

North American Hydrobiidae (Gastropoda: Rissoacea): Redescription and Systematic Relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886

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ABSTRACT

Anatomical details are provided for the type species of *Tryonia* Stimpson, 1865, *Pyrgulopsis* Call and Pilsbry, 1886, *Fontelicella* Gregg and Taylor, 1965, and *Microamnicola* Gregg and Taylor, 1965, in an effort to resolve the systematic relationships of these taxa, which represent most of the generic-level groups of Hydrobiidae in southwestern North America. Based on these and other data presented either herein or in the literature, *Hyalopyrgus* Thompson, 1968 is assigned to *Tryonia*; and *Fontelicella*, *Microamnicola*, *Natricola* Gregg and Taylor, 1965, *Marstonia* F. C. Baker, 1926, and *Mexistiobia* Hershler, 1985 are allocated to *Pyrgulopsis*.

The ranges of both *Tryonia* and *Pyrgulopsis* include parts of eastern and western America and northern Mexico. *Tryonia* is closely related to a group of North and Central American littoridinine genera having an elongate-conic shell and (mammi-form) glandular penial lobes, and *Pyrgulopsis* (Nymphophilinae) is closely allied to *Cincinnatia* Pilsbry, 1891 from eastern North America.

INTRODUCTION

Prosobranch snails of the family Hydrobiidae comprise a major faunal element of North American freshwaters, numbering some 28 genera and 148 species (Burch, 1982). Despite their diversity and ubiquity, North American Hydrobiidae are poorly understood in terms of systematics, as the anatomy of few species is known. While recent advances have been made in the systematic study of southeastern Hydrobiidae (Thompson, 1968, 1969, 1977, 1984; Thompson & McCaleb, 1978), the fauna of other large expanses of territory is virtually unstudied.

One such fauna is that of the arid Southwest. Of the generic-group taxa found in this region, only *Flumini-cola* Stimpson, 1865 has received sufficient morphological study to allow clarification of its relationships (Thompson, 1984). Relatively little is known of *Pyrgulopsis* Call and Pilsbry, 1886, *Tryonia* Stimpson, 1865, and *Fontelicella* Gregg and Taylor, 1965, the latter two of which comprise more than 30 species (mostly unde-

scribed) in the Southwest. Taylor (1966) placed *Tryonia* in the Littoridininae Taylor, 1966 on the basis of its turreted shell and glandular penial lobes. It is clear from the initial descriptions and subsequent studies illustrating the penis (Russell, 1971: fig. 4; Taylor, 1983:16-25) that *Fontelicella* and its subgenera, *Natricola* Gregg and Taylor, 1965 and *Microamnicola* Gregg and Taylor, 1965 belong to the Nymphophilinae Taylor, 1966 (see Thompson, 1979). While the type species of *Pyrgulopsis*, *P. nevadensis* (Stearns, 1883), has not received anatomical study, the penes of several eastern species have been examined by Thompson (1977), who suggested that the genus may be a nymphophiline. The scant published morphological data do not, however, allow meaningful comparisons of the above with other Hydrobiidae.

Our anatomical study of the type species of *Tryonia* and *Hyalopyrgus* Thompson, 1968 showed that *Hyalopyrgus*, endemic to Florida (and placed in the Littoridininae by Davis *et al.*, 1982), should be allocated to *Tryonia*. Similarly, study of type species and published accounts indicated that *Fontelicella*, *Natricola*, *Microamnicola*, as well as *Mexistiobia* Hershler, 1985 (from northern Mexico) and *Marstonia* F. C. Baker, 1926 (widespread in eastern North America) should be allocated to *Pyrgulopsis*. In this paper we redescribe *Tryonia* and *Pyrgulopsis* and briefly discuss their affinities.

MATERIALS AND METHODS

Anatomical illustrations given in this paper are based on study of the following lots (representing fully relaxed alcohol material unless otherwise indicated): *Tryonia clathrata* Stimpson, 1865, Moapa Springs, Clark County, NV, USA, USNM 850291; *Hyalopyrgus aequicostatus* (Pilsbry, 1889), Lake Dora, Lake County, FL, USA, USNM 847212; Alexander Springs, Lake County, FL, USA, UF uncatalogued lot; *Pyrgulopsis nevadensis*, rehydrated (in Bouin's solution) bodies, south end of Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot; *Pyrgulopsis archimedis* S. S. Berry, 1947, unrelaxed, Upper Klamath Lake, Klamath County, OR,

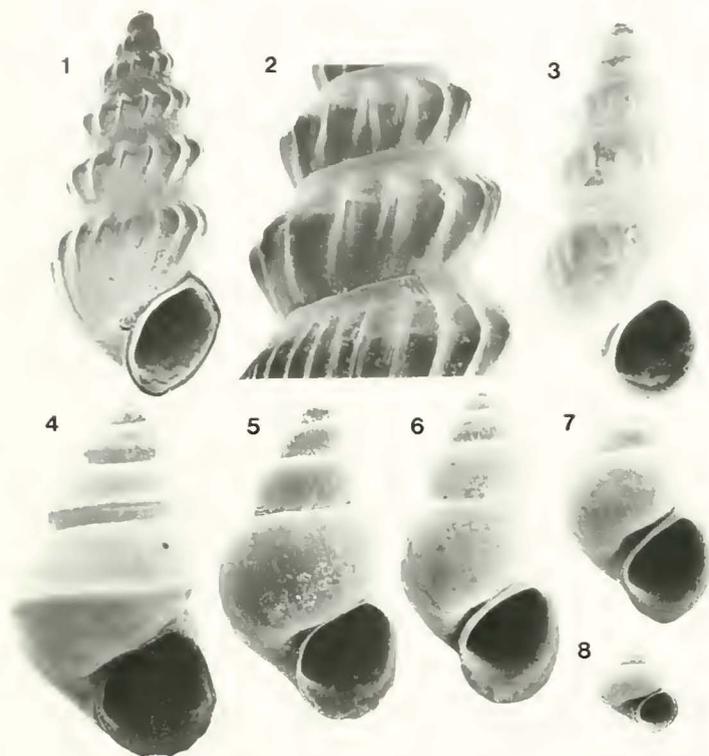


Figure 1. Photograph (SEM) of holotype of *Tryonia clathrata* Stimpson, Colorado Desert, CA, USA (but see Taylor, 1966: 197), ANSP 27969. Shell height is 4.36 mm. **Figure 2.** Close-up photograph of shell of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, showing sculptural pattern. The height of the portion of shell photographed is 2.36 mm. **Figure 3.** Photograph of shell of *Tryonia aequicostata* (Pilsbry), Lake Dora, Lake County, FL, USA, USNM 847212, printed to same enlargement as figure 1. **Figure 4.** Photograph of paratype of *Pyrgulopsis nevadensis*, south end of Pyramid Lake, Washoe County, NV, USA, USNM 75450, printed to same enlargement as figure 1. **Figure 5.** Photograph of shell of *Pyrgulopsis lustrica* (Pilsbry), Little Lakes, Herkimer County, NY, USA, USNM 28085, printed to same enlargement as figure 1. **Figure 6.** Photograph of paratype of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292, printed to same enlargement as figure 1. **Figure 7.** Photograph of shell of *Pyrgulopsis micrococcus* (Pilsbry), Springdale Springs, Nye County, NV, USA, USNM 850297, printed to same enlargement as figure 1. **Figure 8.** Photograph of shell of *Pyrgulopsis manantiali* (Hershler), spring at Tierra Blanca, SW of Cuatro Ciencgas, Coahuila, MEX, ANSP A988SL, printed to same enlargement as figure 1.

USA, ANSP A602b; *Pyrgulopsis letsoni* (Walker, 1901), creek W of Crenshaw Lake, Oakland County, MI, USA, UF 91726; *Pyrgulopsis scalariformis* (Wolf, 1869), Meramec River, 12.0 km SE of Leesburg, Crawford County, MO, USA, UF 91727. *Fontelicella (sensu stricto) californiensis* Gregg and Taylor, 1965, Campo Creek, San Diego County, CA, USA, USNM 850292 (paratypes); *Fontelicella (Microamnicola) micrococcus* (Pilsbry in Stearns, 1893), Springdale Springs, Nye County, NV, USA, USNM 850297; *Mexistiobia manantiali* Hershler,

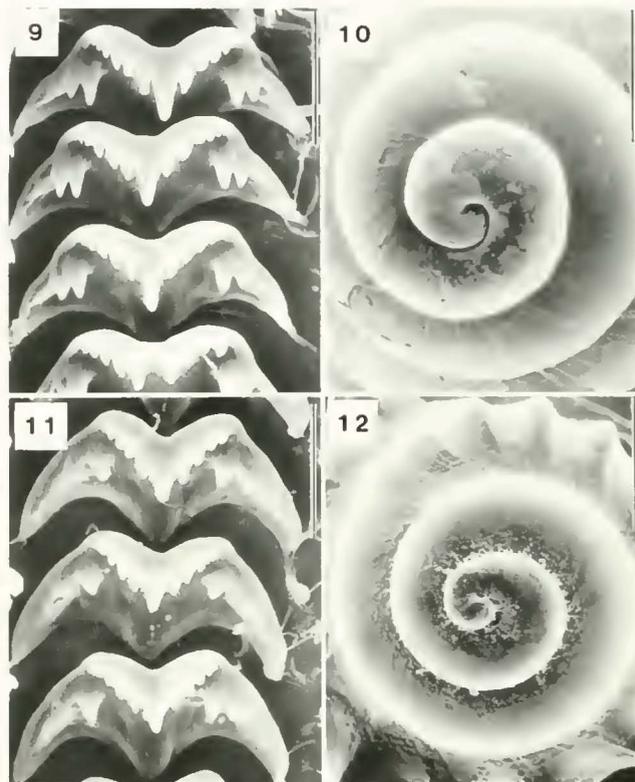


Figure 9. Photograph (SEM) of central radular teeth of *Tryonia aequicostata* (Pilsbry), Lake Dora, Lake County, FL, USA, USNM 847212. Scale bar equals 10 μ m. **Figure 10.** Photograph of protoconch of *Tryonia aequicostata* (Pilsbry) (from same lot as above). Scale bar equals 150 μ m. **Figure 11.** Photograph of central radular teeth of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291. Scale bar equals 10 μ m. **Figure 12.** Photograph of protoconch of *Tryonia clathrata* Stimpson (from same lot as above). Scale bar equals 150 μ m.

1985, small spring at Tierra Blanca, SW of Cuatro Ciencgas, Coahuila, MEX, ANSP A9888J.

Snails were dissected in dilute Bouin's solution at 50 \times using a Wild M-8 dissecting microscope. Ciliation patterns on the cephalic tentacles and penis were examined using a Hitachi S-570 scanning electron microscope, with the animals having first been graded into 100% ETOH and dried using a Denton DCP-1 Critical Point Drier. Shells and radulae were cleaned with Clorox and then photographed using the scanning electron microscope.

SYSTEMATICS

Genus *Tryonia* Stimpson, 1865

Tryonia Stimpson, 1865:54. Type species: *Tryonia clathrata* Stimpson, 1865:54, by original designation; 1865:54

Hyalopyrgus Thompson, 1968:43. Type species: *Bythinella aequicostata* Pilsbry, 1889:86, by original designation; Thompson, 1968:45.

Diagnosis: Shell (figures 1–3) colorless, transparent, elongate-conic to turreted, 1.7–7.0 mm tall with 4.0–8.0

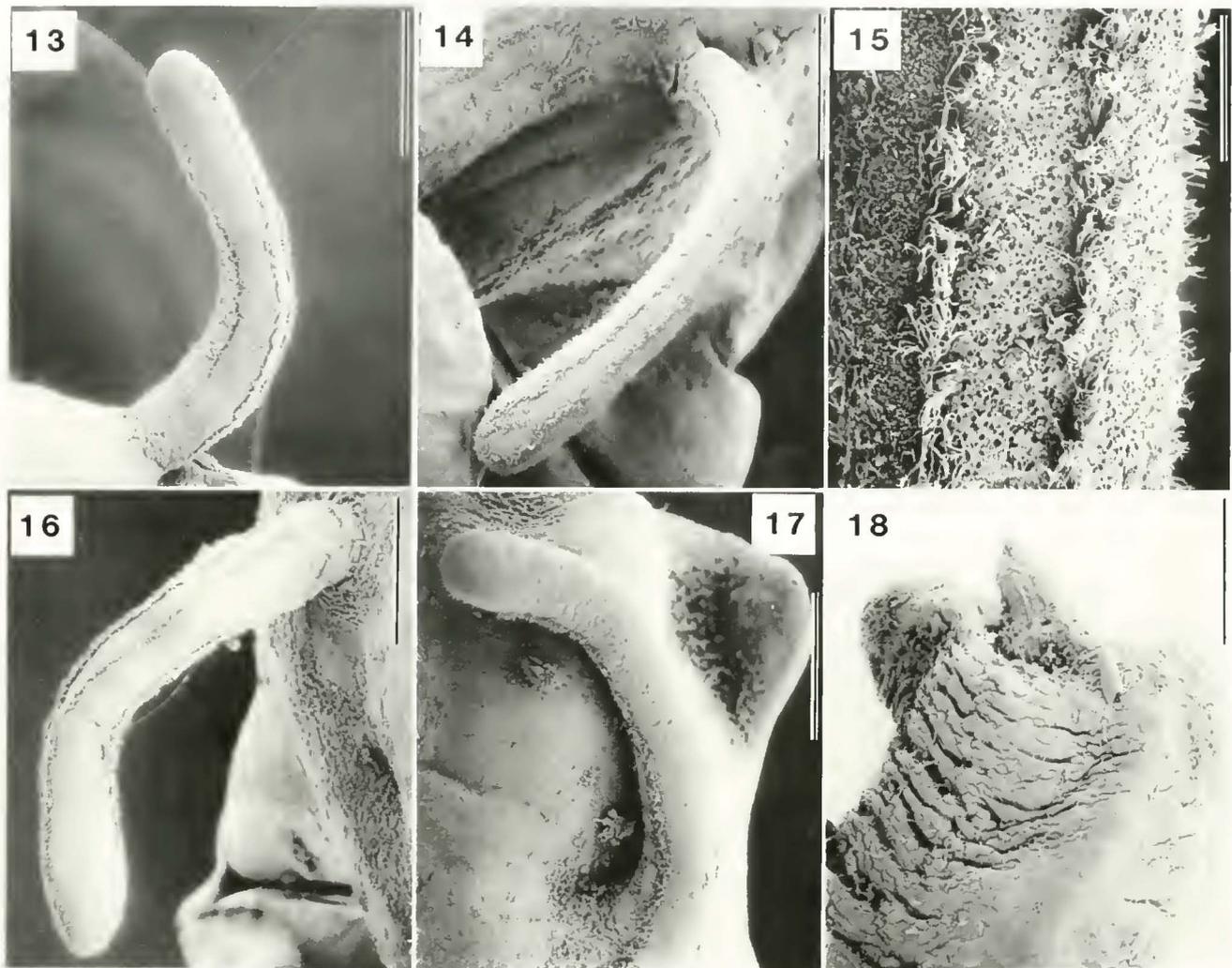


Figure 13. Photograph (SEM) of left tentacle of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, showing ciliary tracts. Scale bar equals 176 μm . **Figure 14.** Photograph of right tentacle of *Tryonia clathrata* Stimpson (from same lot as above). Scale bar equals 170 μm . **Figure 15.** Close-up photograph of ciliary tracts on right tentacle of *Tryonia clathrata* Stimpson (same specimen as above). Scale bar equals 30 μm . **Figure 16.** Photograph of left tentacle of *Tryonia acqicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. Scale bar equals 176 μm . **Figure 17.** Photograph of right tentacle of *Tryonia acqicostata* (Pilsbry) (from same lot as above). Scale bar equals 200 μm . **Figure 18.** Photograph of penial tip of *Tryonia clathrata*, Moapa Springs, Clark County, NEV, USA, USNM 850291, showing sparse ciliation, terminal papilla, and blunt swelling on inner (left) side. Scale bar equals 50 μm .

whorls; typically high-spired with rounded whorls and indented sutures. Aperture simple, unthickened, and complete. Umbilicus narrow or absent. Sexual dimorphism pronounced, with males often half of female shell height. Protoconch (figures 10, 12) flat or slightly protruding, smooth or slightly wrinkled. Teleoconch sculpture consisting of fine growth lines, sometimes coupled with weak spiral lines or collabral striations or varices. Central tooth of radula (figures 9, 11) broader than tall, with 1–3 pairs of basal cusps. Digestive gland without anterior lobe. Cephalic tentacles with several elongate ciliary tracts (figures 13–17). Flattened penis (figures 19, 20) elongate and slender, with a single, enlarged glandular (mammiform) lobe at its base and 1–4 smaller

glandular lobes on the inner curvature. Distal portion of penis ciliated (figure 18) to varying degrees, base sometimes also ciliated. Tip of penis with blunt swelling on inner curvature. Females ovoviviparous, with 3–15 embryos brooded in enlarged capsule gland (figure 21). Capsule gland with muscular sphincter at anterior end. Pallial oviduct reflected posteriorly, albumen gland reduced in size (figure 22, Ag). Small-sized bursa copulatrix and seminal receptacle ventral to albumen gland; coiled seminal receptacle duct opens into short spermathecal duct (figures 23, 24, Osr).

Species included: *Bythinella acqicostata*; *Bythinella brevissima* Pilsbry, 1890:64; *Potamopyrgus cheatumi*

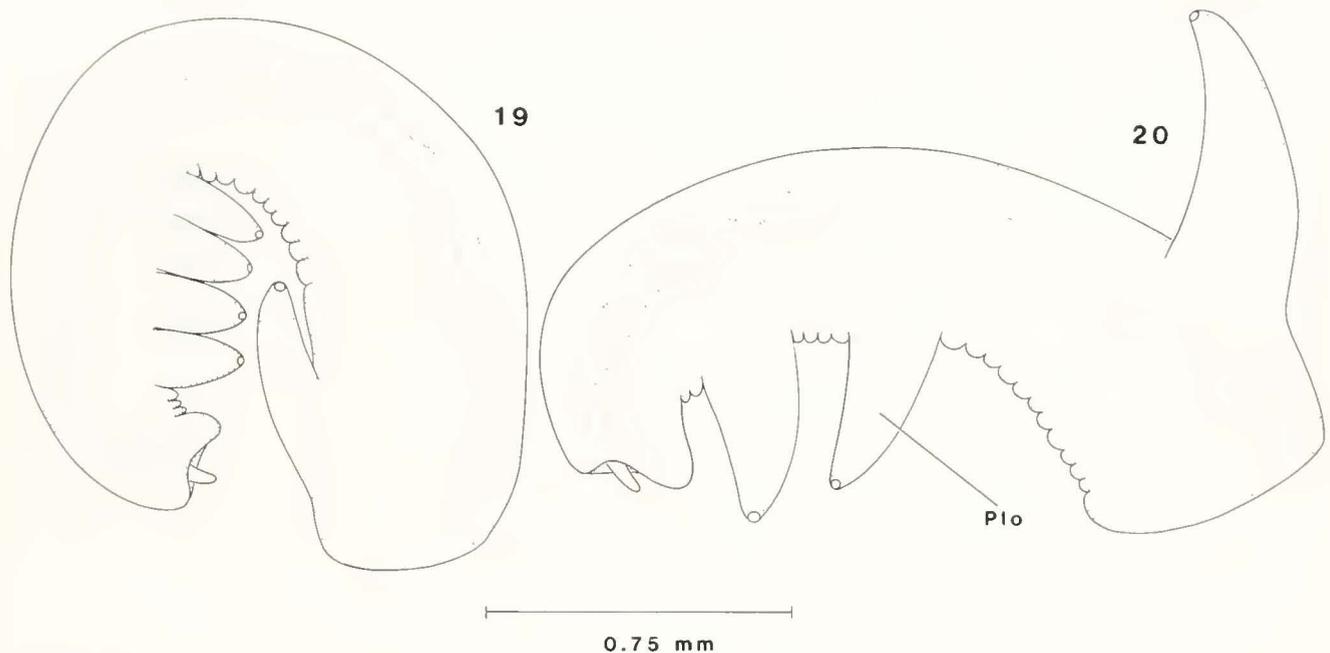


Figure 19. Penis of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291. **Figure 20.** Penis of *Tryonia aequicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. Patterns of ciliation are not shown. Plo = penial lobe.

Pilsbry, 1935:91; *Calipyrgula circumstriata* Leonard and Ho, 1960a:125; *Tryonia clathrata*; *Paludestrina diaboli* Pilsbry and Ferriss, 1906:125; *Paludestrina imitator* Pilsbry, 1899:121; *Calipyrgula pecosensis* Leonard and Ho, 1960b:110; *Amnicola protea* Gould, 1855:129; *Paludestrina stokesi* Arnold, 1903:22.

The identity of the Central and South American taxa assigned to *Tryonia* by Taylor (1966) is uncertain due to lack of anatomical study.

Distribution: *Tryonia* occurs in much of Florida as well as in the arid Southwest, including parts of California,

Nevada, Arizona, New Mexico, and Texas, and northern Mexico.

Remarks: Given the overall similarity between the Floridian and southwestern species, even extending to details of the bursa copulatrix complex (figures 23, 24), there can be no doubt that these species belong to a single genus. *Tryonia* belongs to a group of littoridinines having an elongate-conic shell and mammiform glandular lobes on the penis that includes *Aphaostracan* Thompson, 1968, *Littoridinops* Pilsbry, 1952, *Mexipyrgus* Taylor, 1966, and *Pyrgophorus* Ancy, 1888 (but not *Durangonella* Morrison, 1945; contrary to Hershler, 1985). *Tryonia* is distinguished from the above by its turreted shell and unique position of its penial lobes.

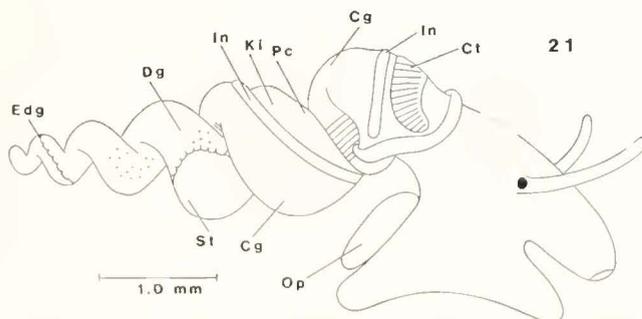


Figure 21. *Tryonia clathrata* Stimpson (without shell), Moapa Springs, Clark County, NV, USA, USNM 850291, viewed from the right side. Note the enlarged capsule gland (Cg) with embryos (dotted circles). The thickened dots on the digestive gland (Dg) are pigment granules. Cg = capsule gland, Ct = ctenidium, Dg = digestive gland, Edg = posterior end of digestive gland, In = intestine, Ki = kidney, Op = operculum, Pc = pericardium, St = stomach.

Genus *Pyrgulopsis* Call and Pilsbry, 1886

Pyrgulopsis Call and Pilsbry, 1886:9. Type species: *Pyrgula nevadensis* Stearns, 1883:173, by original designation; Call and Pilsbry, 1886:9.

Marstonia F. C. Baker, 1926:195. Type species: *Amnicola lusitrica* Pilsbry, 1890:53, by original designation; F. C. Baker, 1926:195.

Fontelicella Gregg and Taylor, 1965:103. Type species: *Fontelicella californiensis* Gregg and Taylor, 1965:109, by original designation; Gregg and Taylor, 1965:104.

Natricola Gregg and Taylor, 1965:108. Type species: *Pomatopsis robusta* Walker, 1908:97, by original designation; Gregg and Taylor, 1965:109.

Microamnicola Gregg and Taylor, 1965:109. Type species: *Amnicola micrococcus* Pilsbry in Stearns, 1893:277, by original designation; Gregg and Taylor, 1965:109.

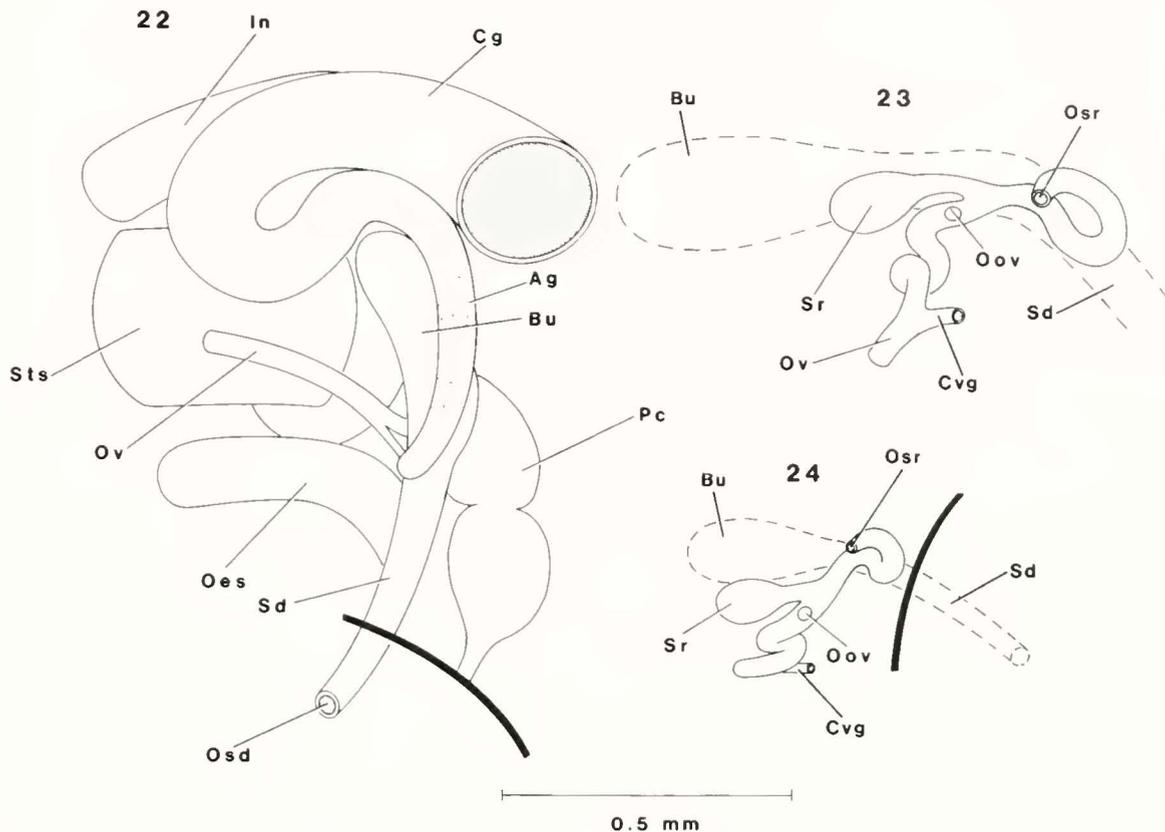


Figure 22. Posterior portion of pallial oviduct and associated organs and structures of *T. clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, viewed from the right. Note the posterior reflection of the pallial oviduct and small albumen gland (Ag). The thickened curving line indicates the posterior end of the pallial cavity. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, In = intestine, Oes = oesophagus, Osd = opening of the spermathecal duct, Ov = oviduct, Pc = pericardium, Sd = spermathecal duct, Sts = style sac. **Figure 23.** Bursa copulatrix complex of *Tryonia clathrata* (from same lot as above), with the bursa removed (position indicated by dashed lines) in order to reveal the underlying structures. The visceral ganglion connective (Cvg) is tightly pressed against the oviduct. Bu = bursa copulatrix, Cvg = visceral ganglion connective, Oov = opening of oviduct into albumen gland, Ov = oviduct, Osr = opening of seminal receptacle into spermathecal duct, Sd = spermathecal duct, Sr = seminal receptacle. **Figure 24.** Bursa copulatrix complex of *Tryonia acquicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. The thickened curving line indicates the posterior end of the pallial cavity. Bu = bursa copulatrix, Cvg = visceral ganglion connective, Oov = opening of oviduct into albumen gland, Osr = opening of seminal receptacle into spermathecal duct, Sd = spermathecal duct, Sr = seminal receptacle.

Mexistiobia Hershler, 1985:46. Type species: *Mexistiobia manantiali* Hershler, 1985:47, by original designation; Hershler, 1985:46.

Diagnosis: Shell (figures 4–8) globose to elongate-conic, 1.2–8.0 mm in height, with 3.0–6.0 whorls. Aperture simple, sometimes loosened from body whorl. Umbilicus absent to open. Protoconch partly or totally covered with wrinkled pits (Thompson, 1977: fig. 4; Hershler, 1985: fig. 11). Teleoconch smooth or uncarinate on periphery (figure 3), usually with fine growth lines. Radula (figures 25–28) typically taenioglossate, with basal cusps on the central teeth. Mantle and/or penial filament (figures 29, 30, 32, 33) often with distinctive pigment markings. Penis (figures 29–33) with small, distal lobe and narrow, elongate filament. Penial surface with one to fifteen glandular ridges, sometimes on stalked crests. Females oviparous; capsule gland with two tissue sections and a

near-terminal opening (figures 34, 35; Thompson, 1977: figs. 5, 7, 10, 11, 18; Hershler, 1985: fig. 14). Oviduct with a single anterior coil on the left side of the albumen gland into which opens the seminal receptacle. Bursa copulatrix typically enlarged and partly posterior to albumen gland; bursa duct and oviduct jointly open into anterior portion of albumen gland.

Species included: *Marstonia agarhecta* Thompson, 1969:243; *Pyrgulopsis archimedis* S. S. Berry, 1947:76; *Fonteliclla californiensis*; *Marstonia castor* Thompson, 1977:130; *Amnicola deserta* Pilsbry, 1916:111; *Marstonia halcyon* Thompson, 1977:128; *Amnicola hendersoni* Pilsbry, 1933:10; *Amnicola idahoensis* Pilsbry, 1933:11; *Pomatiopsis intermedia* Tryon, 1865:220; *Amnicola letsoni* Walker, 1901:113; *Amnicola longinqua* Gould, 1855:130; *Amnicola lustrica*; *Mexistiobia manantiali*; *Amnicola micrococcus*; *Amnicola neonex-*

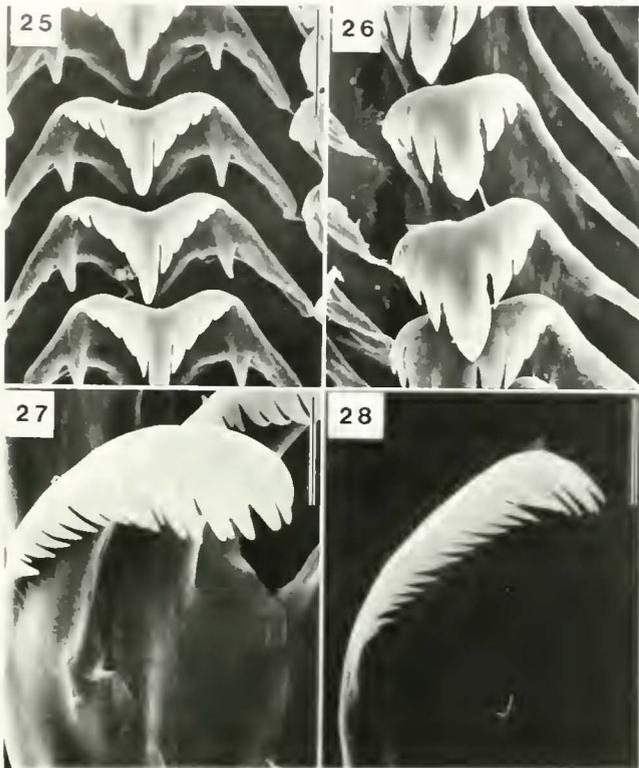


Figure 25. Photograph (SEM) of central radular teeth of *Pyrgulopsis nevadensis* (Stearns), Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot. Scale bar equals 12.0 μ m. **Figure 26.** Photograph of lateral teeth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 12.0 μ m. **Figure 27.** Photograph of inner marginal tooth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 8.6 μ m. **Figure 28.** Photograph of outer marginal tooth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 7.5 μ m.

icana Pilsbry, 1916:111; *Marstonia ogmorphaphe* Thompson, 1977:120; *Annicola olivacca* Pilsbry, 1895:115; *Pyrgulopsis ozarkensis* Hinkley, 1915:588; *Marstonia pachyta* Thompson, 1977:121; *Annicola pilsbryi* Bailly and Bailly, 1952:50; *Pomatiopsis robusta* Walker, 1908:97; *Pyrgula scalariformis* Wolf, 1869:198; *Paludetrina stearnsiana* Pilsbry, 1899:124; *Pyrgulopsis wabashensis* Hinkley, 1908:117.

Fossil species assigned to *Marstonia* and *Fontelicella* by Taylor (1960) and Gregg and Taylor (1965) are not included.

Distribution: *Pyrgulopsis* occurs in much of eastern North America as well as throughout western North America and parts of northern Mexico.

Remarks: Only a limited anatomical study could be made of *Pyrgulopsis nevadensis*, the type species of *Pyrgulopsis*, as only dried bodies were available. We were able to describe its radula (figures 25–28) and penis (figure 29). The species has long been considered endangered (Taylor, 1970) and may now be extinct in the sole locality from which living material was ever found, Pyramid Lake. A recent limnological survey of this lo-

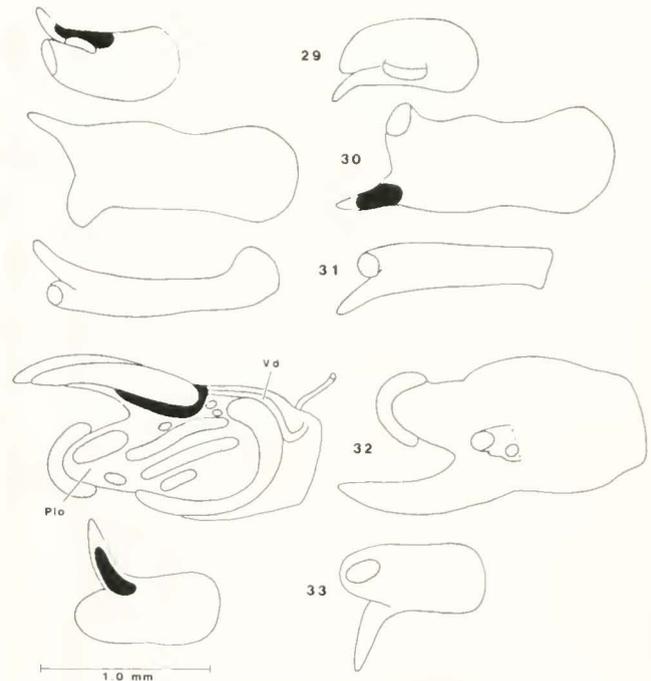


Figure 29. Penis of *Pyrgulopsis nevadensis* (Stearns), south end of Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot. The dorsal aspect is shown to the left and ventral aspect is on the right. The screened areas indicate glandular ridges whereas the darkened areas are pigmented. **Figure 30.** Penis of *Pyrgulopsis letsoni* (Walker), creek W of Crenshaw Lake, Oakland County, MI, USA, UF 91726. **Figure 31.** Penis of *Pyrgulopsis scalariformis* (Wolf), Meramec River, 12.0 km SE of Leesburg, Crawford County, MO, USA, UF 91727. **Figure 32.** Penis of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292. Plo = penial lobe, Vd = vas deferens. **Figure 33.** Penis of *Pyrgulopsis micrococcus* (Pilsbry), Springdale Springs, Nye County, NV, USA, USNM 850297.

cality yielded no live individuals (Galat *et al.*, 1981) of this species, nor were they found during a recent trip to the lake by one of us (F.G.T.).

It is clear from our study that the sole character distinguishing species assigned to *Pyrgulopsis* and other taxa that we consider congeneric is the presence of a peripheral carina on the shell. *Pyrgulopsis* is noteworthy for its diversity in shell and penial morphology. Even within small regions in the Southwest, groups of species show gradations from globose to elongate-conic shells, or gradations from a simple penis with few ridges to a more complex penis with accessory crests and numerous ridges. The eastern species previously assigned to *Marstonia* and *Pyrgulopsis*, united by possession of a penis having few glandular ridges and a broad penial lobe (Berry, 1943: fig. 6; Thompson, 1977: figs. 5, 7, 11, 13, 19, 22, 24), clearly intergrade with western species assigned to *Pyrgulopsis*, *Fontelicella sensu stricto* and *Microannicola*. We have no doubt that *Pomatiopsis robusta*, the type species of *Natricola*, is also a *Pyrgulopsis*, based on anatomical data given by Gregg and Taylor

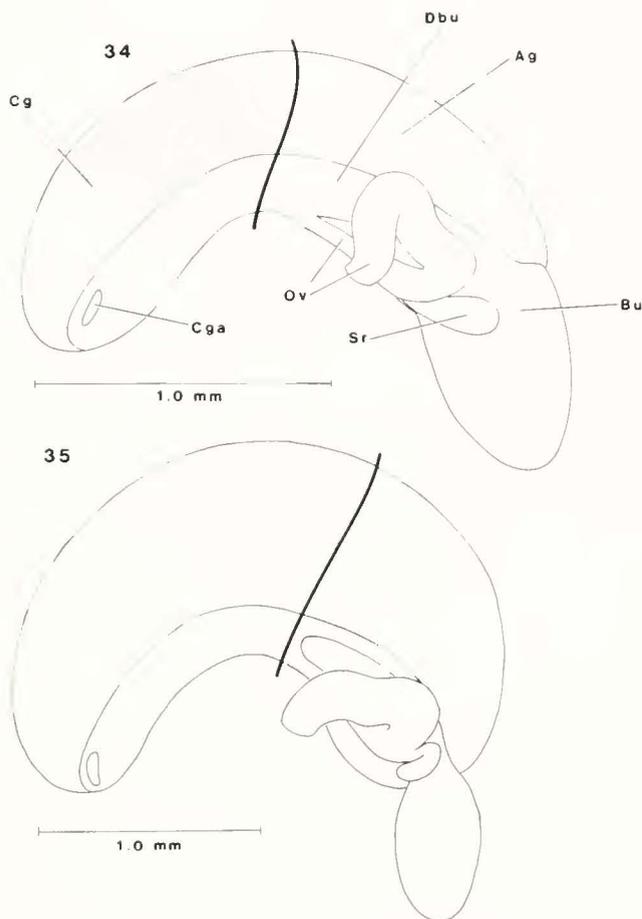


Figure 34. Left lateral aspect of the pallial oviduct and bursa copulatrix complex of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292. The two tissue sections of the capsule gland (Cg) are indicated by the stippled areas. The thickened curving line indicates the posterior end of the pallial cavity. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cga = capsule gland opening, Dbu = duct of the bursa copulatrix, Sr = seminal receptacle. **Figure 35.** Left aspect of the pallial oviduct and bursa copulatrix complex of *Pyrgulopsis archimedis* S. S. Berry, Upper Klamath Lake, Klamath County, OR, USA, ANSP A602B.

(1965:108). The unique, stunted appearance of the bursa copulatrix complex of *P. manantiali* (Hershler, 1985: fig. 14) is probably a result of the extremely minute size of the snail. In other features such as shell form and penial morphology the species clearly conforms to the *Pyrgulopsis* groundplan.

Among nymphophilines that have received anatomical study, *Pyrgulopsis* is most similar to *Cincinnatia* Pilsbry, 1891, which has a somewhat larger and broader shell as well as a more complex penis having a very small filament, a large number of glandular ridges, and numerous accessory crests (Thompson, 1968: figs. 43–47; Davis & Mazurkiewicz, 1985: figs. 11–15).

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