4–6 cusps on outer side;

outer wing well flexed, length 167% width of tooth face. Inner marginal teeth (Figure 18C) with 17–19 cusps, outer marginal teeth with 18–24 cusps.

Prostate gland small, bean-shaped, pallial section 33% of total length. Distal penis weakly tapering, weakly pigmented, stylet small, penial duct nearly straight (Figure 29C). Oviduct loop almost vertical. Brood-pouch opening terminal, slightly muscularized (Figure 14A); brooded embryos 6 or 7. Albumen gland on right side of bursa copulatrix. Bursa copulatrix minute, ovate; seminal receptacle ovate, about as large as and broadly overlapping bursa copulatrix (Figure 14B). Sperm tube fused anteriorly with brood-pouch opening (Figure 14A).

DISTRIBUTION.—Endemic to type locality area, Rio Grande basin, New Mexico.

REMARKS.—This snail is distinguished from other congeners by its penial ornament, consisting of a single papilla along the inner edge.

MATERIAL EXAMINED.—UNITED STATES. *New Mexico:* Ojo Caliente, Socorro County, LACM 2188 (holotype), USNM 854072 (paratypes), USNM 873231, USNM 883959.

Pseudotryonia brevissima (Pilsbry, 1890), new combination

Bythinella brevissima Pilsbry, 1890b:64 [type locality, Haulover Canal, at the head of the Indian River, Florida].

Amnicola harperi Dall, 1910:2 [type locality, swamp at south end of Lake Panasoffkee, six feet [2 m] below the present surface, Sumter County, Florida].—Thompson, 1968:52, 54 [lectotype selection, synonymized with *Hyalopyrgus brevissimus*].

Paludestrina brevissima Walker, 1918:137 [reassignment].

Hydrobia brevissima.—Baker, 1964:171 [reassignment].

Hyalopyrgus brevissimus.—Thompson, 1968:54, 56, figs. 6, 29G, 32C, 39G,H, 49F–I, 58C [disputed type locality; reassignment].

Tryonia brevissima.—Hershler and Thompson, 1992:110 [reassignment].

DIAGNOSIS.—Shell small- to medium-sized, trochiform to ovate-conic. Penial ornament of a small distal papilla along inner edge and a massive, almost basal papilla on outer edge.

DESCRIPTION.—Shell (Figures 15C, 28D,E) 1.3–4.4 mm tall. Shell apex shown in Figure 15G. Males much smaller than females (Thompson, 1968:52–53). Whorls, 3.0–5.0, medium to highly convex, widest above midpoint, sutures impressed, teleoconch sometimes sculptured with faint spiral striae. Aperture narrowly ovate, lip complete, very thin, usually adnate; umbilicus perforate or broadly open. Operculum shown in Figure 16B,F; inner side smooth. Ctenidial filaments about 28, ctenidium abutting pericardium. Stomach with very small posterior caecum. Radula with about 39 rows of teeth, length/width of ribbon 530%. Dorsal edge of central radular teeth (Figure 17C) moderately indented, basal tongue broadly convex, cusps small, central cusps broadly pointed, lateral cusps 5–7, basal cusps 1–3. Lateral teeth (Figure 18A) having 4 cusps on inner side and 4–6 cusps on outer side; outer wing weakly flexed, length 215% width of tooth face. Inner marginal teeth with 18–21 cusps, outer marginal teeth with 16–20 cusps.

Prostate gland small, subglobular, mostly visceral. Distal penis blunt, pigmented, stylet small, penial duct undulating (Figure 29D). Oviduct loop almost vertical. Brood-pouch opening subterminal, slightly muscularized (Figure 14D); brooded embryos 10. Albumen gland on right side of sperm pouch. Posterior bursa copulatrix absent, small bud-like sac on sperm tube in posterior pallial cavity possibly representing anterior vestige. Seminal receptacle globular, with narrow duct continuous with sperm tube (Figure 14E). Sperm tube very narrow, opening adjacent to brood-pouch opening.

DISTRIBUTION.—Central region of Florida Panhandle (Atlantic and Gulf Coastal drainages).

REMARKS.—*Pseudotryonia brevissima* is distinguished from other congeners by its squat shell and unique penial ornament, consisting of a distal papilla on the inner edge and a massive, almost basal papilla on the outer edge. This snail also is unique in the genus in only having a single female sperm pouch.

Thin sections of this species indicate that the female sperm pouch has a thin, muscular wall lacking an inner glandular component, which together with its short duct and typical connection with the oviduct suggests that this structure is homologous with the seminal receptacle and not the bursa copulatrix. Oriented sperm were not seen in the several specimens sectioned, although loose sperm were present in this pouch (and in the renal oviduct). The possibility that the minute anterior sac (opening to the sperm tube) is a remnant of the bursa copulatrix could not be confirmed in section.

MATERIAL EXAMINED.—UNITED STATES. *Florida:* Haulover Canal, at the head of the Indian River, Orange County, ANSP 62418 (holotype, *Bythinella brevissima*); Lake Panasoffkee, Sumter County, USNM 211011 (lectotype, *Amnicola harperi*), USNM 892069.

Pseudotryonia sp.

DIAGNOSIS.—Shell medium-sized, conical. Penial ornament of 2 distal, basally fused papillae on inner edge and 1 medial papilla on outer edge.

DESCRIPTION.—Shell (Figures 15D, 28F) 3.5–5.0 mm tall. Males smaller than females (Thompson, in press, tables 1, 2). Shell apex shown in Figure 15H. Whorls, 5.5–6.5, strongly convex, shouldered, widest above midpoint. Aperture subovate, lip complete, thin, adnate; umbilicus rimate. Operculum shown in Figure 16D,H; inner side smooth. Ctenidial filaments about 28. Stomach with medium-sized posterior caecum. Radula with about 51 rows of teeth, length/width of ribbon 580%. Dorsal edge of central radular teeth (Figure 17D) medium indented, basal tongue broadly convex or V-shaped, central cusps narrowly pointed, lateral cusps 4–6, basal cusps 1. Lateral teeth (Figure 18D) having 3 cusps on inner side and 4–6 cusps on outer side; outer wing medium flexed, length 170% width of tooth face. Inner marginal teeth (Figure 18B) with 17–19 cusps, outer marginal teeth (Figure 18G) with 18–24 cusps.

Prostate gland small, bean-shaped, pallial section 50% of total length. Distal penis rounded, pigmented, stylet small, penial duct undulating (Figure 29F). Oviduct loop posterior-oblique. Brood-pouch opening terminal, muscular (Figure 14C); brooded embryos 7. Albumen gland on right side of bursa copulatrix. Bursa copulatrix small, ovate; seminal receptacle much smaller than bursa copulatrix, ovate or globular (Figure 14F). Sperm duct with small proximal kink. Sperm-tube opening adjacent to brood-pouch opening.

DISTRIBUTION.—Endemic to a single spring in the Tombigbee River basin, Alabama.

REMARKS.—This novelty, which is being described by Thompson (in press), is distinguished from other congeners by the presence of two glandular papillae on the inner edge of the penis. The basally fused condition of these glands is unique among *Tryonia*-like snails.

MATERIAL EXAMINED.—UNITED STATES. *Alabama:* Salt Spring, Clarke County, UF 271517, USNM 860751, USNM 860752, USNM 860755.

Ipnobius Hershler, new genus

TYPE SPECIES.—*Tryonia robusta* Hershler, 1989.

DIAGNOSIS.—Shell ovate-conic to conic, smooth. Penis ornamented with single glandular papilla along outer edge; distal penis evenly rounded. Females ovoviviparous. Bursa copulatrix absent, seminal receptacle present, opening to renal oviduct by an elongate duct; renal oviduct a large, pigmented coil; sperm tube short.

DESCRIPTION.—Shell (Figures 20A, 28G) gray or clear, 1.1–2.2 mm tall, ovate-conic to conic, whorls 3.75–4.75, medium to high convexity. Periostracum thin. Protoconch (Figure 20B) small (<1.0 whorl), blunt, smooth or slightly roughened. Teleoconch smooth, whorls sometimes separated. Aperture small, inner lip complete across parietal wall, umbilicus broadly open. Operculum (Figure 20C,D) thin, ovate or subcircular, multispiral, nucleus eccentric or subcentral, inner side usually with well-developed muscle scar. Snout rectangular, slightly expanded distally; cephalic tentacles narrow, elongate (about 200% length of snout), weakly tapered distally, snout (apart from clear distal lips) and tentacles darkly pigmented with blue-black melanin, eyebrow of yellow granules well developed (from live animals). Ctenidium well developed, abutting pericardium posteriorly; lateral surfaces of ctenidial filaments pleated. Osphradium small, narrow, almost centrally positioned along the ctenidial axis. Kidney having small pallial portion, opening slightly muscularized. Pericardium bulging slightly into pallial cavity. Style sac about as long as remainder of stomach, posterior caecum of stomach absent. Rectum straight, anus near mantle edge. Radula with moderate number of tooth rows, cusps generally narrowly pointed. Central teeth (Figure 21A) trapezoidal, with 1 or 2 pairs of basal cusps. Lateral teeth (Figure 21B) with enlarged central cusp, well-developed basal tongue; outer wing longer than width of tooth face. Inner (Figure 21C) and outer (Figure 21D) marginal teeth with numerous (19–28) cusps borne largely or entirely on outer side; teeth with well-developed wing on outer edge and narrow, raised area extending from face to base. Large testis weakly lobate; seminal vesicle very small, exiting from and tightly coiled against left side of anterior portion of testis. Prostate gland small, ovate. Visceral vas deferens opening to postero-ventral edge of prostate gland, pallial vas deferens exiting from anterodorsal edge of prostate gland. Penis medium-sized, narrow, base expanded; terminal portion ciliated, slightly tapering, rounded and slightly expanded distally, without swelling along inner edge (Hershler, 1989, fig. 58). Penial-duct opening through small stylet. Penis ornamented with single medial, broadly conical papilla along outer edge. Penis pigmented distally with melanin. Females ovoviviparous, brooded young few, of different sizes (having up to 2.0 whorls). Ovary a small, simple sac. Glandular oviduct large, mostly consisting of thin-walled brood pouch, with a posterior fold followed by a broad, circular loop, anterior opening muscular (Figure 19A). Small albumen gland extending posterior to seminal receptacle. Bursa copulatrix absent; seminal receptacle minute, issuing an elongate duct opening to renal oviduct. Proximal to coiled section, oviduct issuing a small gonopericardial duct. Renal oviduct a single, large, posterior-oblique loop; epithelium pigmented. Sperm tube narrow, opening in posterior 33% of pallial cavity.

ETYMOLOGY.—From Classical Greek, *ipnos*, "oven," "furnace;" and *bios*, "life." Referring to endemism of this genus in Death Valley, one of the hottest regions on earth. Gender masculine.

REMARKS.—This monotypic genus is differentiated by the uniquely elongate duct connecting the seminal receptacle and the renal oviduct (Figure 19B), which appears to have lengthened (relative to the typical condition in *Tryonia*-like snails) by splitting in a posterior direction. The penial ornament of this species, a single papilla on the outer edge (Figure 29F), also is unique among cochliopine snails.

The single sperm pouch of this species is considered a seminal receptacle as thin sections reveal thin, muscular walls, absence of a thick inner glandular layer, and presence of oriented sperm (also seen in portions of the renal oviduct).

Ipnobius robustus (Hershler, 1989), new combination

Tryonia robusta Hershler, 1989:208–211, figs. 51d, 52, 55–58, table 2 [type locality, Nevares Springs, spring on travertine mound, Inyo County, California].

DESCRIPTION.—Shell (Figures 20A, 28G) 1.1–2.2 mm tall. Shell apex shown in Figure 20B. Whorls, 3.75–4.75, shouldered. Aperture ovate-pyriform, lip medium thickness, adnate or disjunct. Operculum shown in Figure 20C,D; whorl edges slightly frilled, inner side smooth. Ctenidial filaments about 17, without pleats. Radula with about 54 rows of teeth; length/width of ribbon 580%. Dorsal edge of central radular teeth well indented (Figure 21A); basal tongue broadly V- or U-shaped, central cusp broadly triangular, lateral cusps 5–7, basal cusps 1

or 2 (Figure 21A). Lateral teeth (Figure 21B) with 2–4 cusps on inner side and 4 or 5 cusps on outer side; outer wing weakly flexed, length 160% width of tooth face. Inner marginal teeth (Figure 21C) with 19–24 cusps, outer marginal teeth (Figure 21D) with 21–28 cusps.

Penial duct nearly straight (Figure 29F). Brooded embryos 3. Albumen gland comprising a semicircular loop posterodorsal to seminal receptacle. Seminal receptacle pigmented, ovate (Figure 19B).

DISTRIBUTION.—Endemic to type locality and nearby Travertine Springs, lower Amargosa River basin, California.

REMARKS.—Samples collected in the early 1970s (illustrated herein) differ from more recent (1985) collections of this species (Hershler, 1989, figs. 55, 56d) in that shells are smaller, more loosely coiled, and have a more circular aperture (the operculum also is subcircular rather than ovate). This temporal variation may be attributable to intervening modifications of the type locality associated with spring development.

MATERIAL EXAMINED.—UNITED STATES. *California:* Nevares Springs, Inyo County, USNM 860411 (holotype), USNM 883311, USNM 883313.

Figures

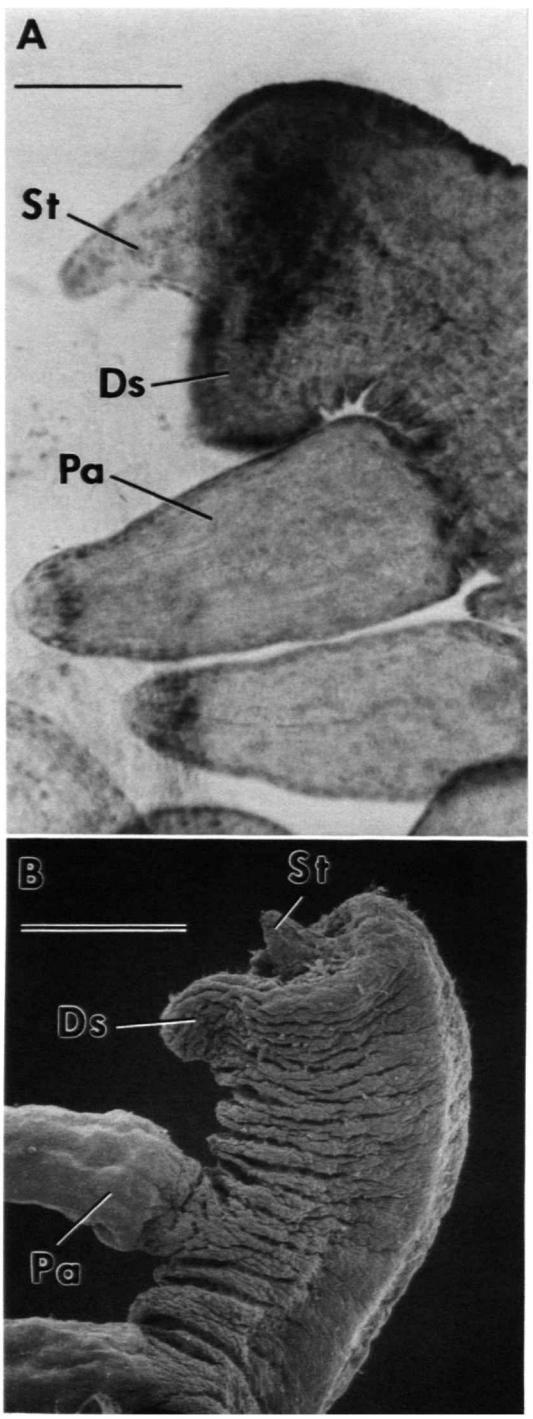


FIGURE 1.—Distal penis (dorsal side) of *Tryonia clathrata:* A, whole mount, USNM 873192 (bar=96 µm); B, scanning electron micrograph, USNM 850291 (bar=86 µm). (Ds=distal swelling, Pa=glandular papilla, St= stylet).

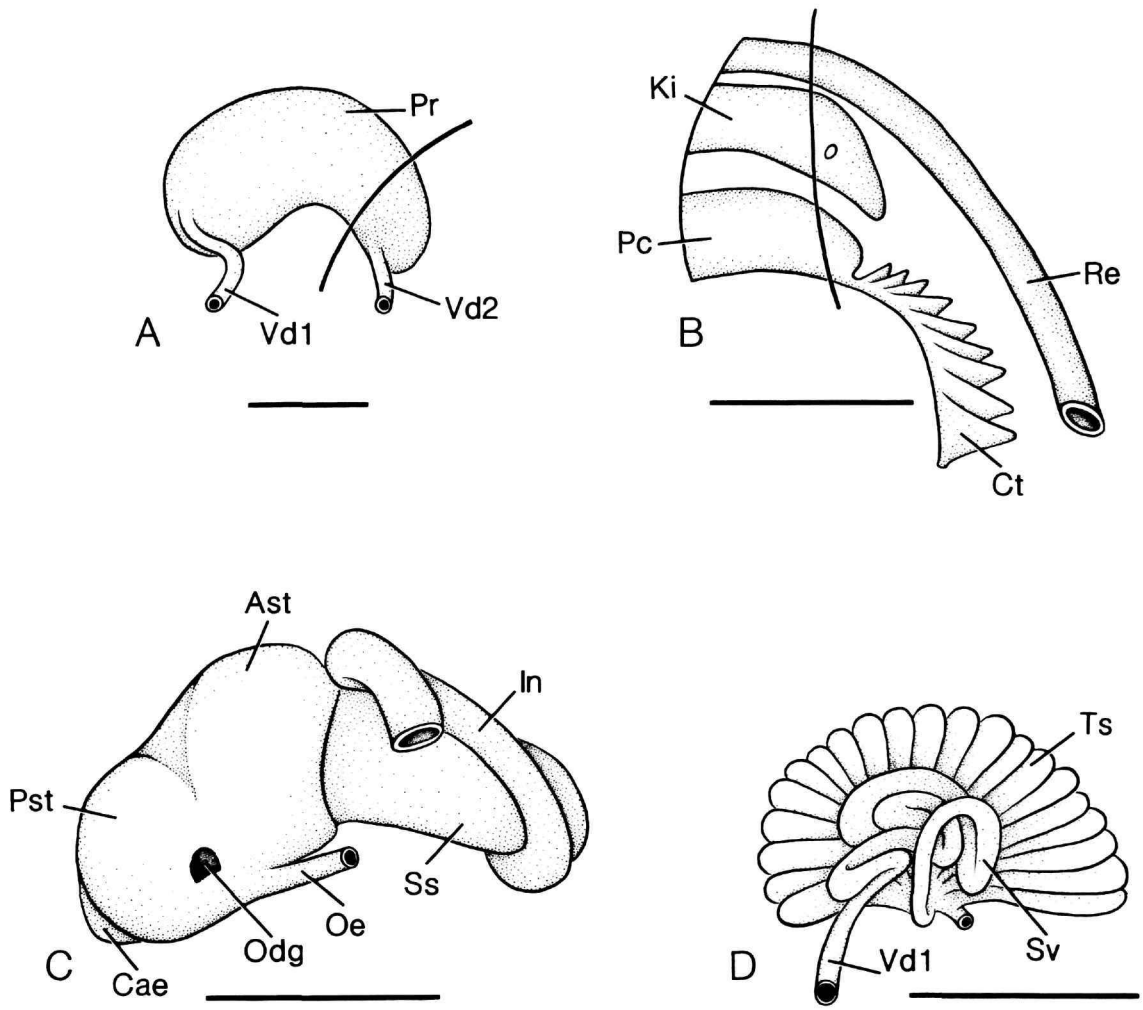


FIGURE 2.—Anatomical details of *Tryonia clathrata*, USNM 850291 (bars=250 μm): A, prostate gland (right side), showing insertion of vas deferens; B, contents of posterior section of pallial cavity, viewed from right side; C, stomach (dorsal side); D, anterior section of testis and abutting seminal vesicle. (Ast=anterior stomach chamber, Cae=posterior caecum, Ct=ctenidium, In=intestine, Ki=kidney, Odg=opening of digestive gland into stomach, Oe=oesophagus, Pc=pericardium, Pr=prostate gland, Pst=posterior stomach chamber, Re=rectum, Ss=style sac, Sv=seminal vesicle, Ts=testis, Vd1=visceral vas deferens, Vd2=pallial vas deferens.)

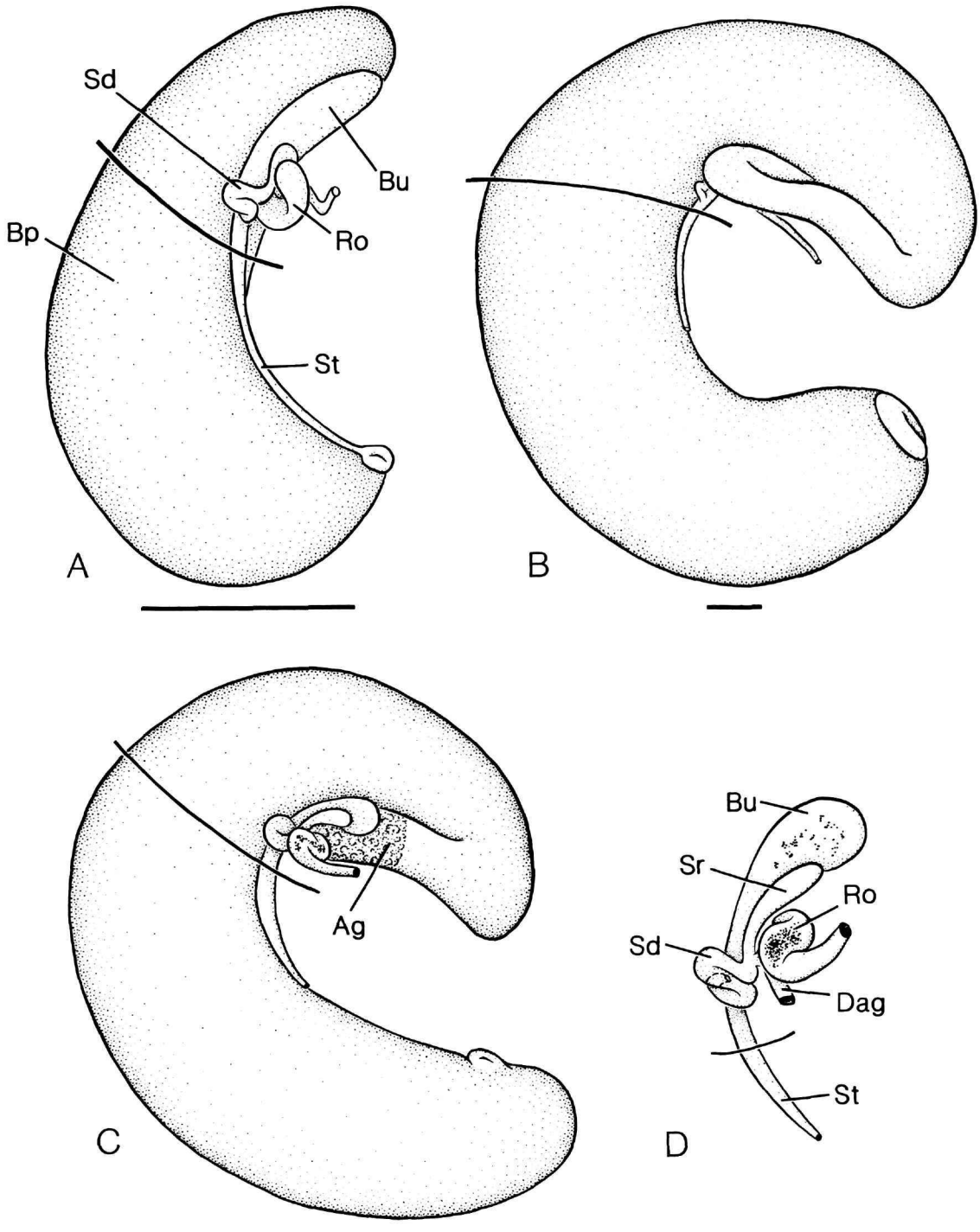


FIGURE 3.—Distal female genitalia (viewed from left side) of *Tryonia* species (bars=200 μm) (gonopericardial-duct not shown): A, *Tryonia ericae,* USNM 850312; B, *Tryonia aequicostata,* USNM 874831; C,D, *Tryonia imitator,* USNM 892057. (Ag=albumen gland, Bp=brood pouch, Bu=bursa copulatrix, Dag=connection between oviduct and albumen gland, Ro=renal oviduct, Sd=sperm duct, Sr=seminal receptacle, St=sperm tube.)

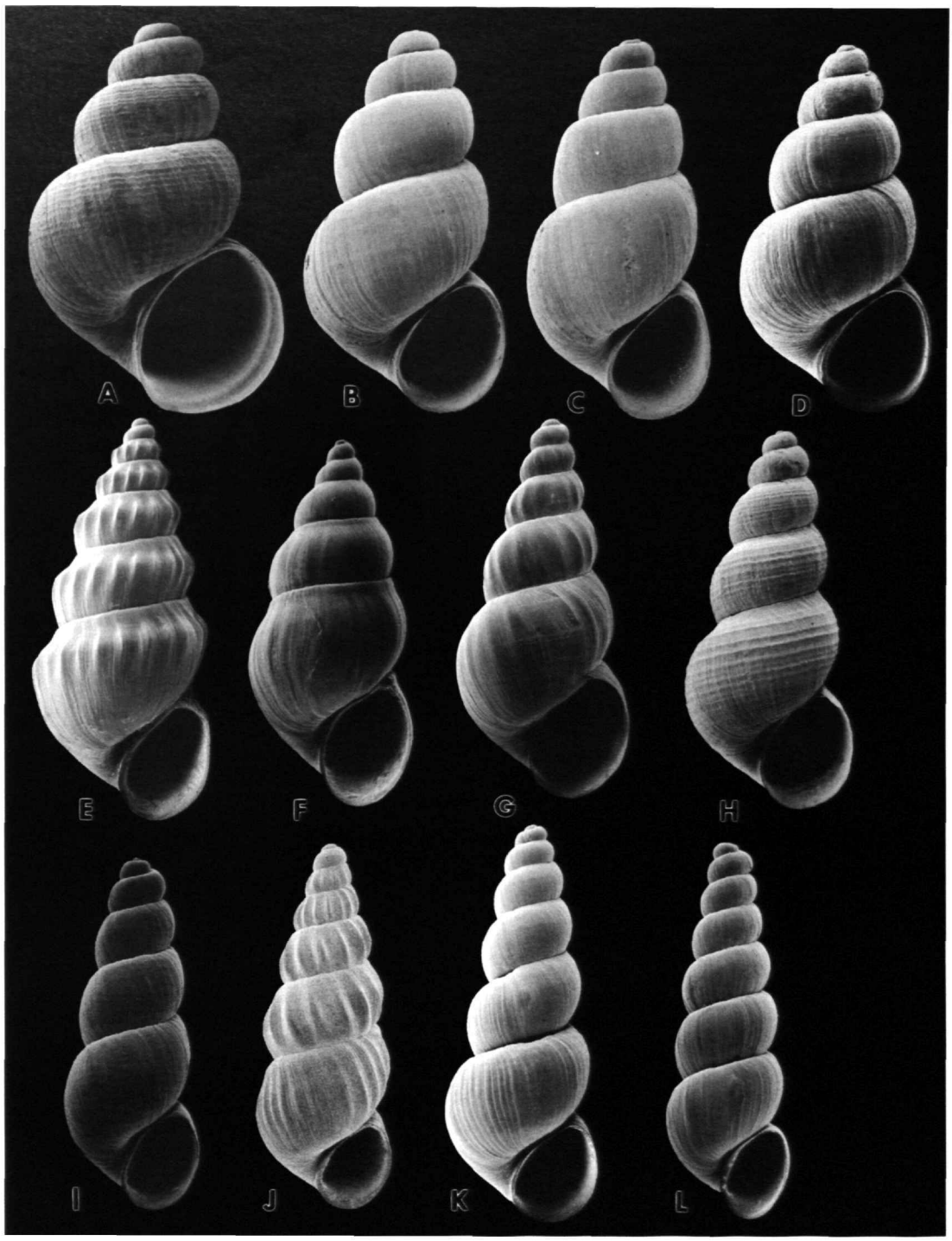


FIGURE 4.—Shell diversity among *Tryonia* species: A, *Tryonia salina,* USNM 857998 (shell height, 2.7 mm); B, *Tryonia quitobaquitae,* USNM 847256 (2.1 mm); C, *Tryonia gilae,* USNM 883956 (2.6 mm); D, *Tryonia hertleini,* USNM 600498 (2.8 mm); E, *Tryonia clathrata,* USNM 791488 (5.5 mm); F, *Tryonia angulata,* USNM 883304 (3.0 mm); G, *Tryonia aequicostata,* USNM 892070 (5.2 mm); H, *Tryonia circumstriata,* USNM 883958 (3.4 mm); I, *Tryonia elata,* USNM 850309 (2.2 mm); J, *Tryonia exigua,* USNM 874034 (6.0 mm); K, *Tryonia porrecta,* USNM 854744 (5.4 mm); L, *Tryonia margae,* USNM 854599 (3.4 mm).

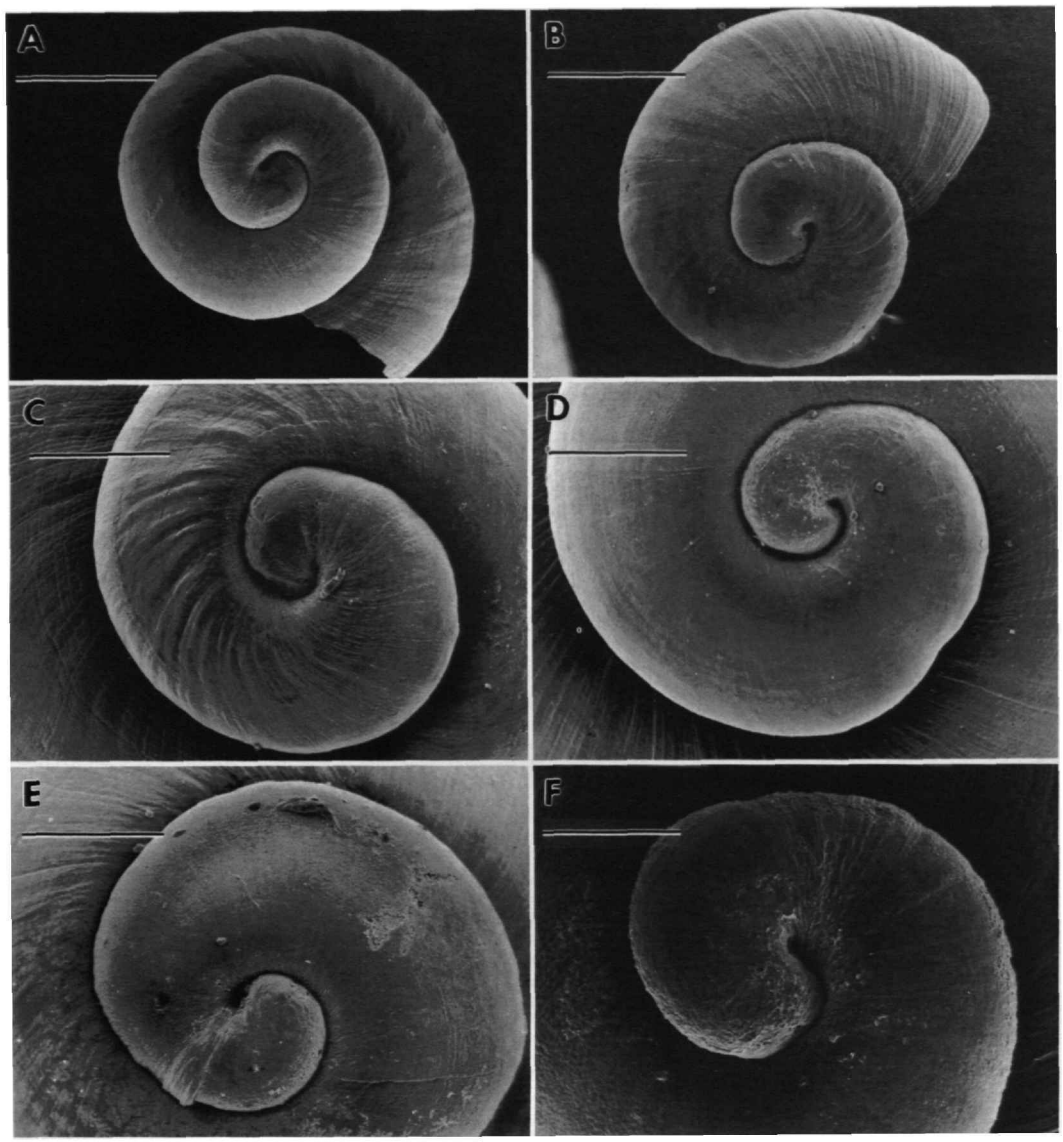


FIGURE 5.—Scanning electron micrographs of shell apices of *Tryonia* species: A, *Tryonia circumstriata* (embryo from brood pouch), USNM 883958 (bar=150 µm); B, *Tryonia imitator* (embryo from brood pouch), USNM 892057 (bar=150 µm); C, *Tryonia circumstriata,* USNM 883958 (bar=92 µm); D, *Tryonia quitobaquitae,* USNM 847256 (bar=75 µm); E, *Tryonia gilae,* showing well-demarcated protoconch, USNM 883956 (bar=75 µm); F, *Tryonia ericae,* close up of protoconch, USNM 850312 (bar=45 µm).

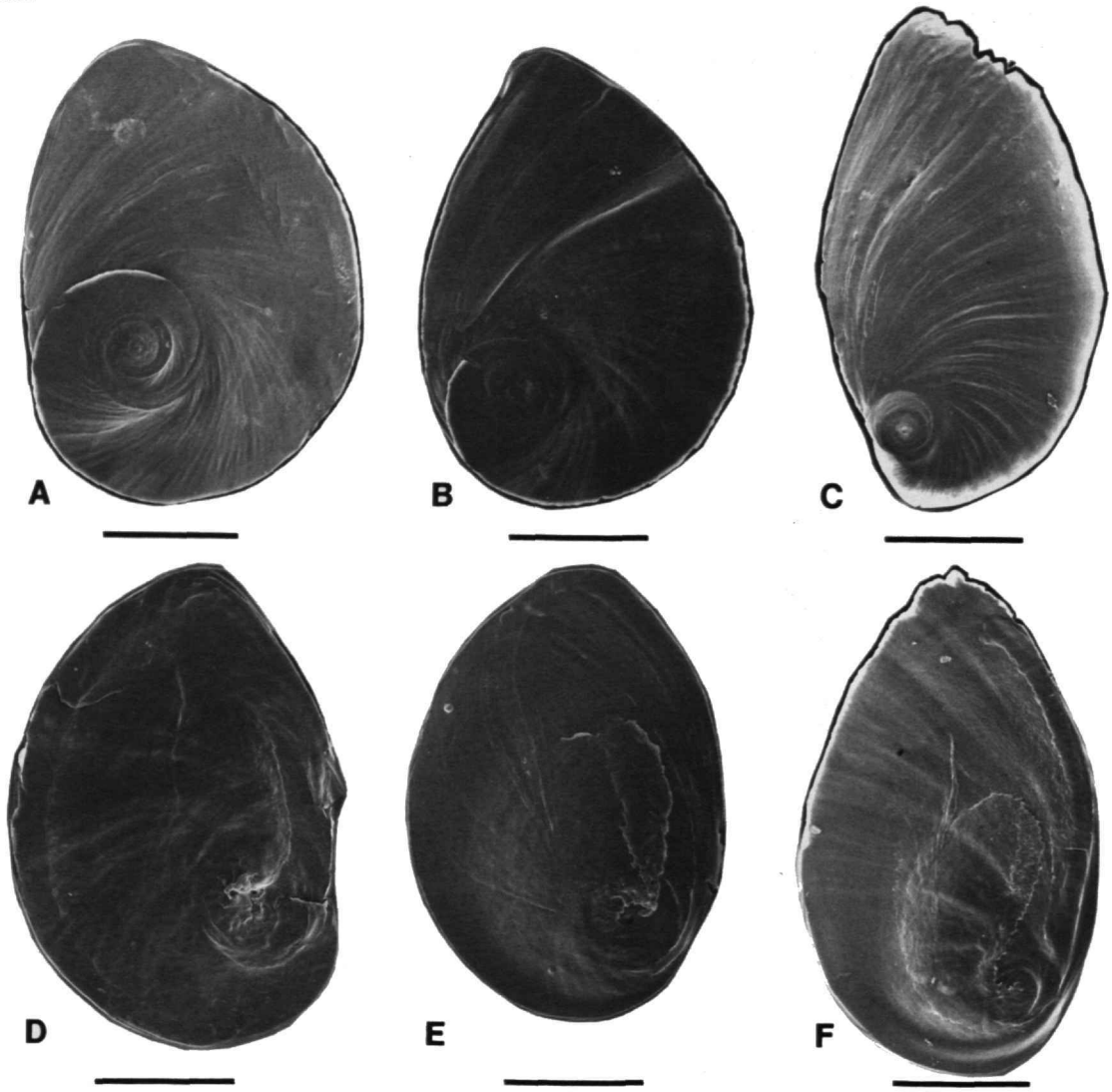


FIGURE 6.—Scanning electron micrographs of opercula (A–C, outer side; D–F, inner side) of *Tryonia* species: A, *Tryonia salina,* USNM 857998 (bar=300 µm); B, *Tryonia cheatumi,* USNM 883957 (bar=333 µm); C,F, *Tryonia clathrata,* USNM 850291 (bars=300 µm); D, *Tryonia circumstriata,* USNM 883406 (bar=240 µm); E, *Tryonia variegata,* USNM 850314 (bar=214 µm).

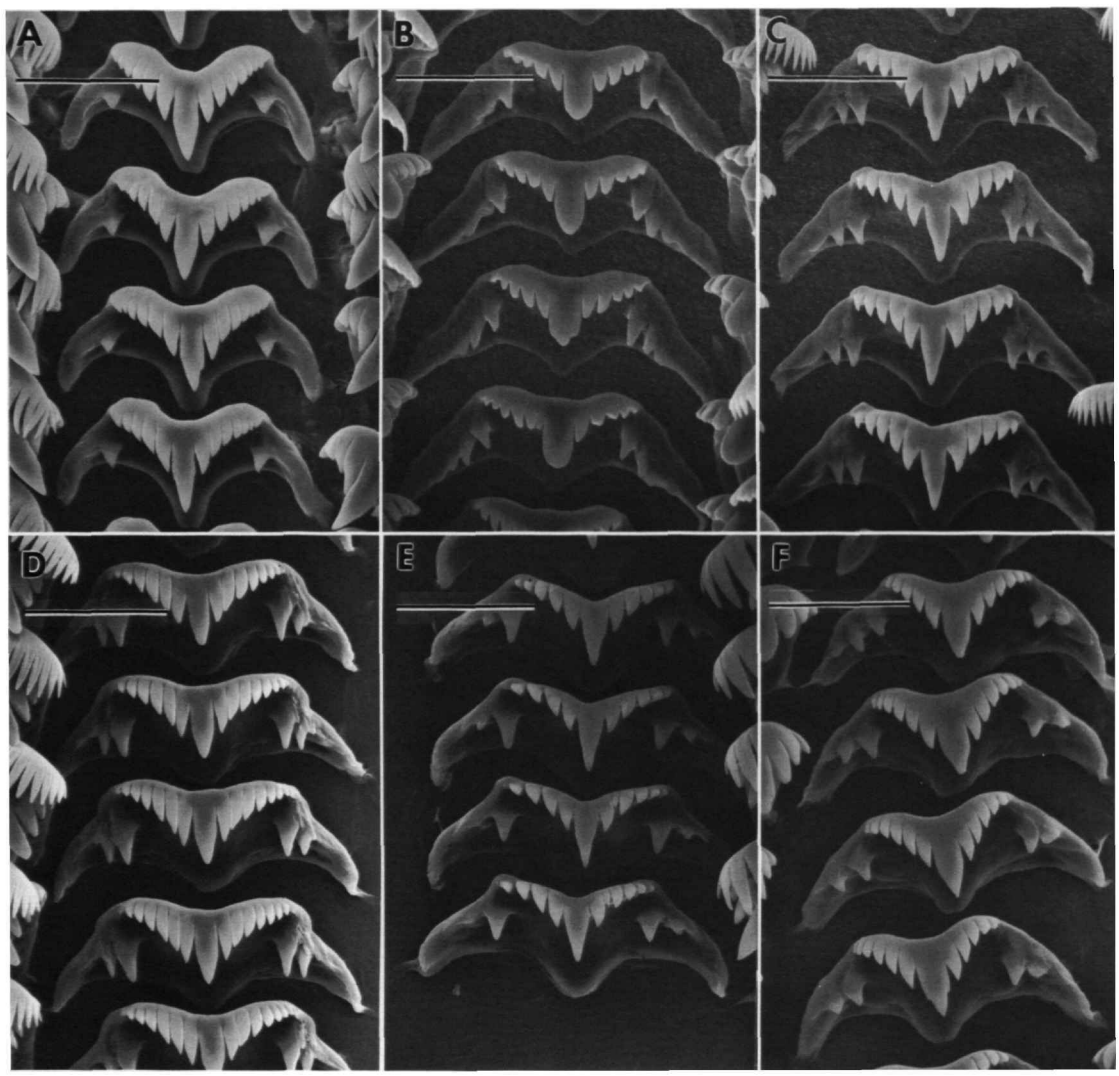


FIGURE 7.—Scanning electron micrographs of central radular teeth of *Tryonia* species: A, *Tryonia rowlandsi,* USNM 857953 (bar=12 μm); B, *Tryonia salina,* USNM 857998 (bar=15 μm); C, *Tryonia porrecta,* USNM 873441 (bar=15 μm); D, *Tryonia clathrata,* USNM 850291 (bar=12 μm); E, *Tryonia angulata,* USNM 883304 (bar=11 μm); F, *Tryonia circumstriata,* USNM 883406 (bar=12 μm).

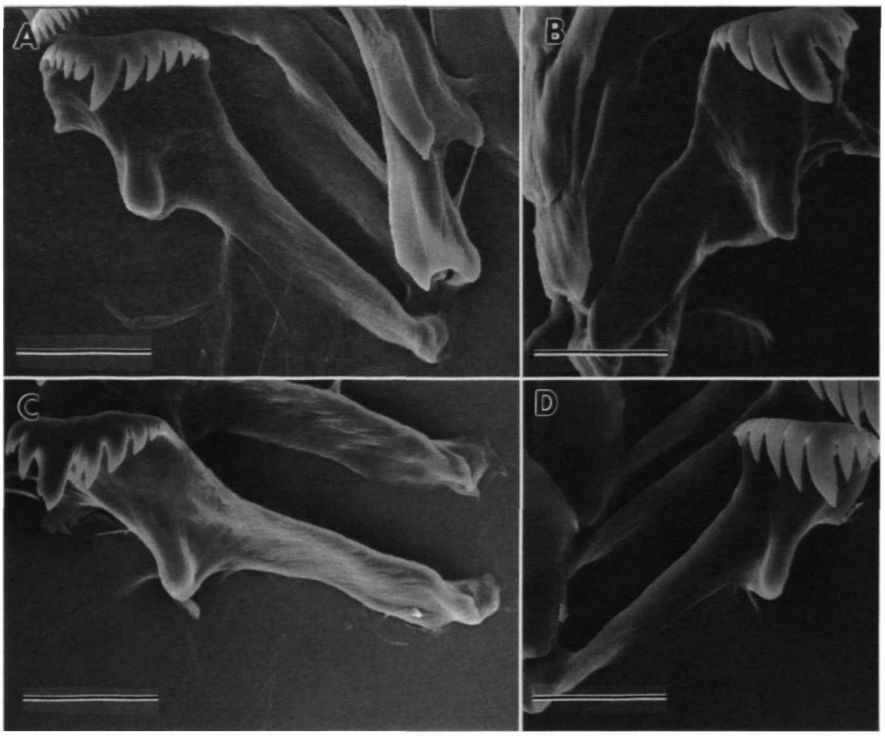


FIGURE 8.—Scanning electron micrographs of lateral radular teeth of *Tryonia* species: A, *Tryonia clathrata,* USNM 850291 (bar=12 μm); B, *Tryonia cheatumi,* USNM 883957 (bar=17 μm); C, *Tryonia imitator,* USNM 892057 (bar=15 μm); D, *Tryonia elata,* USNM 850309 (bar=10 μm).

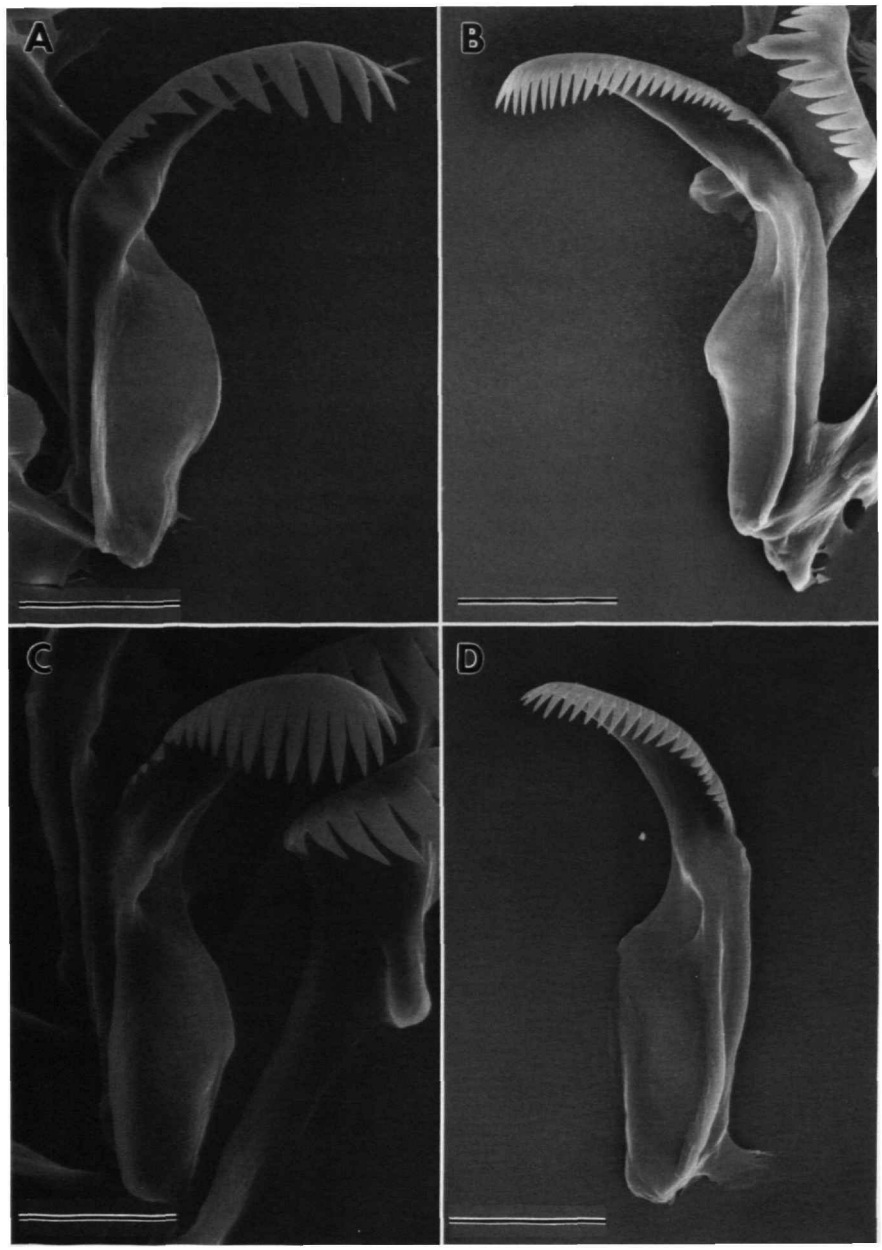


FIGURE 9.—Scanning electron micrographs of inner marginal radular teeth of *Tryonia* species: A, *Tryonia angulata*, USNM 883304 (bar=12 µm); B, *Tryonia porrecta*, USNM 873441 (bar=17 µm); C, *Tryonia elata*, USNM 850309 (bar=8 µm); D, *Tryonia circumstriata*, USNM 883406 (bar=13 µm).

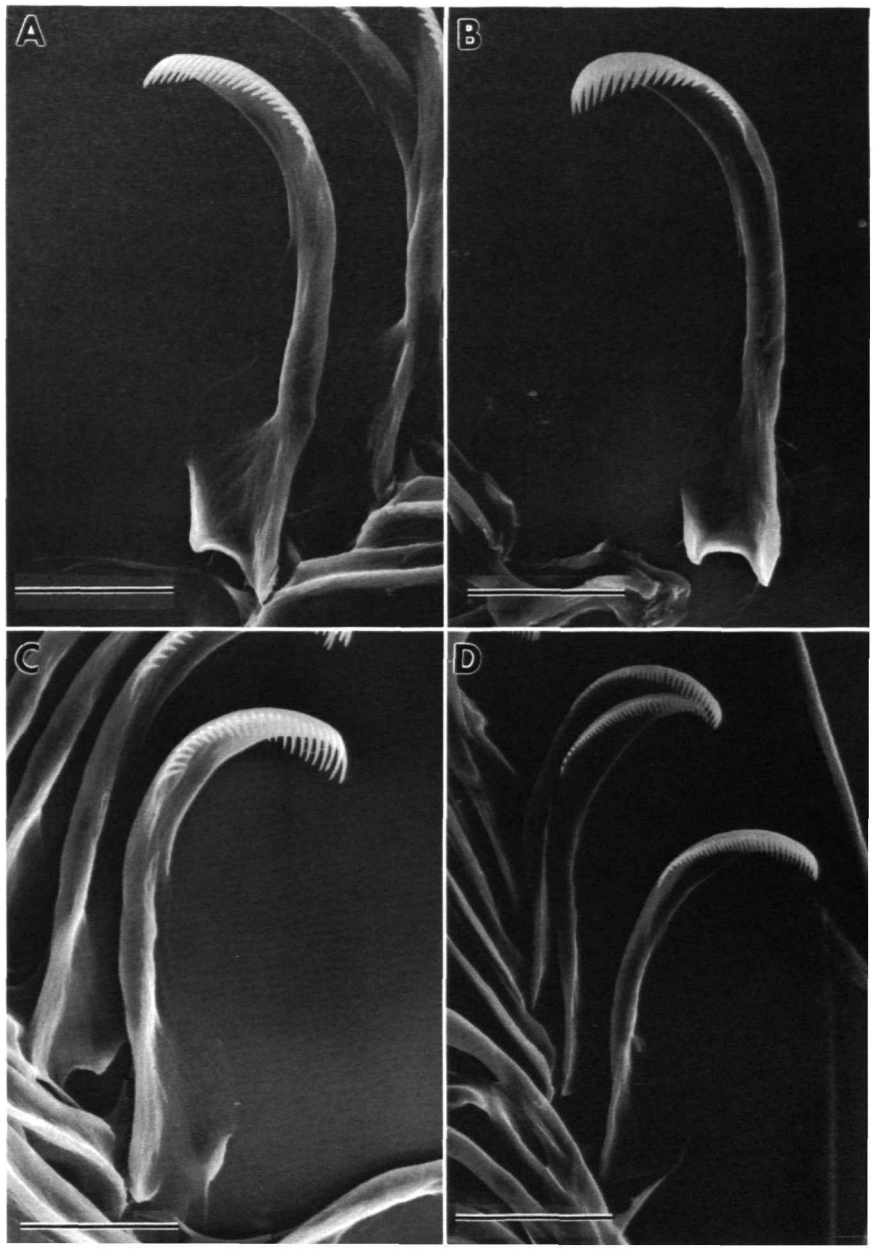


FIGURE 10.—Scanning electron micrographs of outer marginal radular teeth of *Tryonia* species: A, *Tryonia gilae*, USNM 883956 (bar=9 μm); B, *Tryonia rowlandsi*, USNM 857953 (bar=10 μm); C, *Tryonia margae*, USNM 883308 (bar=10 μm); D, *Tryonia variegata*, USNM 850314 (bar=13 μm).

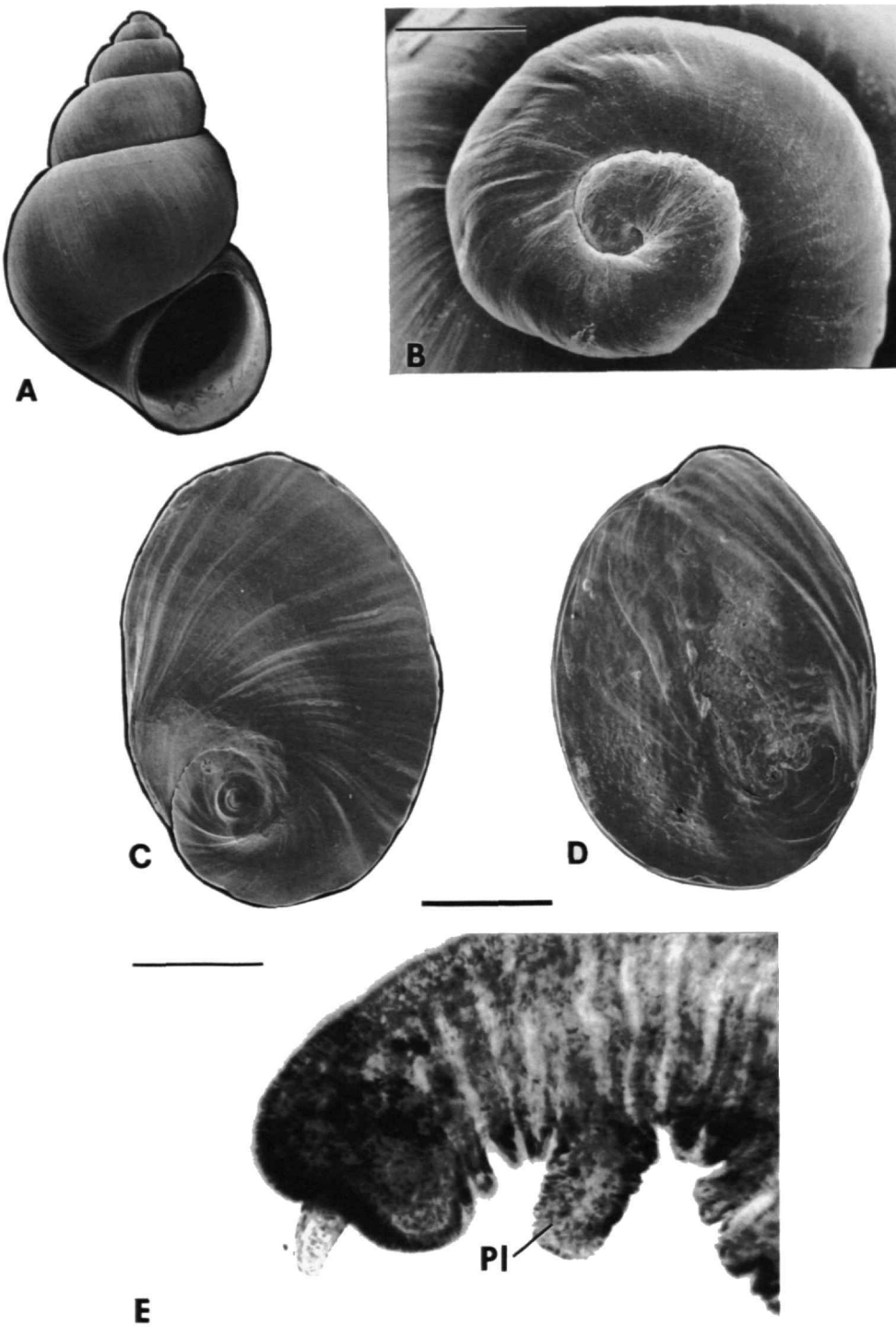


FIGURE 11.—Morphology of *Durangonella kosteri:* A, scanning electron micrograph of shell, USNM 854727 (shell height, 3.2 mm); B, scanning electron micrograph of shell apex, USNM 854727 (bar=133 µm); C,D, scanning electron micrographs of opercula (outer and inner sides, respectively), USNM 883771 (bar=90 µm); E, whole mount of distal section of penis showing non-glandular lobe, USNM 854957 (bar=96 µm). (Pl=penial lobe.)

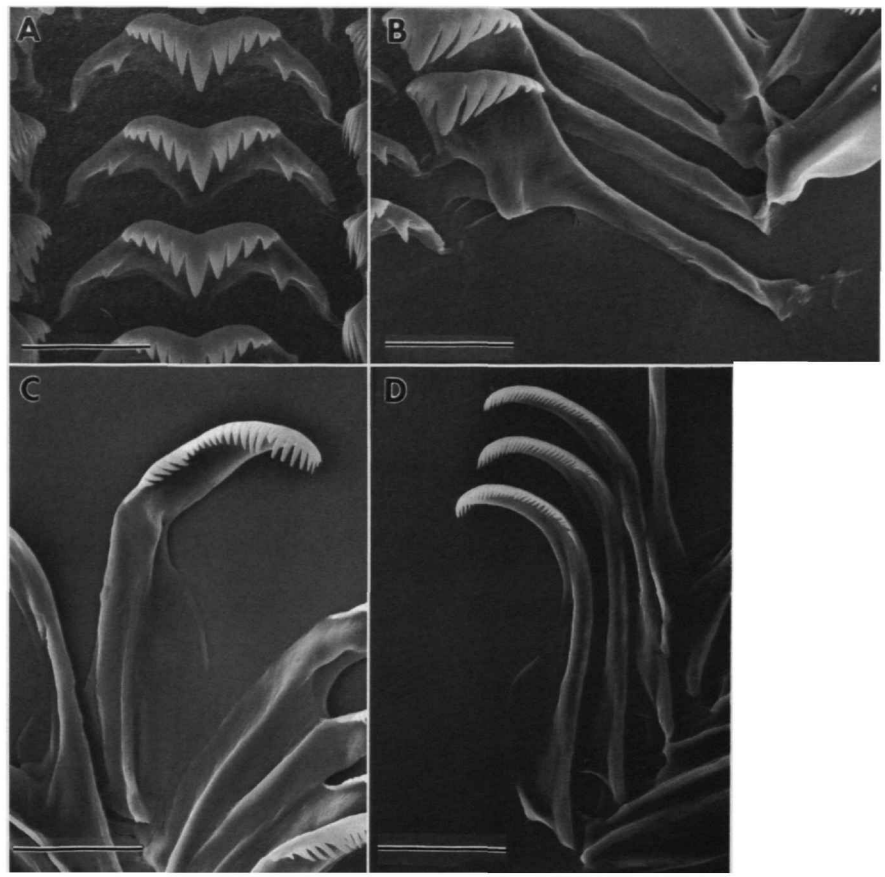


FIGURE 12.—Scanning electron micrographs of radula of *Durangonella kosteri,* USNM 883771: A, central teeth (bar=12 μm); B, lateral teeth (bar=15 μm); C, inner marginal tooth (bar=13 μm); D, outer marginal teeth (bar=17 μm).

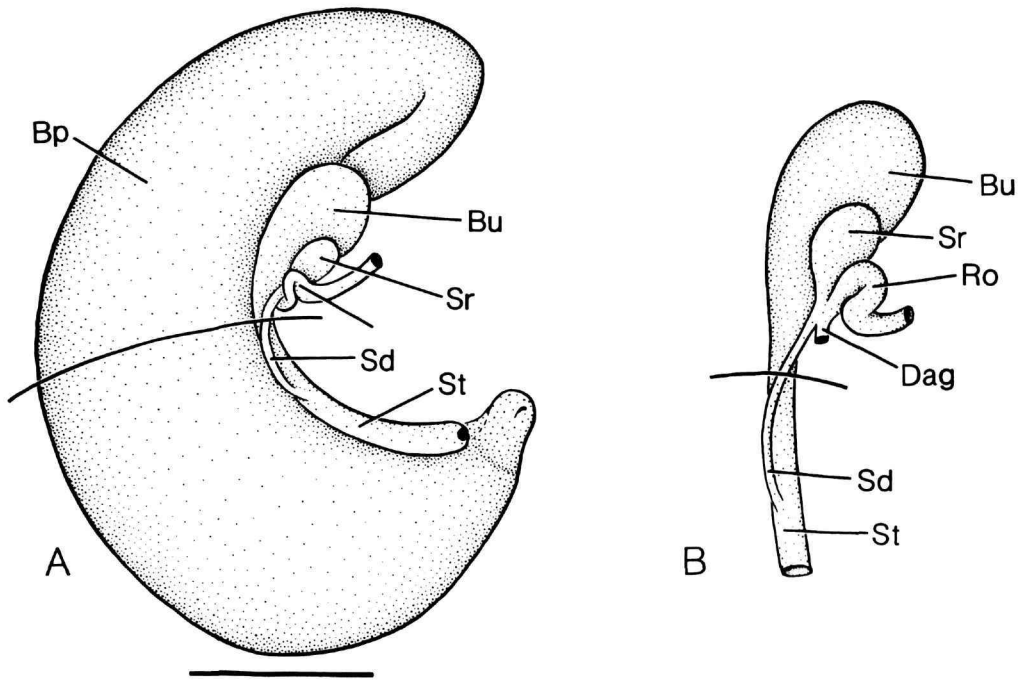


FIGURE 13.—Distal female genitalia (viewed from left side) of *Durangonella kosteri*, USNM 854957 (bar=500 µm) (gonopericardial duct not shown): A, brood pouch and associated structures; B, bursa copulatrix and associated structures, with brood pouch removed. (Bp=brood pouch, Bu=bursa copulatrix, Dag=connection between oviduct and albumen gland, Ro=renal oviduct, Sd=sperm duct, Sr=seminal receptacle, St=sperm tube.)

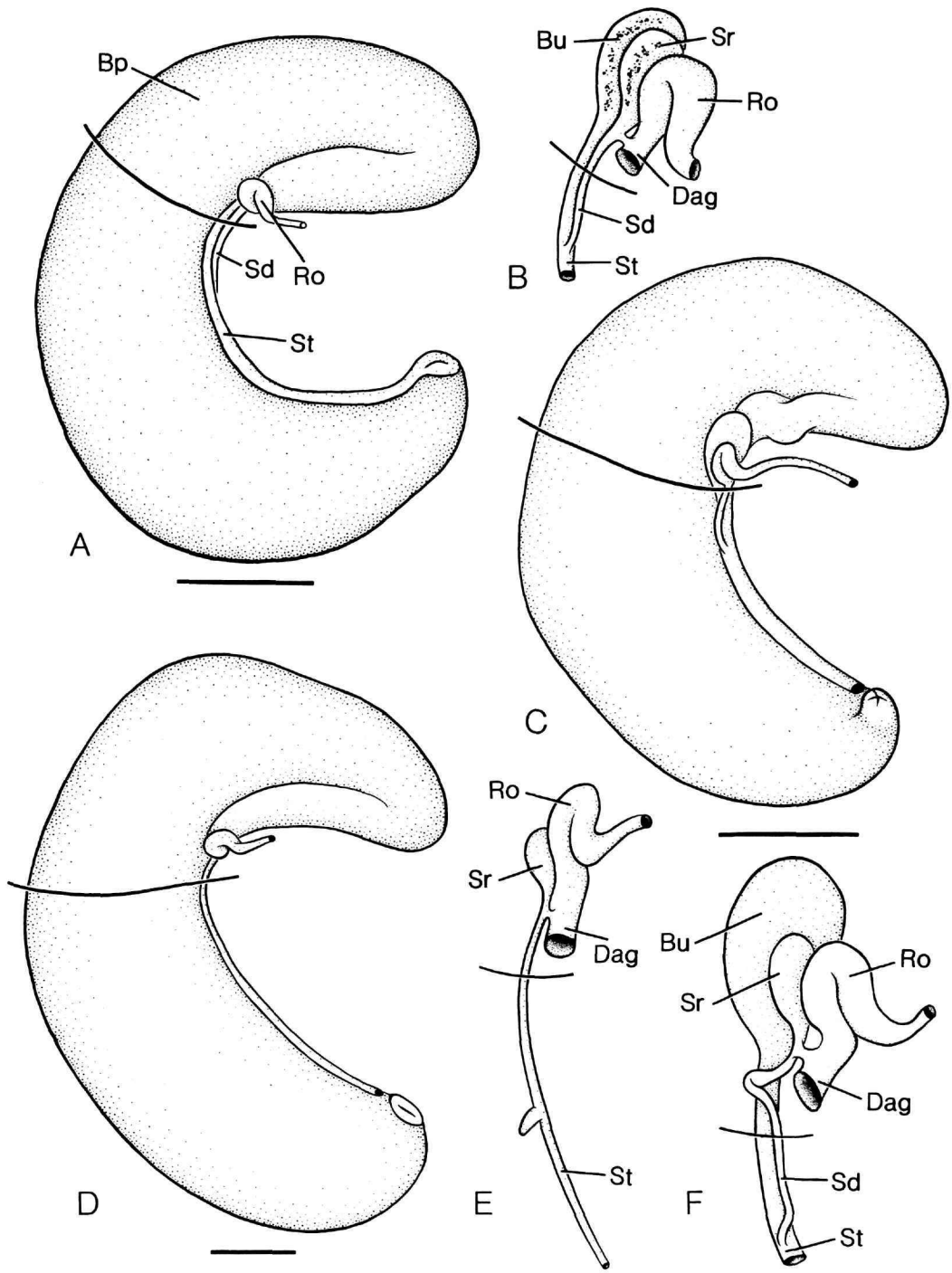


FIGURE 14.—Distal female genitalia (viewed from left side) of *Pseudotryonia* species (bars=250 µm) (gonopericardial duct not shown): A,B, *Pseudotryonia alamosae*, USNM 883959; C,F, *Pseudotryonia* sp., USNM 860751; D,E, *Pseudotryonia brevissima*, USNM 892069. (Note the minute sac opening to sperm tube in pallial cavity. Bp =brood pouch, Bu=bursa copulatrix, Dag=connection between oviduct and albumen gland, Ro=renal oviduct, Sd=sperm duct, Sr=seminal receptacle, St=sperm tube.)

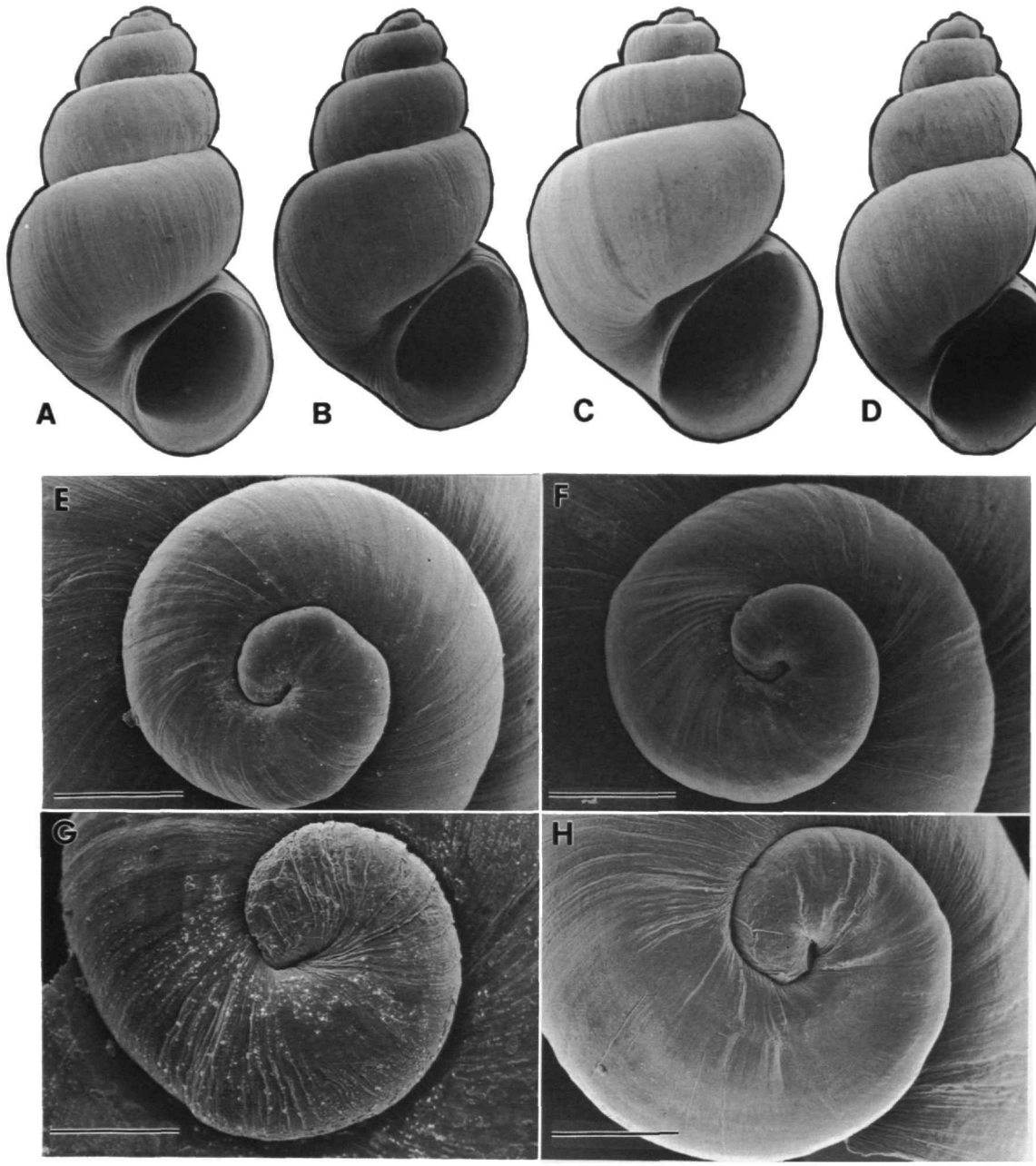


FIGURE 15.—Scanning electron micrographs of entire shells (A–D) and shell apices (E–H) of *Pseudotryonia* species: A, *Pseudotryonia adamantina*, USNM 874915 (shell height, 2.3 mm); B, *Pseudotryonia alamosae*, USNM 883959 (2.1 mm); C, *Pseudotryonia brevissima*, USNM 892069 (3.4 mm); D, *Pseudotryonia* sp., USNM 860755 (3.5 mm); E, *Pseudotryonia adamantina*, USNM 874915 (bar=100 µm); F, *Pseudotryonia alamosae*, USNM 883959 (bar=100 µm); G, *Pseudotryonia brevissima*, USNM 892069 (bar=75 µm); H, *Pseudotryonia* sp., USNM 860752 (bar=75 µm).

FIGURE 16.—Scanning electron micrographs of opercula (A–D, outer side; D–H, inner side) of *Pseudotryonia* species: A,E, *Pseudotryonia adamantina,* USNM 874915 (bars=222, 214 µm, respectively); B,F, *Pseudotryonia brevissima,* USNM 892069 (bars=360, 400 µm, respectively); C,G, *Pseudotryonia alamosae,* USNM 873231 (bars=222, 231 µm, respectively); D,H, *Pseudotryonia* sp., USNM 860752 (bars=360 µm).

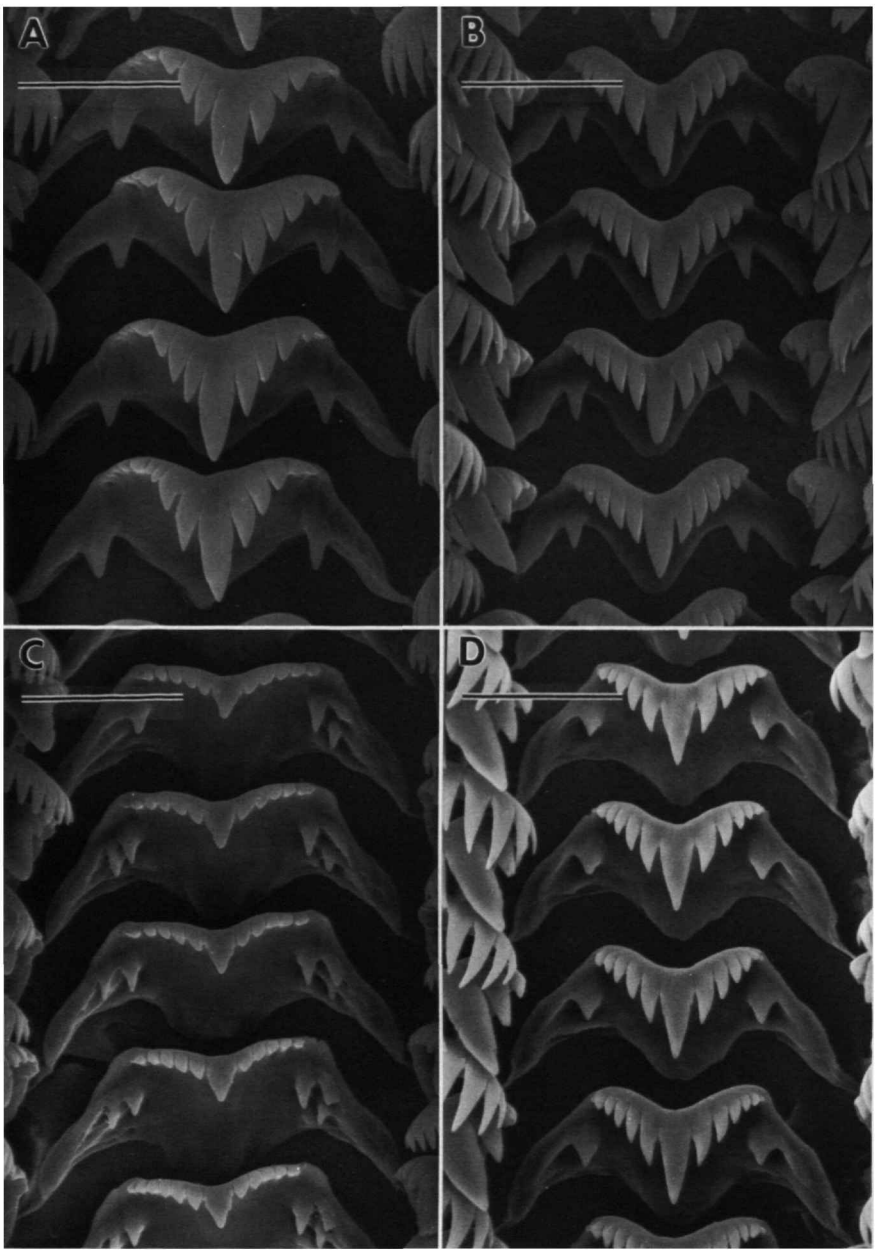


FIGURE 17.—Scanning electron micrographs of central radular teeth of *Pseudotryonia* species: A, *Pseudotryonia adamantina,* USNM 874915 (bar=8.6 μm); B, *Pseudotryonia alamosae,* USNM 873231 (bar=8.6 μm); C, *Pseudotryonia brevissima,* USNM 892069 (bar=12 μm); D, *Pseudotryonia* sp., USNM 860752 (bar=15 μm).

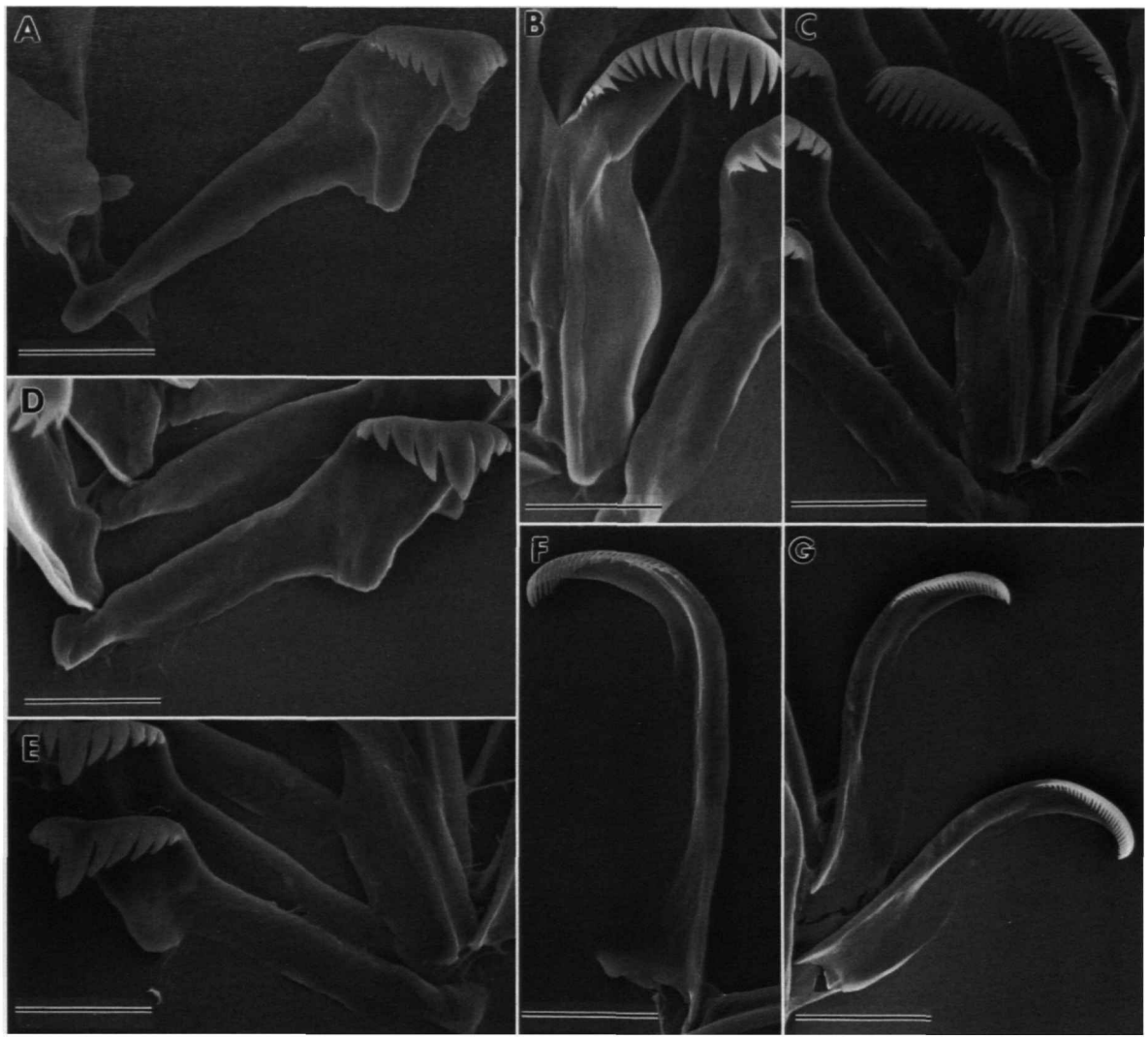


FIGURE 18.—Scanning electron micrographs of lateral (A,D,E), inner marginal (B,C) and outer marginal (F,G) radular teeth of *Pseudotryonia* species: A, *Pseudotryonia brevissima,* USNM 892069 (bar=10 µm); B,D,G, *Pseudotryonia* sp., USNM 860752 (bars=15, 15, 20 µm, respectively); C,E, *Pseudotryonia alamosae,* USNM 873231 (bars=11 µm); F, *Pseudotryonia adamantina,* USNM 874915 (bar=15 µm).

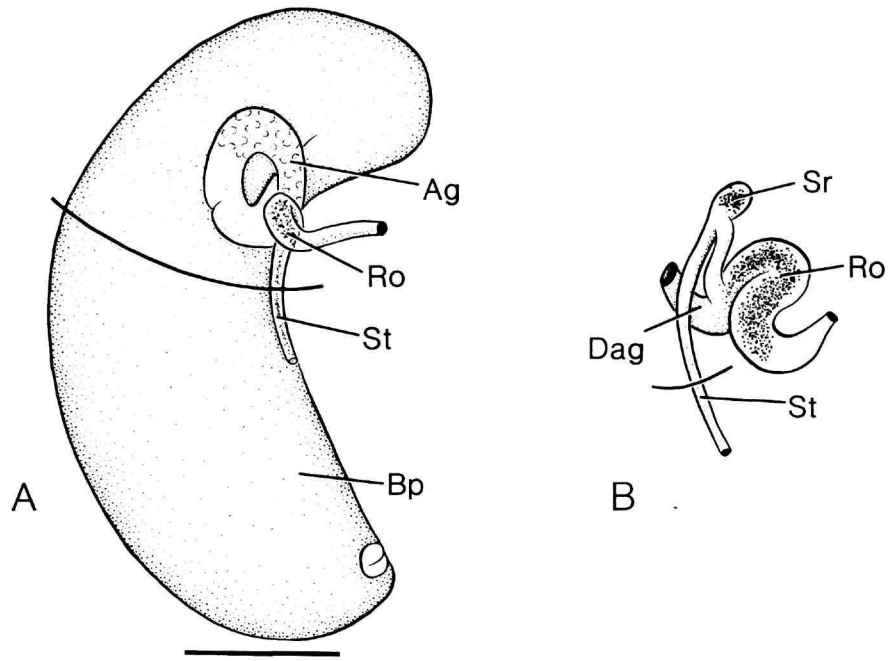


FIGURE 19.—Distal female genitalia (viewed from left side) of *Ipnobius robustus*, USNM 883313 (bar=250 μm) (gonopericardial duct not shown): A, brood pouch and associated structures; B, seminal receptacle and associated structures. (Ag=albumen gland, Bp=brood pouch, Dag=connection between oviduct and albumen gland, Ro=renal oviduct, Sr=seminal receptacle, St=sperm tube.)

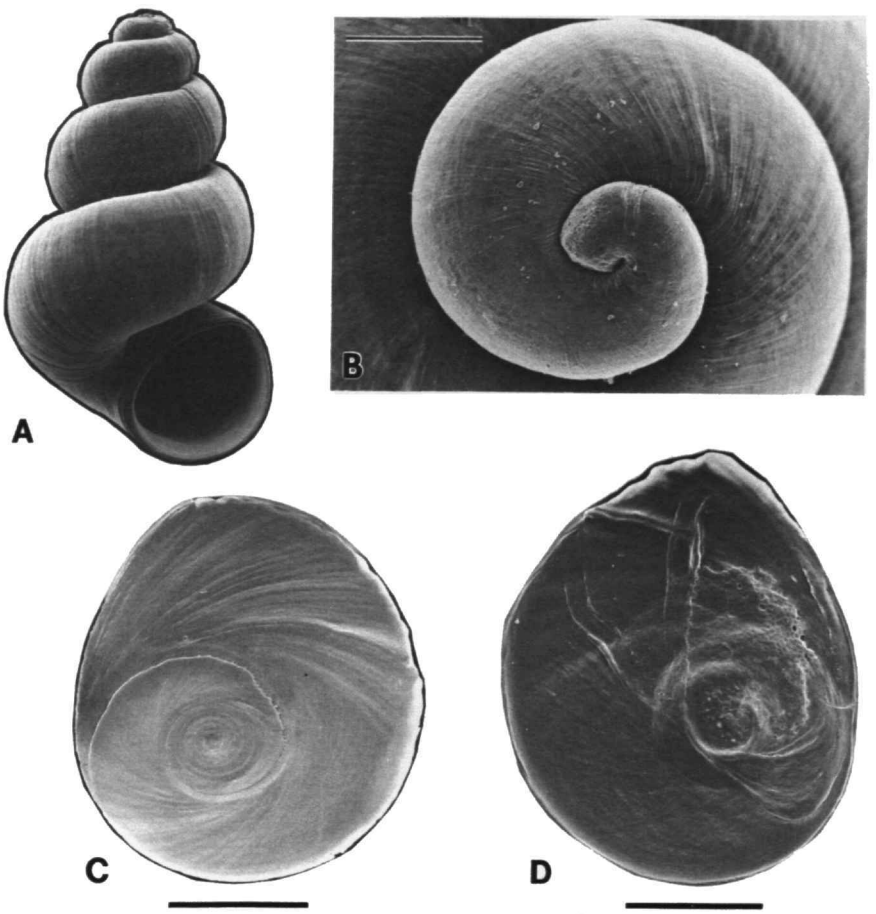


FIGURE 20.—Scanning electron micrographs of morphology of *Ipnobius robustus,* USNM 883313: A, shell (height, 2.2 mm); B, shell apex (bar=86 µm); C, outer side of operculum (bar=230 µm); D, inner side of operculum (bar=207 µm).

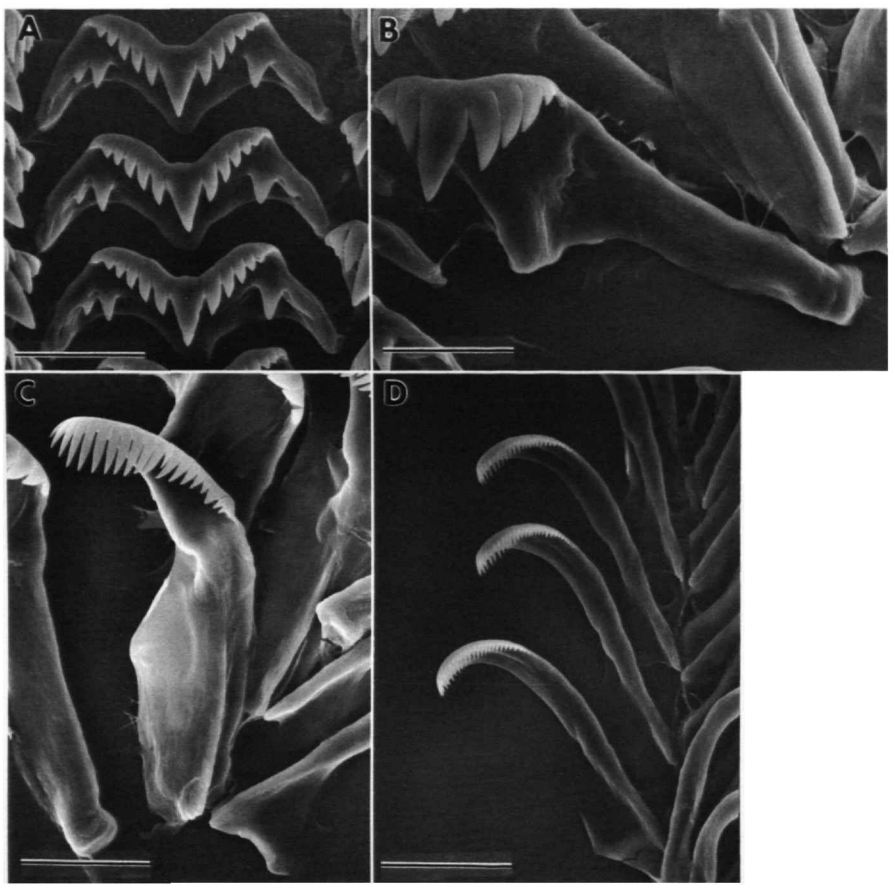


FIGURE 21.—Scanning electron micrographs of radula of *Ipnobius robustus*, USNM 883313: A, central teeth (bar = 12 μm); B, lateral tooth (bar = 11 μm); C, inner marginal tooth (bar = 12 μm); D, outer marginal teeth (bar = 15 μm).

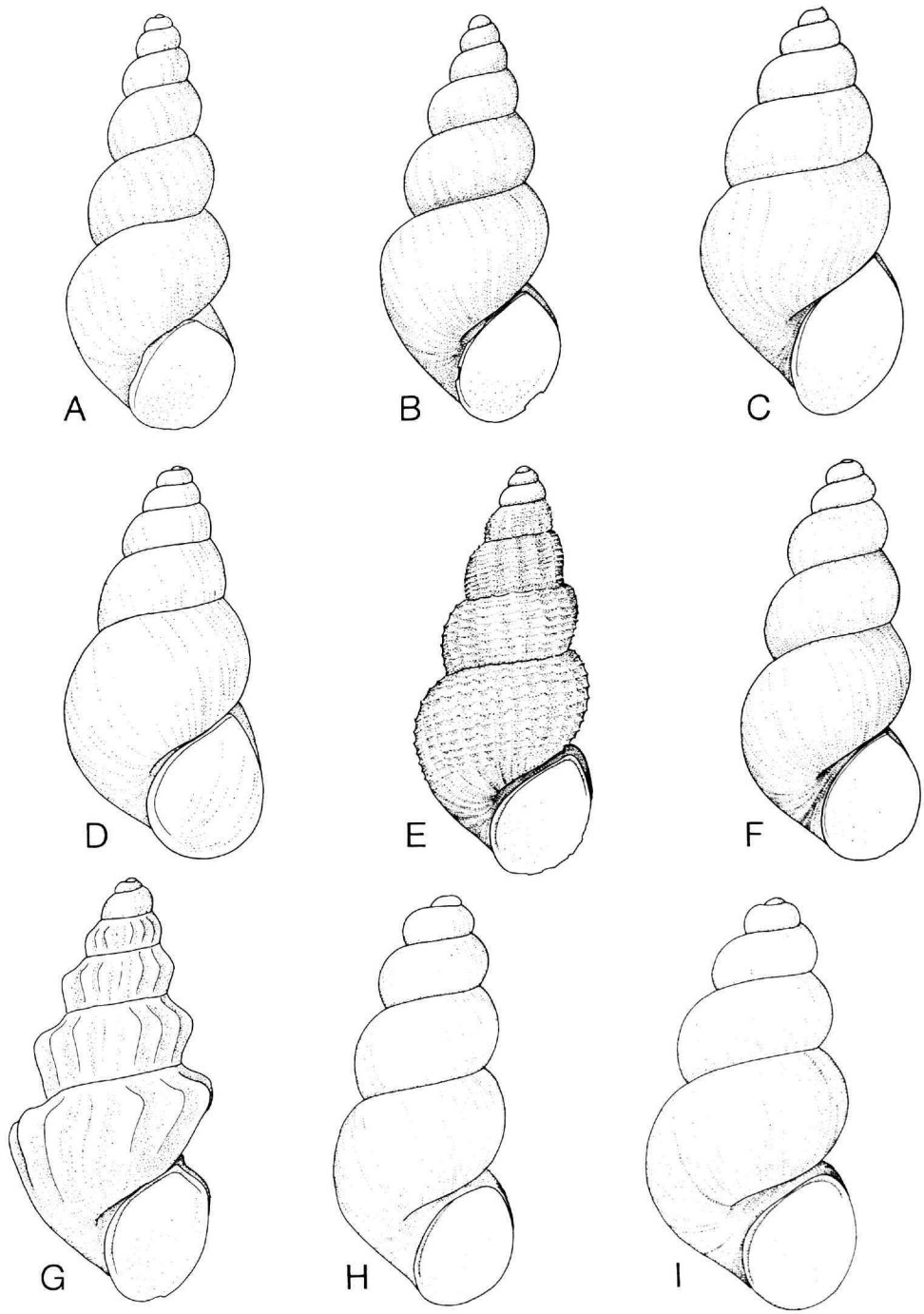


FIGURE 22.—Type specimens of *Tryonia* species and junior synonyms thereof (shells not drawn to same scale): A, holotype, *T. aequicostata,* ANSP 27985 (shell height, 6.0 mm); B, holotype, *Fontigens oxybeles* (=*T. aequicostata*), ANSP 186751 (5.5 mm); C, holotype, *T. angulata,* USNM 859151 (3.6 mm); D, lectotype, *T. cheatumi,* ANSP 16388 (3.9 mm); E, holotype, *T. circumstriata,* USNM 440734 (5.3 mm); F, paratype, *T. stocktonensis* (=*T. circumstriata*), USNM 854092 (3.3 mm); G, lectotype, *T. clathrata,* ANSP 27969 (5.0 mm); H, holotype, *T. elata,* USNM 859159 (1.8 mm); I, holotype, *T. ericae,* USNM 859162 (1.7 mm).

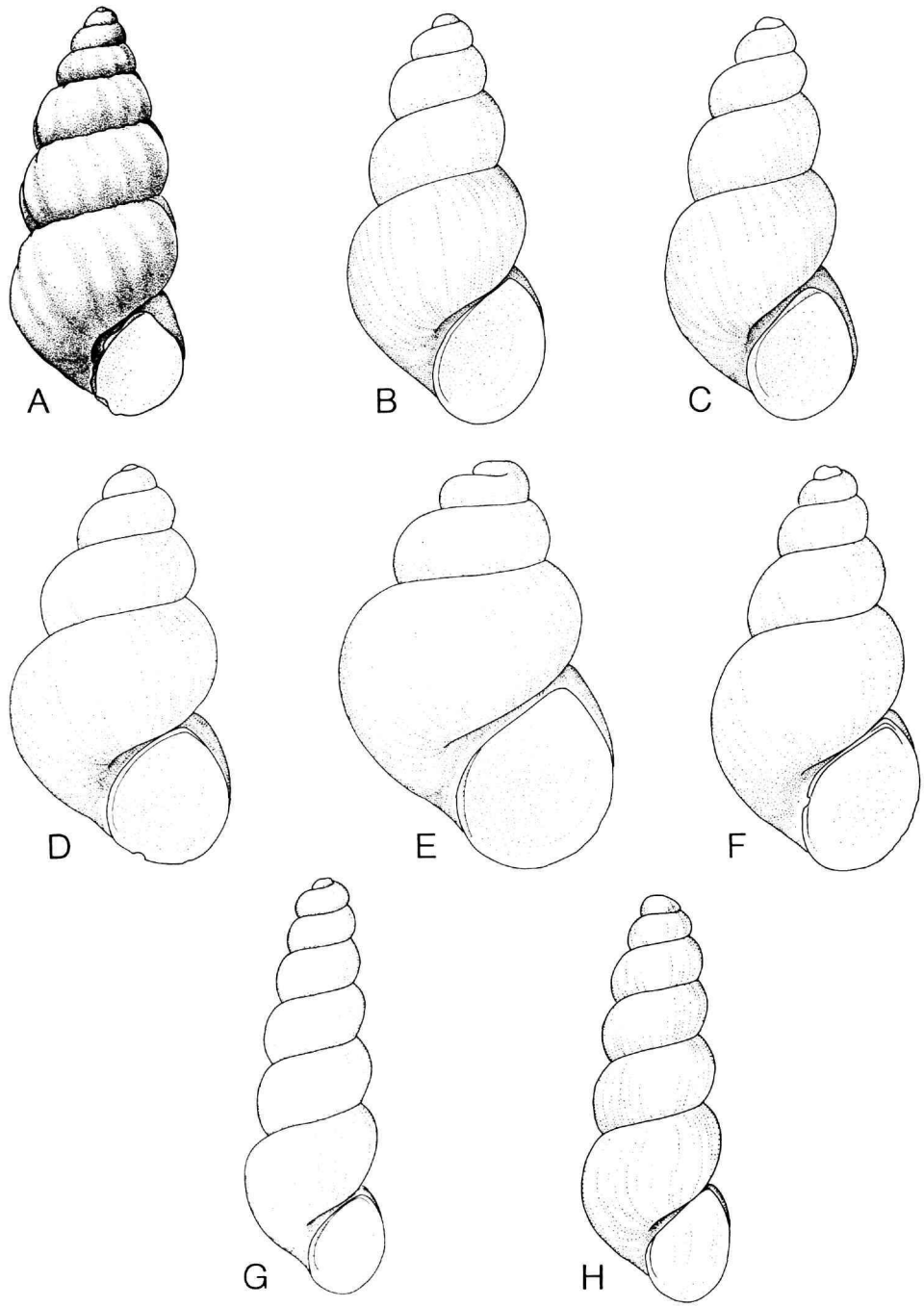


FIGURE 23.—Type specimens of *Tryonia* species and junior synonyms thereof (shells not drawn to same scale): A, lectotype, *T. exigua*, BMNH 1893.2.4.1769 (shell height, 7.3 mm); B, paratype, *T. gilae* Taylor, USNM 854074 (3.0 mm); C, holotype, *T. gilae* Hershler, 1988=*T. gilae* Taylor, 1988), USNM 859059 (3.4 mm); D, paratype, *T. hertleini*, CAS 64919 (2.6 mm); E, lectotype, *T. imitator*, ANSP 62670 (2.5 mm); F, holotype, *Paludestrina curta* (=*T. imitator*), USNM 162542 (3.5 mm); G, holotype, *T. margae*, USNM 860408 (3.5 mm); H, holotype, *T. monitorae*, USNM 892046 (3.0 mm).

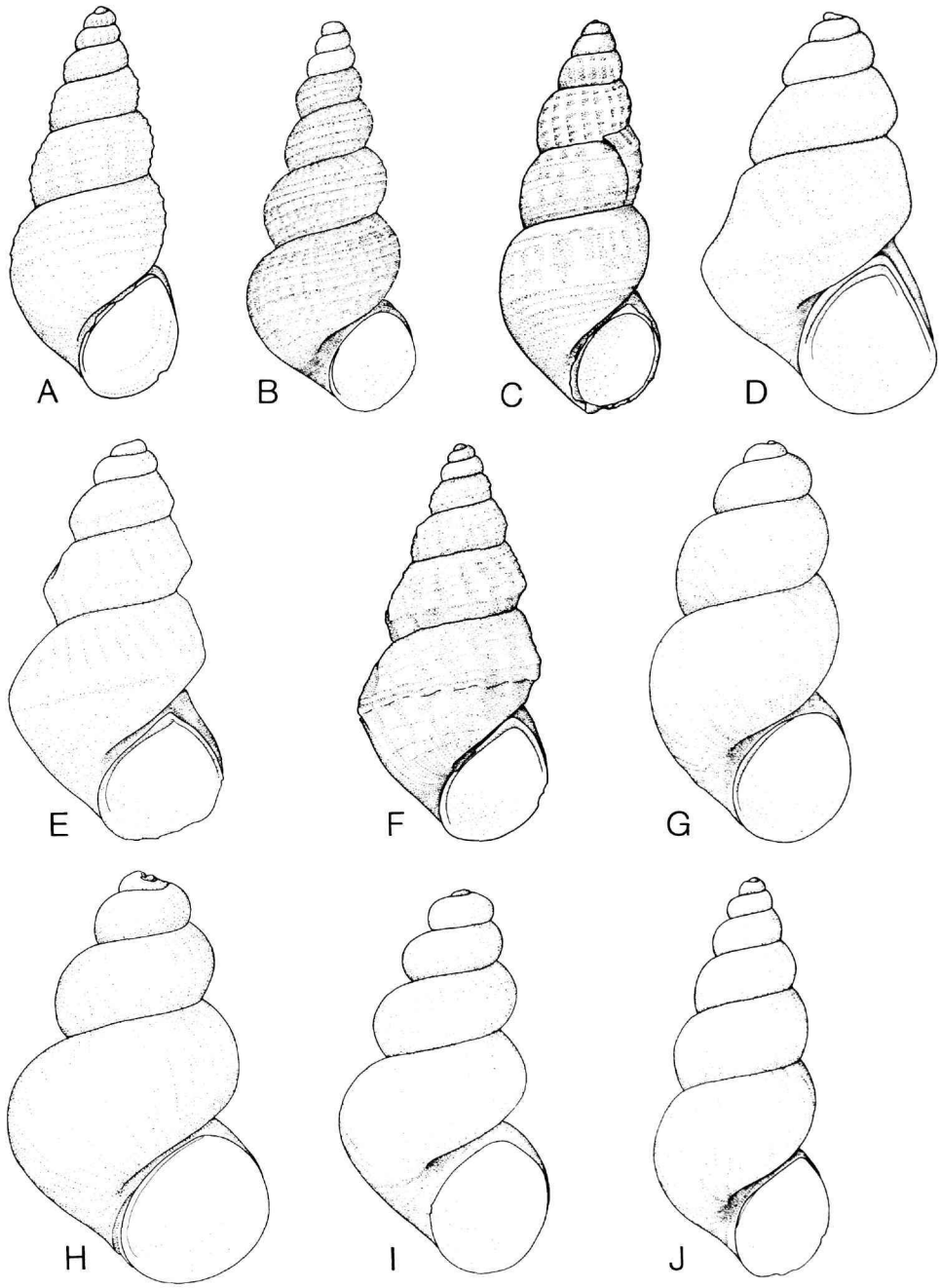


FIGURE 24.—Types and other historical specimens of *Tryonia* species and junior synonyms thereof (shells not drawn to same scale): A, possible syntype, *T. porrecta*, BMNH 1995123 (shell height, 6.7 mm); B, lectotype, *Amnicola protea* (=*T. porrecta*), USNM 120174 (5.4 mm); C, lectotype, *Melania exigua* (=*T. porrecta*), ANSP 27965 (4.6 mm); D, holotype, *Pyrgulopsis imminens* (=*T. porrecta*), SBMNH 35497 (3.8 mm); E, holotype, *Pyrgulopsis blakeana* (=*T. porrecta*), SBMNH 35500 (4.2 mm); F, holotype, *Pyrgulopsis cahuillarum* (=*T. porrecta*), SBMNH 35503 (5.7 mm); G, holotype, *T. quitobaquitae*, USNM 859061 (2.0 mm); H, holotype, *T. rowlandsi*, USNM 860409 (2.2 mm); I, holotype, *T. salina*, USNM 860410 (3.3 mm); J, holotype, *T. variegata*, USNM 859166 (4.0 mm).

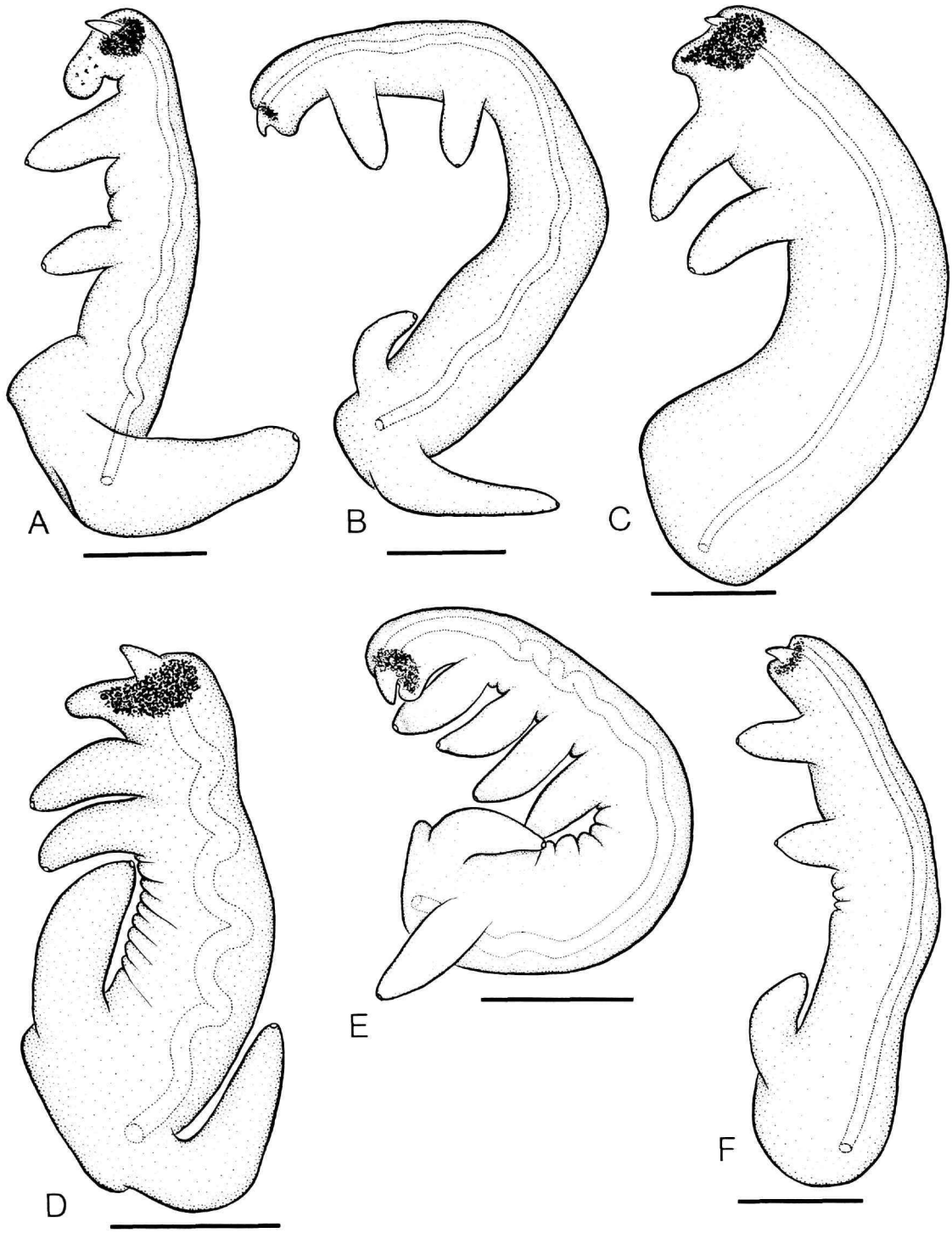


FIGURE 25.—Penes (dorsal side) of *Tryonia* species (bars=250 µm): A, *Tryonia aequicostata,* USNM 874831; B, *Tryonia angulata,* USNM 850299; C, *Tryonia cheatumi,* USNM 883952; D, *Tryonia circumstriata,* USNM 892020; E, *Tryonia clathrata,* USNM 873192; F, *Tryonia elata,* USNM 850309. (Pigmented areas indicated by dense stipple; penial ducts indicated by stippled lines.)

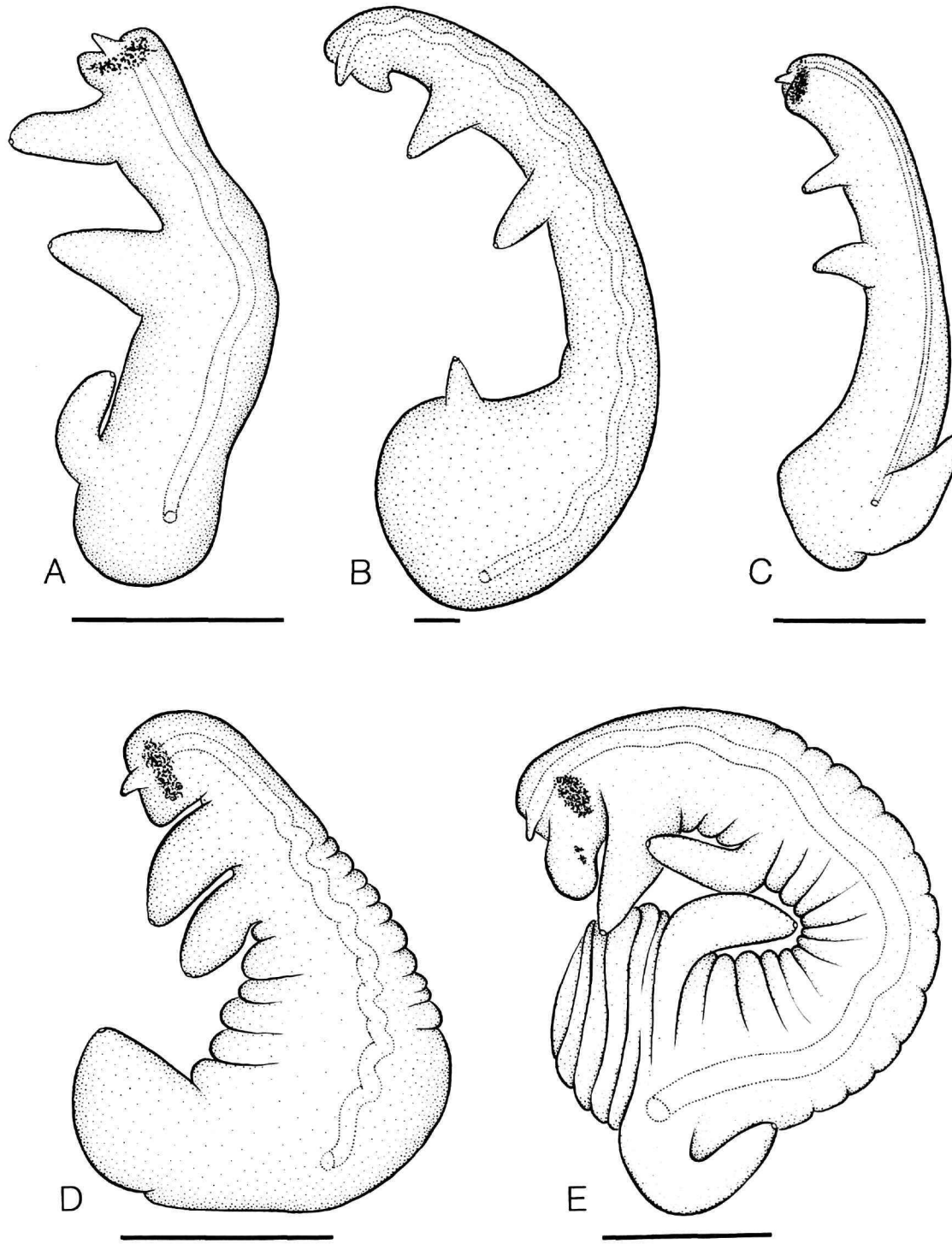


FIGURE 26.—Penes (dorsal side) of *Tryonia* species (bars=250 μm): A, *Tryonia ericae*, USNM 850312; B, *Tryonia exigua*, USNM 874034; C, *Tryonia gilae*, USNM 847253; D, *Tryonia hertleini*, UMMZ uncat.; E, *Tryonia imitator*, USNM 892057. (Pigmented areas indicated by dense stipple; penial ducts indicated by stippled lines.)

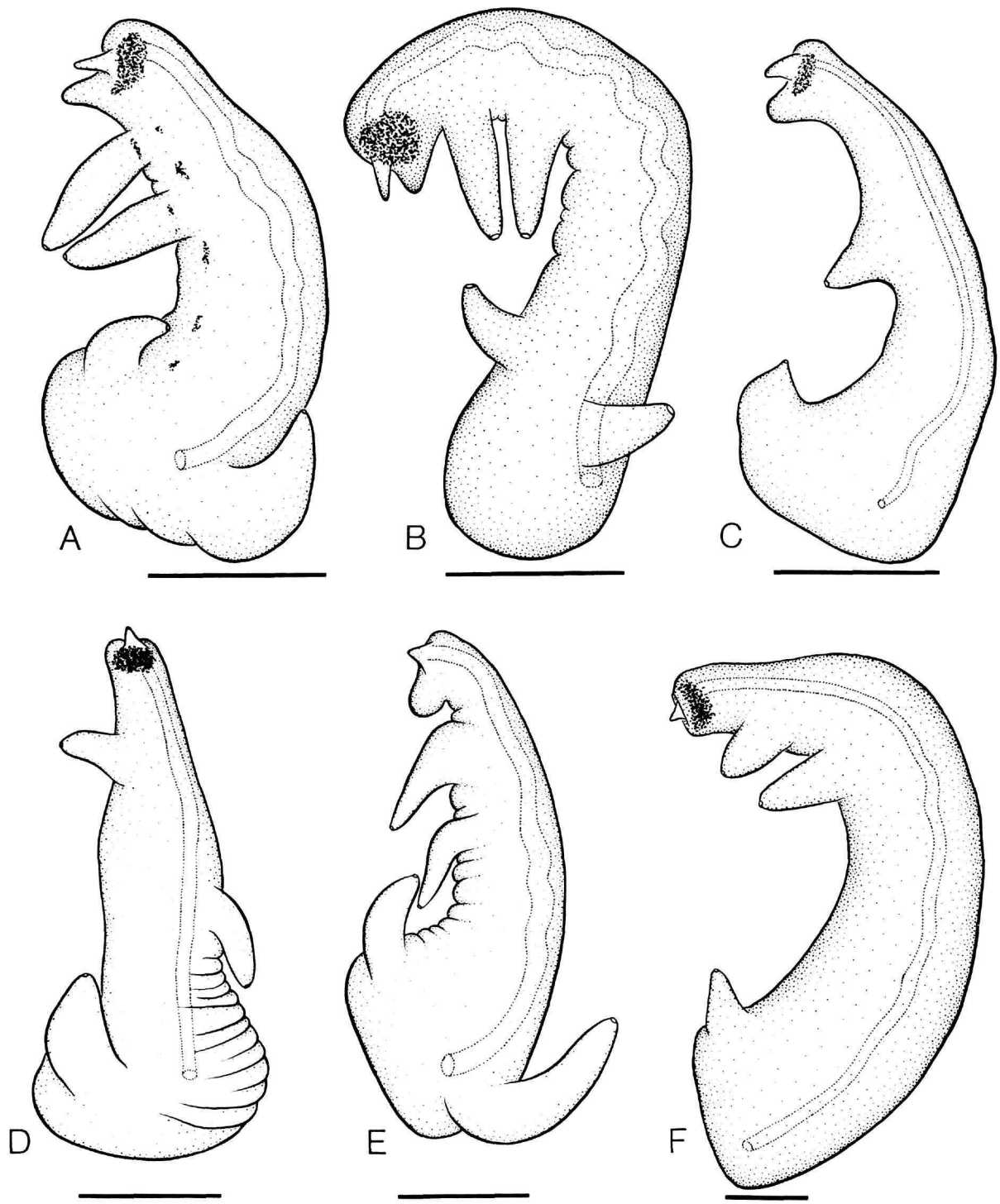


FIGURE 27.—Penes (dorsal side) of *Tryonia* species (bars=250 µm): A, *Tryonia margae*, USNM 857952; B, *Tryonia monitorae*, USNM 860760; C, *Tryonia quitobaquitae*, USNM 847256; D, *Tryonia rowlandsi*, USNM 857953; E, *Tryonia salina*, USNM 883326; F, *Tryonia variegata*, USNM 850314. (Pigmented areas indicated by dense stipple; penial ducts indicated by stippled lines.)

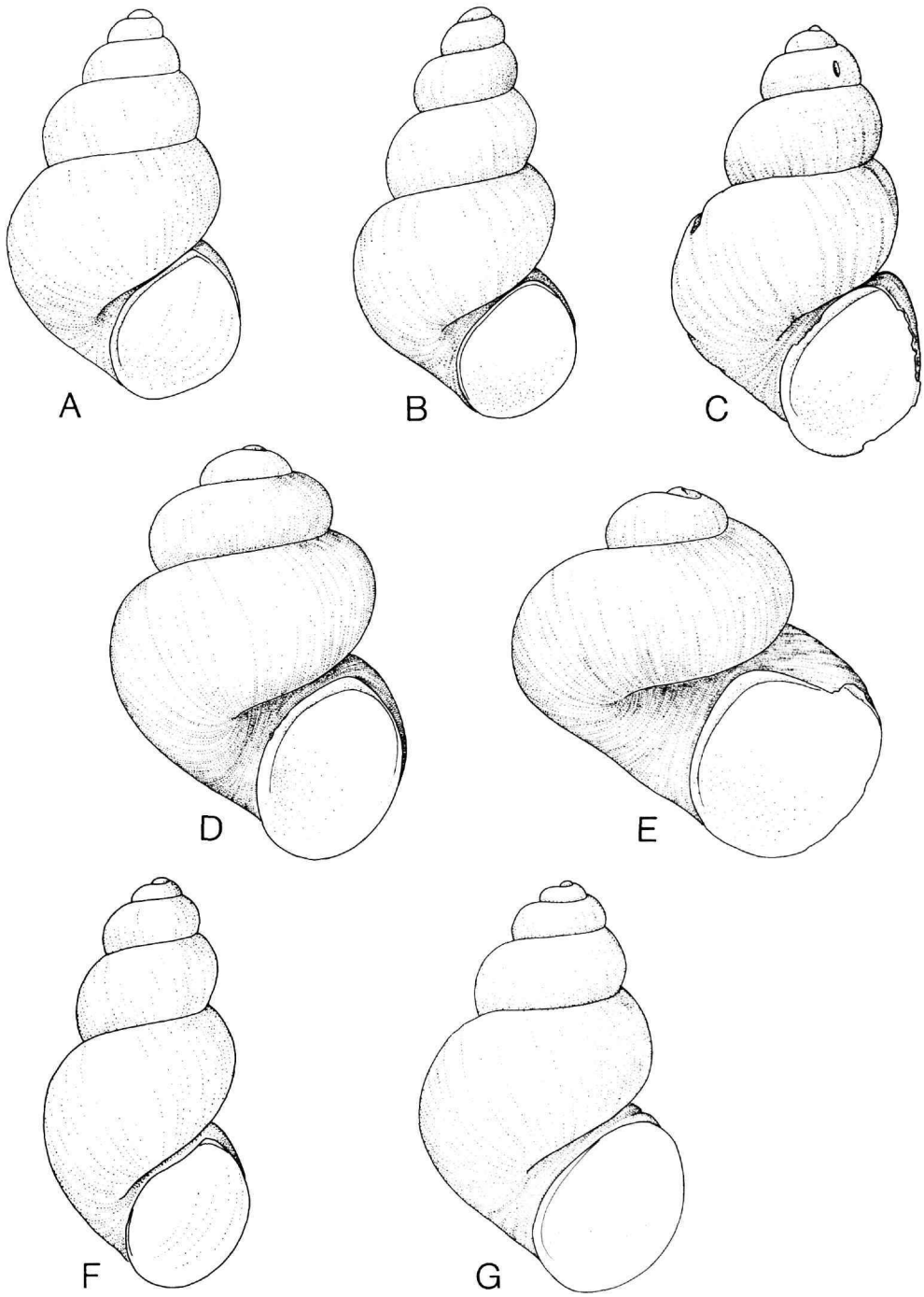


FIGURE 28.—Type and other representative specimens of species of *Durangonella, Pseudotryonia,* and *Ipnobius,* and junior synonyms thereof (shells not drawn to same scale): A, paratype, *Durangonella kosteri,* USNM 854091 (shell height, 4.0 mm); B, paratype, *Pseudotryonia adamantina,* USNM 854075 (3.3 mm); C, paratype, *Pseudotryonia alamosae,* USNM 854072 (3.2 mm); D, holotype, *Bythinella brevissima* (= *P. brevissima*), ANSP 62418 (3.0 mm); E, lectotype, *Amnicola harperi* (=*P. brevissima*), USNM 211011 (1.3 mm); F, *Pseudotryonia* sp., UF 271517 (4.2 mm); G, holotype, *Ipnobius robustus,* USNM 860411 (1.9 mm).

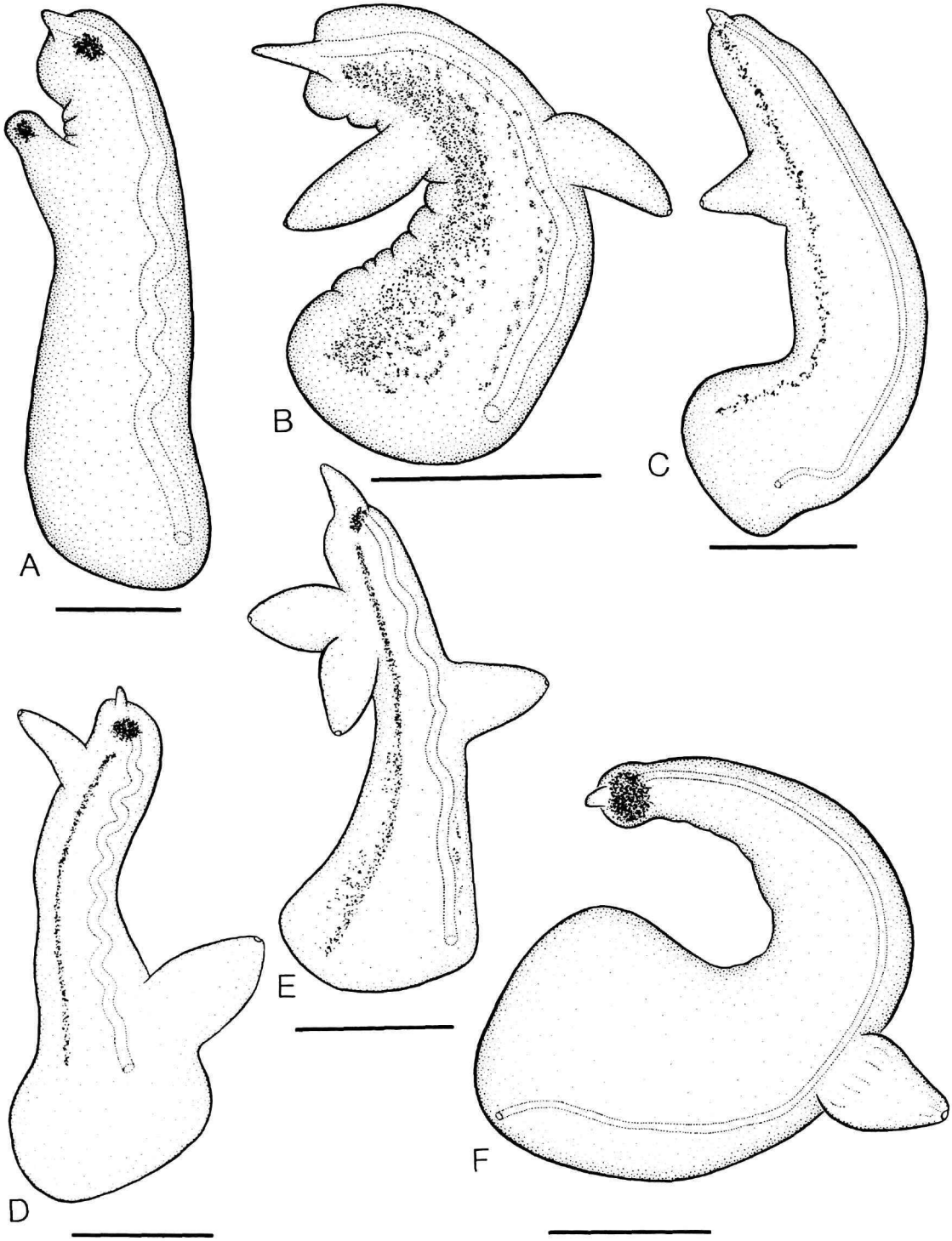


FIGURE 29.—Penes (dorsal side) of species of *Durangonella*, *Pseudotryonia*, and *Ipnobius* (bars=200 μm): A, *Durangonella kosteri*, USNM 854957; B, *Pseudotryonia adamantina*, USNM 873125; C, *Pseudotryonia alamosae*, USNM 873231; D, *Pseudotryonia brevissima*, USNM 892069; E, *Pseudotryonia* species, USNM 860751; F, *Ipnobius robustus*, USNM 883313.

Literature Cited

Arnold, R.

1903. The Paleontology and Stratigraphy of the Marine Pliocene and Pleistocene of San Pedro, California. *Memoirs of the California Academy of Sciences*, 3: 420 pages, 37 plates.

Athens, J.S., and J.V. Ward

1993. Paleoenvironmental Investigations at Hamakua Marsh, Kailua, O'ahu, Hawai'i. 50 pages. Unpublished report, International Archaeological Research Institute, Inc., Honolulu. [Report prepared for Ducks Unlimited, Inc., Western Regional Office, Sacramento.]

Baily, J.L., Jr., and R.I. Baily

1951–1952. Further Observations on the Mollusca of the Relict Lakes in the Great Basin. *The Nautilus*, 65(2, 3):46–53, 85–93.

Baker, H.B.

1964. Type Land Snails in the Academy of Natural Sciences of Philadelphia, Part III: Limnophile and Thalassophile Pulmonata; Part IV: Land and Fresh-Water Prosobranchia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 116(4):149–193.

Bequaert, J.C., and W.B. Miller

1973. *The Mollusks of the Arid Southwest, with an Arizona Check List.* 271 pages. Tucson: University of Arizona Press.

Berry, E.G.

1948 ("1947"). Snails Collected for the Schistosomiasis Investigations. *Bulletin of the United States National Institute of Health*, 189:55–69. [Date on title page is 1947; actually published in 1948.]

Binney, W.G.

1865. Land and Fresh-Water Shells of North America, Part III: Ampullariidae, Valvatidae, Viviparidae, Fresh-Water Rissoidae, Cyclophoridae, Truncatellidae, Fresh-Water Neritidae, Helicinidae. *Smithsonian Miscellaneous Collections*, 7(3): 120 pages.

Brot, A.D.M.

1862. *Matériaux pour servir a l'étude de la famille des Mélaniens; Catalogue systématique des espèces qui composent la famille des Mélaniens.* 72 pages. Genève: Jules-Guillaume Fick.

Conrad, T.

1855. Description of a New Species of *Melania*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7:269.

1871. Descriptions of New Fossil Shells of the Upper Amazon. *American Journal of Conchology*, 6:192–198, plates 10, 11.

Cowie, R.H.

1995. *Catalog of the Native Land and Freshwater Molluscs of the Hawaiian Islands.* 248 pages. Leiden: Backhuys Publishers.

1997. Catalog and Bibliography of the Nonindigenous Nonmarine Snails and Slugs of the Hawaiian Islands. *Occasional Papers of the Bernice P. Bishop Museum*, 50: 66 pages.

Dall, W.H.

1877. Note on "Die Gasteropoden Fauna Baikalsees." *Proceedings of the Boston Society of Natural History*, 19:43–47.

1910. A New Floridian *Amnicola*. *The Nautilus*, 24(1):2.

Drake, R.J.

1956. A New Species of Amnicolid Snail from Chihuahua, Mexico. *Bulletin of the Southern California Academy of Sciences*, 55(1):44–46.

Fischer, P., and H. Crosse

1880–1902. *Études sur les Mollusques terrestres et fluviatiles; Mission scientifique au Mexique et dans l'Amérique Centrale ouvrage publié par Order du Ministre de L'Institution Publique; Recherches Zoologiques publiées sous la direction de M. Milne Edwards, membre de l'Institut, septième partie.* Volume II, 731 pages, plates XXXII–LXXII. Paris: Imprimerie Nationale.

Frauenfeld, G.R. von

1863. Vorläufige Aufzählung der Arten der Gattungen *Hydrobia* Htm. und *Amnicola* Gld, Hldm. in der Kaiserlichen und in Cuming's Sammlung. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 13:1017–1032.

Giusti, F., F. Manganelli, and M. Bodon

1998. Case 3087: *Hydrobia* Hartmann, 1821 and *Cyclostoma acutum* Draparnaud, 1805 (Currently *Hydrobia acuta*; Mollusca, Gastropoda): Proposed Conservation by Replacement of the Lectotype of *H. acuta* with a Neotype; *Ventrosia* Radoman, 1977: Proposed Designation of *Turbo ventrosus* Montagu, 1803 as the Type Species; and Hydrobiina Mulsant, 1844 (Insecta, Coleoptera): Proposed Emendation of Spelling to Hydrobiusina, so Removing the Homonymy with Hydrobiidae Troschel, 1857 (Mollusca). *Bulletin of Zoological Nomenclature*, 55(3):139–145.

Goodrich, C., and H. van der Schalie

1937. Mollusca of Petén and North Alta Vera Paz, Guatemala. *University of Michigan Museum of Zoology, Miscellaneous Publications*, 34: 50 pages, plate I, map 1.

Gould, A.A.

1855. New Species of Land and Fresh-Water Shells from Western (N.) America. *Proceedings of the Boston Society of Natural History*, 5:127–130.

1857. Catalogue of the Recent Shells, with Descriptions of the New Species. *In* W.P. Blake, *Geological Report, in Reports of Explorations and Surveys for Railroad Routes to Connect with the Routes near the 35th and 32d Parallels of North Latitude by Lieutenant R.S. Williamson, 1853, in Reports of Explorations and Surveys, to Ascertain the Most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific Ocean Made under the Direction of the Secretary of War, in 1853–4, According to Acts of Congress of March 3, 1853, May 31, 1854, and August 5, 1854.* Volume 5, part II, appendix, article III, pages 330–336, plate 11. Washington, D.C.: A.O.P. Nicholson.

Haas, F.

1938. Neue Binnen-Mollusken aus Nordost-Brasilien. *Archiv für Molluskenkunde*, 70(1):46–51.

1949. On Fresh Water Mollusks from the Amazonian Region. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México*, 20:301–314.

Hershler, R.

1985. Systematic Revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Ciénegas Basin, Coahuila, México. *Malacologia*, 26(1–2):31–123.

1989. Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa River (Exclusive of Ash Meadows) Drainages, Death Valley System, California-Nevada. *Proceedings of the Biological Society of Washington*, 102(1):176–248.

1994. A Review of the North American Freshwater Snail Genus *Pyrgulopsis* (Hydrobiidae). *Smithsonian Contributions to Zoology*, 554: 115 pages.

1998. A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States, Part I: Genus *Pyrgulopsis*. *The Veliger*, 41(1): 132 pages.

1999. A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States, Part II: Genera *Colligyrus*, *Eremopyrgus*, *Fluminicola*, *Pristinicola*, and *Tryonia*. *The Veliger*, 42(4):306–337.

Hershler, R., and T.J. Frest

1996. A Review of the North American Freshwater Snail Genus *Fluminicola* (Hydrobiidae). *Smithsonian Contributions to Zoology*, 583: 41 pages.

Hershler, R., and J.J. Landye
1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). *Smithsonian Contributions to Zoology,* 459: 63 pages.
Hershler, R., H.-P. Liu, and M. Mulvey
1999. Phylogenetic Relationships within the Aquatic Snail Genus *Tryonia*: Implications for Biogeography of the North American Southwest. *Molecular Phylogenetics and Evolution,* 13(2):377–391.
Hershler, R., M. Mulvey, and H.-P. Liu
1999. Biogeography in the Death Valley Region: Evidence from Springsnails (Hydrobiidae: *Tryonia*). *Zoological Journal of the Linnean Society,* 126:335–354.
Hershler, R., and W.F. Ponder
1998. A Review of Morphological Characters of Hydrobioid Snails. *Smithsonian Contributions to Zoology,* 600: 55 pages.
Hershler, R., and D.W. Sada
1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, Amargosa Basin, California–Nevada. *Proceedings of the Biological Society of Washington,* 100(4):776–843.
Hershler, R., and F.G. Thompson
1987. North American Hydrobiidae (Gastropoda: Rissoacea): Redescription and Systematic Relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886. *The Nautilus,* 101(1):25–32.
1992. A Review of the Aquatic Gastropod Subfamily Cochliopinae (Prosobranchia: Hydrobiidae). *Malacological Review,* supplement 5: 140 pages.
Johnson, R.I.
1949. Jesse Wedgwood Mighels with a Bibliography and a Catalogue of His Species. *Occasional Papers on Mollusks, Museum of Comparative Zoology (Harvard),* 1(14):213–231.
Kabat, A.R., and R. Hershler
1993. The Prosobranch Snail Family Hydrobiidae (Gastropoda: Rissoacea): Review of Classification and Supraspecific Taxa. *Smithsonian Contributions to Zoology,* 547: 94 pages.
Kellogg, M.G.
1985. Contributions to our Knowedge of *Tryonia imitator* (Pilsbry, 1899). 78 pages. Master's thesis, Department of Biology, San Francisco State University, California.
Küster, H.C.
1852–1853. Die Gattungen *Paludina, Hydrocaena* und *Valvata*. *In* H.C. Küster et al., *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Volume 1, part 21: 96 pages, 14 plates. Nürnberg: V. Bauer and Raspe.
Leonard, A.B., and T.-Y. Ho
1960. New *Calipyrgula* from Pleistocene of Texas and Notes on *Cochliopa riograndensis*. *The Nautilus,* 73(4):125–129, plates 12, 13.
Meffe, G.K., and P.C. Marsh
1983. Distribution of Aquatic Macroinvertebrates in Three Sonoran Desert Springbrooks. *Journal of Arid Environments,* 6:363–371.
Mighels, J.W.
1845. Descriptions of Shells from the Sandwich Islands, and Other Localities. *Proceedings of the Boston Society of Natural History,* 2:18–25.
Minckley, W.L., and C.O. Minckley
1986. *Cyprinodon pachycephalus*, a New Species of Pupfish (Cyprinodontidae) from the Chihuahuan Desert of Northern México. *Copeia,* 1986:184–192.
Morelet, A.
1851. *Testacea Novissima Insulæ Cubanæ et Americæ Centralis*. 30 pages. Paris: J-B. Ballière.
Morrison, J.P.E.
1940. A New Species of *Fluminicola* with Notes on "Colorado Desert" Shells, and on the Genus *Clappia*. *The Nautilus,* 53(4):124–127.
1945. *Durangonella*, a New Hydrobiine Genus from Mexico, with Three New Species. *The Nautilus,* 59(1):18–23, plate 3.
Mulvey, M., and R. Hershler
Ms. Genetic Diversity in Great Basin Springsnails (*Tryonia protea*): Implications for the Origin and Age of a Widespread Parthenogen.
Newton, A.F., Jr., and M.K. Thayer
1990. Comment on the Proposed Placement of Hydrobiidae Troschel, 1857 (Mollusca, Gastropoda) on the Official List of Family-Group Names. *Bulletin of Zoological Nomenclature,* 47(4):286–287.
Norton, A.H.
1927. Jesse Wedgwood Mighels—Pioneer Conchologist. *Maine Naturalist,* 7(2):63–74.
Nuttall, C.P.
1990. A Review of the Tertiary Non-Marine Molluscan Faunas of the Pebasian and Other Inland Basins of North-Western South America. *Bulletin of the British Museum (Natural History), Geology Series,* 45(2):167–371.
Parodiz, J.J.
1969. The Tertiary Non-marine Mollusca of South America. *Annals of the Carnegie Museum,* 40: 242 pages, 19 plates.
Pilsbry, H.A.
1890a ("1889"). New and Little-Known American Molluscs, No. 1. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 1889: 81–89, plate III. [Date on title page is 1889; actually published in 1890.]
1890b. Notices of New Amnicolidae. *The Nautilus,* 4(6):63–64.
1899. Catalogue of the Amnicolidae of the Western United States. *The Nautilus,* 12:121–127.
1934. Pliocene Fresh-Water Fossils of the Kettleman Hills and Neighboring California Oil Fields. *The Nautilus,* 48(1):15–17.
1935. Western and Southwestern Amnicolidae and a New *Humboldtiana*. *The Nautilus,* 48(3):91–94.
1950. New Fountain Snails from Florida. *The Nautilus,* 64(2):37–39, plate 3.
Reeve, L.A.
1859–1861. Monograph of the Genus *Melania*. In *Conchologia Iconica: Or, Illustrations of the Shells of Molluscous Animals*. Volume 12, 59 unnumbered pages, 59 plates, 6 pages of index. London: Reeve and Bonham.
Sandberger, C.L.F.
1870–1875. *Die Land-und Süsswasser-Conchylien der Vorwelt*. 1000 pages, 36 plates, fold-out table. Wiesbaden: C.W. Kreidel.
Stearns, R.E.C.
1893. Report on the Land and Fresh-Water Shells Collected in California and Nevada by the Death Valley Expedition, Including a Few Additional Species Obtained by Dr. C. Hart Merriam and Assistants in Parts of the Southwestern United States. *North American Fauna,* 7:269–283.
1901. The Fossil Fresh-Water Shells of the Colorado Desert, Their Distribution, Environment, and Variation. *Proceedings of the United States National Museum,* 24:271–299, plates XIX–XXIV.
Stephenson, L.W.
1941. The Larger Invertebrate Fossils of the Navarro Group of Texas (Exclusive of Corals and Crustaceans and Exclusive of the Fauna of the Escondido Formation). *The University of Texas Publication,* 4101: 641 pages, plates 1–95, tables 1–6.
Stimpson, W.
1865. Diagnoses of Newly Discovered Genera of Gasteropods, Belonging to the Sub-fam. Hydrobiinae, of the Family Rissoidae. *American Journal of Conchology,* 1:52–54.
Sykes, E.R.
1900. Mollusca. *In* D. Sharp, editor, *Fauna Hawaiiensis, or the Zoology of the Sandwich (Hawaiian) Isles: Being Results of the Explorations Instituted by the Joint Committee Appointed by the Royal Society of London for Promoting Natural Knowledge and the British Association for the Advancement of Science and Carried on with the Assistance of those Bodies and of the Trustees of the Bernice Pauaji Bishop Museum at Honolulu*. Volume 2, part IV, pages 271–441, plates XI, XII. Cambridge, England: The University Press.

Tate, R.
1870. On the Land and Fresh-Water Mollusca of Nicaragua. *American Journal of Conchology,* 5:151–162.

Taylor, D.W.
1950. Three New *Pyrgulopsis* from the Colorado Desert, California. *Leaflets in Malacology,* 1(7):27–33.
1966a. Summary of North American Blancan Nonmarine Mollusks. *Malacologia,* 4(1):1–172.
1966b. A Remarkable Snail Fauna from Coahuila, México. *The Veliger,* 9(2):152–228.
1975. Index and Bibliography of Late Cenozoic Freshwater Mollusca of Western North America. *University of Michigan Museum of Zoology, Papers on Paleontology,* 10: 384 pages.
1981. Freshwater Mollusks of California: A Distributional Checklist. *California Fish and Game,* 67(3):140–163.
1985. Evolution of Freshwater Drainages and Molluscs in Western North America. *In* C.J. Smiley, editor, *Late Cenozoic History of the Pacific Northwest,* pages 265–321. San Francisco: American Association for the Advancement of Science (Pacific Division).
1987. Fresh-Water Molluscs from New Mexico and Vicinity. *Bulletin of the New Mexico Bureau of Mines and Mineral Resources,* 116: 50 pages.

Thompson, F.G.
1968. *The Aquatic Snails of the Family Hydrobiidae of Peninsular Florida.* xv + 268 pages. Gainesville: University of Florida Press.
In press. A New Hydrobiid Snail from a Saline Spring in Southern Alabama (Gastropoda, Prosobranchia, Rissooidea). *American Malacological Bulletin,* 16.

Troschel, F.H.
1856–1863. *Das Gebiss der Schnecken zur Bergründung einer Natürlichen Classification.* Volume 1, 252 pages. Berlin: Nicolaische Verlagsbuchhandlung.

Tryon, G.W., Jr.
1866. [Review of] Researches upon the Hydrobiinae and Allied Forms. *American Journal of Conchology,* 2:152–158.
1883. *Structural and Systematic Conchology: An Introduction to the Study of the Mollusca.* Volume 2, 430 pages, plates 28–91. Philadelphia: Privately published.

United States Department of the Interior [USDI]
1991. Endangered and Threatened Wildlife and Plants; Final Rule to List the Alamosa Springsnails and the Socorro Springsnail as Endangered. *Federal Register,* 56(189):49646–49649.
1997. Endangered and Threatened Wildlife and Plants; Review of Plant and Animal Taxa that Are Candidates or Proposed for Listing as Endangered or Threatened, Annual Notice of Findings on Recycled Petitions, and Annual Description of Progress on Listing Actions. *Federal Register,* 62(182):49398–49411.

Walker, B.
1918. A Synopsis of the Classification of the Fresh-Water Mollusca of North America, North of Mexico, and a Catalogue of the More Recently Described Species, with Notes. *University of Michigan Museum of Zoology, Miscellaneous Publications,* 6: 213 pages.

Wenz, W.
1922. Die Entwicklungsgeschichte der Steinheimer Planorben und ihre Bedeutung für die Deszendenzlehre. *Senckenbergerische Naturforschende Gesellschaft,* 52(3–4):135–158.
1925. Zur Nomenklatur Tertiärer Land- und Süßwasser-Gastropoden, VII. *Senckenbergiana,* 7(3):124–125.

Wesselingh, F.P.
1996. Geological-Paleontological Research in the Tertiary and Quaternary of Central America, III: New Pliocene Fresh Water Gastropods from Guatemala. *Documenta Naturae,* 100:23–36.

Williams, J.E., D.B. Bowman, J.E. Brooks, A.A. Echelle, R.J. Edwards, D.A. Hendrickson, and J.J. Landye
1985. Endangered Aquatic Ecosystems in North American Deserts with a List of Vanishing Fishes of the Region. *Journal of the Arizona-Nevada Academy of Science,* 20(1): 62 pages.

Woodring, W.P., M.N. Bramlette, and W.S.W. Kew
1946. Geology and Paleontology of Palos Verdes Hills, California. *United States Geological Survey Professional Paper,* 207: 145 pages, 37 plates, map.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼″ margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title** page with only title and author and no other information; **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "...Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number):pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from the Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustation should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when the manuscript is submitted.