North American Hydrobiidae (Gastropoda: Rissoaceae): 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, Fonticella 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, 1965 is assigned to Tryonia; and Fonticella, Microamnicola, Natricola Gregg and Taylor, 1965, Marstonia F. C. Baker, 1926, and Mexistobia 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 littoridinid genera having an elongate-cone shell and (mam-miform) 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 25 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, 1965, 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 Fluminicola 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 Fonticella Gregg and Taylor, 1965, the latter two of which comprise more than 50 species (mostly undescribed) in the Southwest. Taylor (1966) placed Tryonia in the Littoridininae Taylor, 1966 on the basis of its turretted 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 Fonticella 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, 1965 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 Fonticella, Natricola, Microamnicola, as well as Mexistobia 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 acquiscostatus (Pilsbry, 1889), Lake Dora, Lake County, FL, USA, USNM 847212; Alexander Springs, Lake County, FL, USA, UF uncatalogued lot; Pyrgulopsis nevadensis, rehydrated (in Bonin's solution) bodies, south end of Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot; Pyrgulopsis archimedes S. S. Berry, 1947, unrelaxed, Upper Klamath Lake, Klamath County, OR,
USA, ANSP A602b; *Pyrgulopsis lutosi* (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* (Microannulica) *micrococcus* (Pilsbry in Stearns, 1893), Springdale Springs, Nye County, NV, USA, USNM 850297; *Mexistioxia manantiali* Herschler.

**SYSTEMATICS**

**Genus Tryonia Stimpson, 1865**

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


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

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**Figure 1.** Photograph (SEM) of holotype of *Tryonia aequicostata* Stimpson, Colorado Desert, CA, USA (but see Taylor, 1966:197), ANSP 27069. 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 lastrica* (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* (Herschler), spring at Tierra Blanca, SW of Cuatro Cienegas, Coahuila, MEX, ANSP A98881, printed to same enlargement as figure 1.

1985, small spring at Tierra Blanca, SW of Cuatro Cienegas, Coahuila, MEX, ANSP A98881.

Snails were dissected in dilute Bouin's solution at 50× 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.
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 acquisostata*; *Bythinella brevissima* Pilsbry, 1890:64; *Potamopyrgus cheatum

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 Ancey, 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.

**Genus Pyrgulopsis Call and Pilsbry, 1886**

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


**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 unarciinate 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 pigmentation 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 agarheta* Thompson, 1969:243; *Pyrgulopsis archimedis* S. S. Berry, 1947:76; *Fontelicella 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 longinququa* Gould, 1855:130; *Amnicola lustrica*; *Mexistoibia manantiali*; *Amnicola micrococcus*; *Amnicola neomexi...
icana Pilsbry, 1916:111; Marstonia ogmorphaphe
Thompson, 1977:120, Annicola olivacea Pilsbry, 1895:
115; Pyrgulopsis ozarkensis Hinkley, 1915:588; Mar-
stonia pachyla Thompson, 1977:121; Annicola pilbryi
Baily and Baily, 1952:50; Pomatiopsis robusta Walker,
1905:91; Pyrgula scalariformis Wolf, 1869:195; Pul-
destrina steamsiana Pilsbry, 1899:124; Pyrgulopsis
wabashensis Hinkley, 1905:117.

Fossil species assigned to Marstonia and Fontellicella
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 endan-
gered (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-
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 dis-
tinguishing 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 Mar-
stonia 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 as-
signed to Pyrgulopsis, Fontellicella sensu stricto and Mi-
croamnicola. We have no doubt that Pomatiopsis ro-
busta, the type species of Naticola, is also a Pyrgulopsis,
based on anatomical data given by Gregg and Taylor.

Figure 29. Penis of Pyrgulopsis nevadensis (Stearns), south
end of Pyramid Lake, Washoe County, NV, USA, UF unca-
tagolued 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 lessoni (Walker), creek W of Crenshaw
Lake, Oakland County, MI, USA, UF 91726. Figure 31. Pe-
nis of Pyrgulopsis scalariformis (Wolf), Meramec River, 120
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.
The unique, stunted appearance of the 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 ovicduct 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* (Herschler, 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).

**ACKNOWLEDGEMENTS**

Drs. G. M. Davis (ANSP), A. Bogan (ANSP), and W. L. Pratt (Museum of Natural History, University of Nevada at Las Vegas), as well as J. J. Landye (Arizona Game and Fish) and K. Auffenberg (Florida State Museum, University of Florida) loaned material necessary for the completion of this report. Mrs. M. Ryan assisted with the preparation of the illustrations. We thank two anonymous reviewers for their useful criticisms.

**LITERATURE CITED**


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