

Species composition and geographic distribution of Virginia's freshwater gastropod fauna: A review using historical records*

Timothy W. Stewart¹ and Robert T. Dillon, Jr.²

¹ Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011, U.S.A., twstewar@iastate.edu

² Department of Biology, College of Charleston, Charleston, South Carolina 29424, U.S.A.

Abstract: Survey data from electronic databases and the literature were used to summarize knowledge of the composition and geographic distribution of Virginia's freshwater gastropod fauna. After excluding records likely based on misidentifications, we concluded that 53 species of freshwater gastropods occur in Virginia now or historically. A map and/or narrative description of statewide distribution was produced for each species. Several species appeared to be restricted to a few sites and highly endangered, including the hydrobiids *Fontigens bottimeri*, *Fontigens morrisoni*, *Holsingeria unthankensis*, and *Holsingeria* sp. 1. Absence of recent records for the hydrobiid *Somatogyrus virginicus*, the pomatiopsid *Pomatiopsis cincinnatiensis*, the pleurocerids *Elimia arachnoidea* and *Pleurocera gradata*, and the lymnaeid *Stagnicola neopalustris* indicated these species might also be imperiled if not already extirpated from Virginia. Although we have a good understanding of distributions of *Fontigens* spp., *Holsingeria* spp., and of several river-dwelling pleurocerids in southwest Virginia, other species and geographic regions (e. g., eastern shore and Big Sandy River drainage) are undersurveyed. We provide data to assist in designing surveys to fill these knowledge gaps and to monitor temporal changes in species' distributions. Comparisons of historic and future data from field surveys will facilitate protection and management of endangered species by providing evidence of restricted or shrinking geographic ranges.

Key words: Macroinvertebrates, biogeography, endangered species, snails

In 1817, Thomas Say published the first descriptions of species of freshwater gastropods in North America (Say 1817, Martin 1999). Although our understanding of this continent's freshwater gastropod fauna has advanced since that time, large gaps remain. For example, taxonomic confusion precludes accurate estimates of numbers of species inhabiting North America and makes it difficult to determine the geographic distribution, environmental requirements, ecological importance, and conservation status for many taxa (Neves *et al.* 1997). Additionally, many species are thought to have experienced dramatic population declines, but quantitative evidence to confirm this is rarely available. It has been determined, however, that at least 42 species have become extinct following European settlement of North America, and living specimens of several other species have not been seen in nearly a century (Neves 1991, Neves *et al.* 1997, Bogan 1998). Clearly, the lack of attention to freshwater gastropods has been costly.

Field surveys provide critical evidence of changes in freshwater gastropod assemblages, including population declines and shrinking or restricted geographic ranges. Although large quantities of survey data exist for many North American species, many data are scattered among museum

collections and unpublished and published literature that are difficult to obtain. These data must be summarized and disseminated to gain a complete understanding of the distribution and conservation status of our freshwater gastropods and to identify geographic regions requiring additional surveys.

We reviewed and summarized data from field surveys in electronic databases and the literature to describe the species composition and geographic distribution of freshwater gastropods in Virginia, U.S.A. Geographic information associated with collection records was used to produce maps and narrative descriptions of distributions of species inhabiting Virginia now or historically. This is the first comprehensive review of Virginia's freshwater gastropod fauna in 30 years. Beetle (1973a) used museum collections to construct a checklist of Virginian species with names of counties or cities, but not specific locality data. Burch (1950) and Burch (1952) published regional species checklists for the James River Basin and Hanover County. Other surveys in Virginia concentrated on specific drainage basins or taxonomic groups (Clench and Boss 1967, Stansbery and Clench 1974a, Stansbery and Clench 1974b, Stansbery and Clench 1977, Dillon and Benfield 1982, Hershler *et al.* 1990).

* From the symposium "The Biology and Conservation of Freshwater Gastropods" presented at the annual meeting of the American Malacological Society, held 3-7 August 2002 in Charleston, South Carolina, USA.

METHODS

Study area

Virginia extends from 36°30'N to 39°30'N in latitude, and from 75°13'W to 83°40'W in longitude. Approximately 102,830 km² is contained within state boundaries (Woodward and Hoffman 1991). Because of Virginia's variable physiography and climate, the state supports a diverse assemblage of freshwater species. Many boreal species reach the southern limit of their geographic distribution in northern Virginia and many austral species reach the northern limit of their ranges in southern Virginia (Woodward and Hoffman 1991). Additionally, Virginia's major rivers flow in different directions, restricting gene flow between populations and contributing to high species richness. Rivers east of the New River flow southeast to the Atlantic Ocean, the New River flows north to the Ohio River, the Levisa and Russel Rivers of the Big Sandy watershed flow northwest to the Ohio, and other rivers west of the New River flow southwest to the Tennessee River (Fig. 1, Woodward and Hoffman 1991).

Study design

Distributional information was obtained from (1) published literature, (2) unpublished literature authored by R. T. Dillon, (3) museum records, and (4) the Virginia Department of Game and Inland Fisheries. With exception of unattainable publications, we reviewed all peer-reviewed literature that might contain records of freshwater gastropods in Virginia. Information from one unpublished report and a

Ph.D. dissertation was also used (Dillon 1977, Dillon 1982). We also included all museum records available on the World Wide Web, specifically those in the Florida Museum of Natural History (FMNH 2002) and the Illinois Natural History Survey Mollusk Collection (INHS 2003). The Virginia Museum of Natural History (VMNH) also provided records. Additional records were obtained from the Virginia Fish and Wildlife Information Service (VDGIF 1998).

A map and/or narrative description of geographic distribution was produced for each species occurring in Virginia now or historically. Records likely resulting from misidentified species were excluded from maps, but are discussed. Species' names and their authorities were based on Turgeon *et al.* (1998).

RESULTS AND DISCUSSION

Our review suggests that 53 species of freshwater gastropods occur in Virginia now or historically. Distributions and ecological requirements for these taxa are discussed below. Our review also uncovered records of eight species that we consider questionable. Records for questionable species are provided with rationale for why we feel they never occurred in Virginia (Table 1).

Family Valvatidae

Valvata tricarinata (Say, 1817). This species reaches the southern extent of its geographic range in Virginia (Clarke

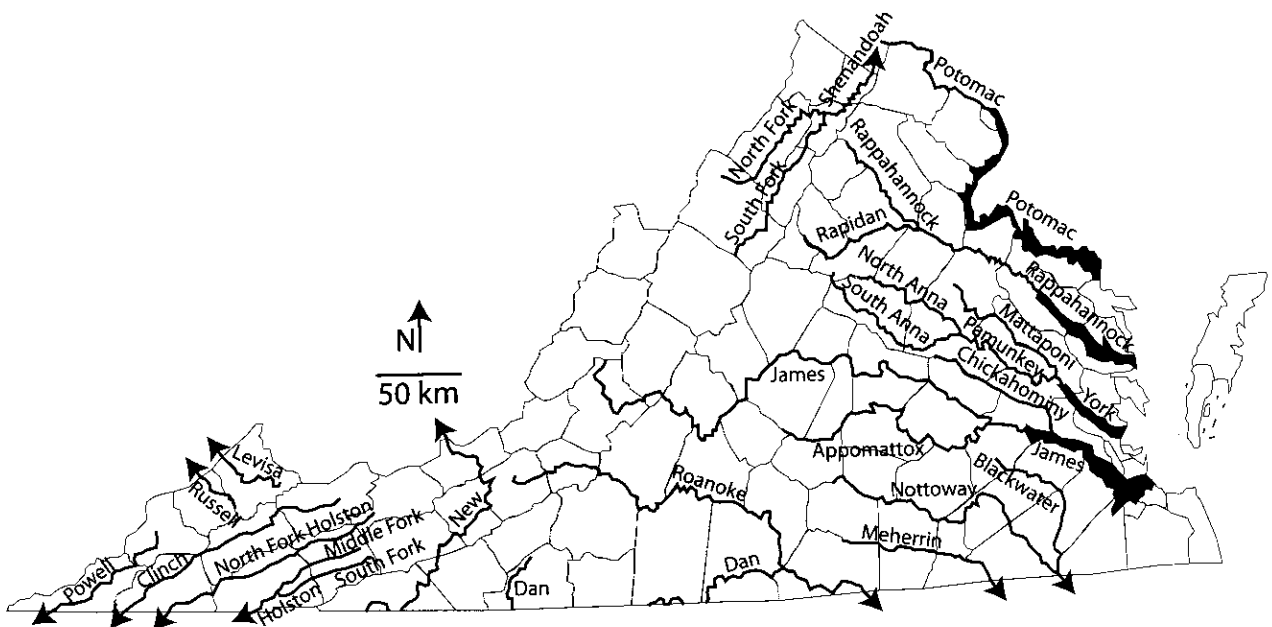


Figure 1. Major rivers of Virginia. Arrows indicate direction of flow (map adapted from Woodward and Hoffman 1991).

Table 1. Although these species were reported from Virginia, it is unlikely that they ever occurred there.

Species	Records (and reference)	Rationale for conclusion
Family Hydrobiidae		
<i>Birgella subglobosus</i>	Fairfax County (Thompson 1977, 1984)	No other records occur near Virginia (Thompson 1977, 1984)
<i>Pyrgulopsis lustrica</i>	Fairfax County (Thompson 1977, 1984)	See <i>Birgella subglobosus</i>
<i>Cincinnatia integra</i>	Norfolk (FMNH 2002)	Occurs in the midwestern United States (Burch 1989)
Family Pleuroceridae		
<i>Elimia carinifera</i>	Tazewell County (Beetle 1973a)	Inhabits Alabama River drainage and southern Tennessee River drainage (Burch 1989)
<i>Leptoxis clipeata</i>	Roanoke River, Montgomery County (FMNH 2002)	Now extinct, but occurred in the Coosa River drainage, Alabama (Palmer 1985, Burch 1989)
<i>Lithasia obovata</i>	Augusta and Washington Counties (Burch 1950, FMNH 2002)	Occurs in Ohio River drainage, including states adjacent to Virginia (Burch 1989)
Family Lymnaeidae		
<i>Stagnicola caperata</i>	Fairfax, Page, and Shenandoah Counties (Beetle 1973a)	A northern species that occurs as far south as Maryland (Burch 1989)
<i>Stagnicola oronoensis</i>	Gretna, Pittsylvania County (FMNH 2002)	Inhabits Maine and Ontario (Burch 1989)

1981, Burch 1989, VDGIF 1998). *Valvata tricarinata* is restricted to calcium-rich, permanent, slow-moving waters including lakes and backwaters of large rivers (Baker 1928a, Jokinen 1983, Strayer 1987). Such habitats occur in western Virginia, where this snail has most often been encountered (Woodward and Hoffman 1991, VDGIF 1998). *Valvata tricarinata* has been recorded from Fairfax County, from the Powell River near Back Valley in Lee County, and from the Clinch River near Honaker and Fort Blackmore in Russell and Scott counties (Figs. 1-2, Beetle 1973a, VDGIF 1998).

Family Viviparidae

Viviparus georgianus (Lea, 1834). This is one of four freshwater gastropods to invade Virginia. Presumably due to introductions by aquarists, this native of Florida, Georgia, and Alabama is now discontinuously distributed across the United States (Clench 1962, Clench and Fuller 1965, Mills *et al.* 1993). Populations occupy soft substrates in large, slow-moving bodies of water (Clench and Fuller 1965, Clarke 1981, Strayer 1987). *Viviparus georgianus* has been recorded from the Potomac River near Hunter's Point, from Little Hunting Creek and Mount Vernon in Fairfax County, from Great Creek in Chesterfield County, and from the Wytheville Fish Hatchery in Wytheville, Wythe County (Clench 1962, FMNH 2002).

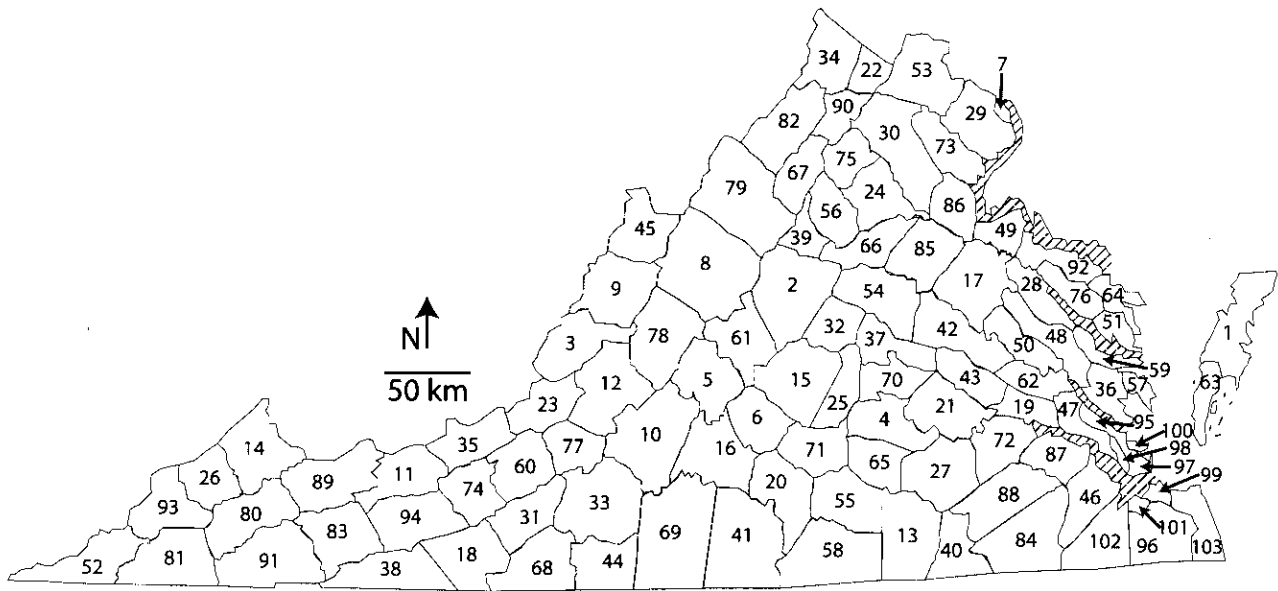
Cipangopaludina chinensis (Reeve, 1863) (= *Viviparus chinensis*, *Viviparus malleatus* [Reeve, 1863]). This Asian snail has invaded much of North America (Jokinen 1982, Mills *et al.* 1993). It inhabits soft substrata in static or slow-moving waters (Clarke 1981). It is rare in Virginia, but has been reported from the Dyke Marsh in Fairfax County and from the Azalea Gardens in Norfolk (VMNH).

Campeloma decisum (Say, 1817) (= *Campeloma decisa*, *Campeloma integra* Say, 1821, *Campeloma rufa* [Haldeman, 1841]). Taxonomic confusion surrounds the genus *Campeloma* (Baker, 1928a). Although we found records of *Campeloma crassula* (Rafinesque, 1819) and *Campeloma limum* (Anthony, 1860), these species appear to occur outside of Virginia (Clench and Boss 1967, Dillon 1977, Burch 1989). Thus, we assigned all records of *Campeloma* to *C. decisum*. *Campeloma* has been collected from rivers and streams within the Atlantic, New River, and Tennessee River drainages (Fig. 3A, Goodrich 1913, Burch 1950, Burch 1952, Clench and Boss 1967, Beetle 1973a, Dillon 1977, FMNH 2002, VDGIF 1998, VMNH). This burrowing snail is often abundant in low-gradient rivers and pools with soft substrates (Clench 1962, Clarke 1981, Jokinen 1983).

Lioplax subcarinata (Say, 1816). This species occurs on soft substrates in the Atlantic drainage (Baker 1928a, Clench and Turner 1955, Burch 1989). It has been recorded from Swift Creek in Chesterfield County, the James River near Cartersville in Cumberland County, near Maidens in Powhatan County, Mount Vernon and the Potomac River near Great Falls in Fairfax County, and Fluvanna County (Clench and Turner 1955, Clench and Boss 1967, Beetle 1973a, FMNH 2002).

Family Bithyniidae

Bithynia tentaculata (Linnaeus, 1758) (= *Bulimus tentaculatus*). Most authors feel that North American populations of *B. tentaculata* descended from European snails introduced into the Great Lakes in the 19th century (Baker 1928b, Mills *et al.* 1993). This species is common in the Great Lakes, but uncommon in Virginia where it reaches the



Counties

- | | | | |
|------------------|--------------------|--------------------|---------------------|
| 1. Accomack | 28. Essex | 55. Lunenburg | 82. Shenandoah |
| 2. Albemarle | 29. Fairfax | 56. Madison | 83. Smyth |
| 3. Alleghany | 30. Fauquier | 57. Mathews | 84. Southampton |
| 4. Amelia | 31. Floyd | 58. Mecklenburg | 85. Spotsylvania |
| 5. Amherst | 32. Fluvanna | 59. Middlesex | 86. Stafford |
| 6. Appomattox | 33. Franklin | 60. Montgomery | 87. Surry |
| 7. Arlington | 34. Frederick | 61. Nelson | 88. Sussex |
| 8. Augusta | 35. Giles | 62. New Kent | 89. Tazewell |
| 9. Bath | 36. Gloucester | 63. Northampton | 90. Warren |
| 10. Bedford | 37. Goochland | 64. Northumberland | 91. Washington |
| 11. Bland | 38. Grayson | 65. Nottoway | 92. Westmoreland |
| 12. Botetourt | 39. Greene | 66. Orange | 93. Wise |
| 13. Brunswick | 40. Greensville | 67. Page | 94. Wythe |
| 14. Buchanan | 41. Halifax | 68. Patrick | 95. York |
| 15. Buckingham | 42. Hanover | 69. Pittsylvania | |
| 16. Campbell | 43. Henrico | 70. Powhatan | Independent Cities |
| 17. Caroline | 44. Henry | 71. Prince Edward | 96. Chesapeake |
| 18. Carroll | 45. Highland | 72. Prince George | 97. Hampton |
| 19. Charles City | 46. Isle of Wight | 73. Prince William | 98. Newport News |
| 20. Charlotte | 47. James City | 74. Pulaski | 99. Norfolk |
| 21. Chesterfield | 48. King and Queen | 75. Rappahannock | 100. Poquoson |
| 22. Clarke | 49. King George | 76. Richmond | 101. Portsmouth |
| 23. Craig | 50. King William | 77. Roanoke | 102. Suffolk |
| 24. Culpeper | 51. Lancaster | 78. Rockbridge | 103. Virginia Beach |
| 25. Cumberland | 52. Lee | 79. Rockingham | |
| 26. Dickenson | 53. Loudoun | 80. Russell | |
| 27. Dinwiddie | 54. Louisa | 81. Scott | |

Figure 2. Counties and selected independent cities of Virginia (map adapted from Woodward and Hoffman 1991).

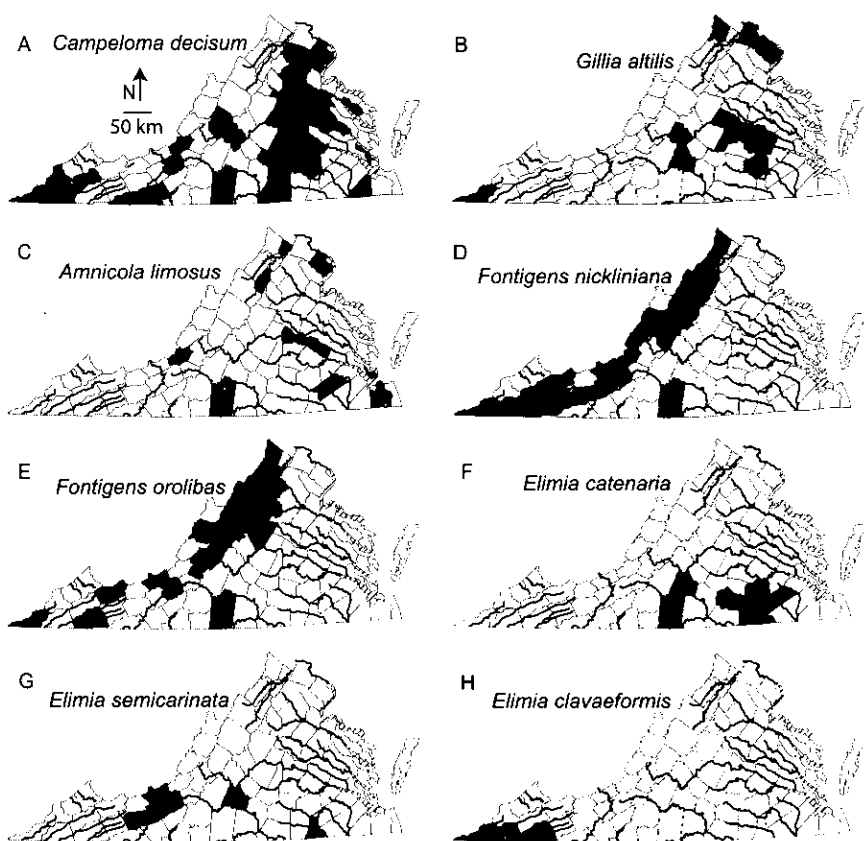


Figure 3. Distributions of (A) *Campeloma decisum*, (B) *Gillia altilis*, (C) *Amnicola limosus*, (D) *Fontigens nickliniana*, (E) *Fontigens orolibas*, (F) *Elimia catenaria*, (G) *Elimia semicarinata*, and (H) *Elimia clavaeformis* in Virginia. Shading indicates counties and independent cities where the taxon has been found. Specific localities of occurrence, if known, are indicated by dots. Filled dots represent records collected during or after 1952. Unfilled circles indicate earlier records. See figures 1-2 for names of rivers, counties, and independent cities.

southern extent of its North American range (Baker 1928a, Burch 1989). It has been recorded from Rockbridge County, and from the Potomac River near Alexandria and Mount Vernon in Fairfax County in the 1920s and 1930s (Pilsbry 1932, Marshall 1933, Beetle 1973a, Dundee 1974).

Family Hydrobiidae

Littoridinops tenuipes (Couper, 1844) (= *Amnicola tenuipes*, *Bythinella tenuipes*). This species inhabits the Atlantic drainage in streams that are brackish for part of the year (Pilsbry, 1952; Hershler and Thompson, 1992). It has been reported from Hampton, Newport News, and Norfolk cities, and from King George and Northampton counties (Beetle 1973a).

Gillia altilis (Lea, 1841). This species is common in inland rivers and streams (Fig. 3B, Clench and Boss 1967,

Beetle 1973a, Thompson 1984, FMNH 2002). Most authors consider *G. altilis* to be restricted to the Atlantic drainage, so Beetle's (1973a) record from Lee County, Virginia (Tennessee drainage) should be examined further (Thompson 1984, Burch 1989).

Somatogyrus virginicus (Walker, 1904). This is one of the most endangered species of freshwater gastropods in North America. The species was described from a population in the Rapidan River at Barnard's Ford, Culpeper County, Virginia (Walker 1904a). Neves (1991) recognized the rarity of records of *S. virginicus* for Virginia, but was unsure if the Rapidan had been sampled after 1904. *Somatogyrus virginicus* has also been reported from North Carolina, but its status there is also uncertain (Neves *et al.* 1997). *Somatogyrus virginicus* is a candidate for federal endangered species status (Neves *et al.* 1997).

Amnicola limosus (Say, 1817) (= *Amnicola limosa*). This species occurs in a variety of habitats of the Atlantic drainage, including lakes, rivers, and permanent streams (Fig. 3C, Rehder 1949, Beetle 1973a, Hershler and Thompson 1988, FMNH 2002, VDGIF 1998).

Lyogyrus granum (Say, 1822) (= *Amnicola grana*). This species is also restricted to the Atlantic drainage, and is often associated with physical structure in eutrophic, slow-moving, permanent waters (Clarke 1981, Burch 1989). It has been reported from Norfolk City, and

from Fairfax, Hanover, Henrico, and New Kent counties (Beetle 1973a).

Holsingeria unthankensis (Hershler, 1989). The "thankless ghostsnail" was described as a tiny, pale-colored, stream-dwelling snail inhabiting undersides of stones in Unthanks Cave, Lee County, Virginia (Hershler 1989, Kabat and Hershler 1993). This species is listed as "endangered" by the Virginia Department of Conservation and Recreation, but has not been provided federal protection under the Endangered Species Act (Roble 2001). Before Hershler's (1989) taxonomic revision, *H. unthankensis* and the yet unnamed *Holsingeria* sp. 1 were grouped under the name *Fontigens holsingeri* (Burch 1989, Kabat and Hershler 1993).

Holsingeria sp. 1 *sensu* Hershler (1989). Populations of the "skyline caverns snail" have been collected only from

streamside pools in Skyline Caverns, Warren County, Virginia (Hershler 1989, Batie 1991). Although its taxonomic status remains uncertain, this species is certainly imperiled due to limited geographic range (Roble 2001).

Fontigens nickliniana (Lea, 1838). This species and its congeners occur in cool, calcium-rich waters of western Virginia (Hershler *et al.* 1990). It inhabits caves, springs, streams, and small lakes (Fig. 3D, Haldeman 1842, Goodrich 1913, Baker 1928a, Burch 1950, Beetle 1973a, Holsinger and Culver 1988, Hershler *et al.* 1990, Richardson *et al.* 1991, FMNH 2002, VDGIF 1998, VMNH). Hershler *et al.* (1990) list synonyms for this species.

Fontigens orolibas (Hubricht, 1957). This species inhabits springs and cave streams in western Virginia (Fig. 3E, Haldeman 1840-1845, Hubricht 1957, Beetle 1973a, Holsinger and Culver 1988, Hershler *et al.* 1990, Richardson *et al.* 1991, FMNH 2002, VMNH). Hershler *et al.* (1990) list synonyms for this species.

Fontigens morrisoni (Hershler, Holsinger, and Hubricht, 1990). This is another endangered species that is not protected by law, although it is found at only four sites: Blowing and Butler caves in Bath County, and two springs near Mustoe in Highland County (Hubricht 1976, Holsinger and Culver 1988, Hershler *et al.* 1990, Roble 2001). Environmental requirements and life history features are poorly known.

Fontigens bottimeri (Walker, 1925) (= *Palustrina bottimeri*). This species is limited to a few caves and springs, but has not been granted legal protection (Hershler *et al.* 1990, Roble 2001). In Virginia, it is known only from Ogden's Cave in Frederick County (Hershler *et al.* 1990).

Family Pomatiopsidae

Pomatiopsis cincinnatiensis (Lea, 1840). Limited historic distribution and absence of recent records suggest *P. cincinnatiensis* is imperiled in or extirpated from Virginia. Goodrich (1913) recorded this species from brooks near Cleveland, in Russell County, and Beetle (1973a) reported sightings from Lee and Scott counties. *Pomatiopsis cincinnatiensis* is described as a semiaquatic species (van der Schalie and Dundee 1955). Its habitat consists of a narrow, moist zone on riverbanks (Baker 1928a, van der Schalie and Getz 1962).

Pomatiopsis lapidaria (Say, 1817). This species is also semiaquatic (Baker 1931, Berry 1943). It has more generalized habitat requirements than *Pomatiopsis cincinnatiensis*, and occurs in swampy areas and wet pastures as well as stream edges (Baker 1931, van der Schalie and Dundee 1955). Beetle (1973a) recorded this species from Arlington, Buchanan, Fairfax, Giles, Grayson, Lee, Mecklenburg, Montgomery, New Kent, Patrick, Prince William, Scott, Smyth, Washington, and Wythe counties and from the city of Newport News.

Family Pleuroceridae

Elimia arachnoidea (Anthony, 1854) (= *Goniobasis arachnoidea*, *Goniobasis spinella* Lea, 1862). This species is limited to small streams in Tennessee and southwestern Virginia (Goodrich 1940, Burch 1989). Goodrich (1913) recorded populations from Little and Big Moccasin Creeks near Gate City in Scott County, and Goodrich (1940) found it in Lee County. Lack of recent records for *E. arachnoidea* makes its present status unclear.

Elimia catenaria (Say, 1822) (= *Goniobasis catenaria*). This species of the Atlantic Coastal Plain has been recorded from several streams and rivers in southcentral Virginia (Fig. 3F, Goodrich 1942, VMNH).

Elimia semicarinata (Say, 1829) (= *Goniobasis semicarinata*). This species occurs in the upper New River and surrounding tributaries and in Campbell and Greensville counties (Fig. 3G, Goodrich 1942, Dillon 1977, Dillon and Davis 1980, Dillon 1982, VDGIF 1998). The discontinuous distribution probably indicates an incomplete understanding of its geographic range.

Elimia aterina (Lea 1863) (= *Goniobasis aterina*). This rare species is restricted to a few springs and small streams in Tennessee and southwest Virginia (Goodrich 1913, Burch 1989, FMNH 2002). It has been recorded from Beaver Creek near Bristol in Washington County, and from Stock Creek and a mountain brook near Gate City in Lee County (Goodrich 1913, FMNH 2002). The most recent record was from 1914, so the present status of *E. aterina* is uncertain.

Elimia clavaeformis (Lea, 1841) (= *Goniobasis clavaeformis*). This species is restricted to streams and small rivers in the Tennessee River drainage (Goodrich 1940, Burch 1989). It occurs in tributaries of the Powell and Holston Rivers (Fig. 3H, Goodrich 1913, Beetle 1973a, Dillon 1989, FMNH 2002, VDGIF 1998).

Elimia simplex (Say, 1825) (= *Goniobasis simplex*). This species occurs in the Tennessee and New River drainages (Fig. 4A, Goodrich 1940, Burch 1989). Populations in the New River drainage are restricted to a few small creeks (Fig. 4A, Dillon 1977, Dillon and Davis 1980, Dillon 1982). In the Tennessee drainage, however, *E. simplex* occurs in both small and large rivers, including the Clinch and Holston rivers (Fig. 4A, Say 1825, Tryon 1873, Goodrich 1913, Stansbery and Clench 1974a, 1974b, 1977, Goudreau *et al.* 1993, FMNH 2002, VDGIF 1998, VMNH). This species has also been collected from cave streams (Holsinger 1964, Holsinger and Culver 1988).

Elimia proxima (Say, 1825) (= *Elimia symmetrica* [Haldeman, 1841], *Goniobasis proxima*, *Goniobasis symmetrica*). This species inhabits Atlantic and Tennessee drainages (Goodrich 1942, Goodrich 1950, Dillon and Keferl 2000). Populations inhabit small streams in addition to large rivers or

Fig. 4
Io flu
Pleur
the t
Filled
recon
ducti
lished
rivers

spray
1950.
Davis
A po
entire
taries
E
This i
in lar
Burch
2002,
corde
establ
from
FMNH

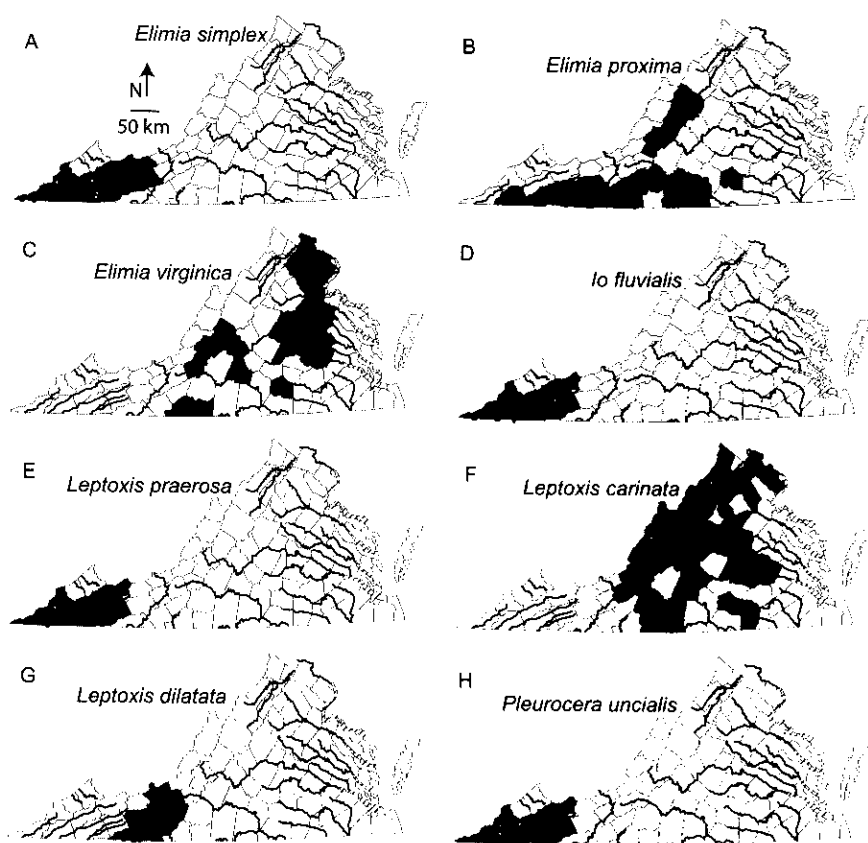


Figure 4. Distributions of (A) *Elimia simplex*, (B) *Elimia proxima*, (C) *Elimia virginica*, (D) *Io fluviialis*, (E) *Leptoxis praerosa*, (F) *Leptoxis carinata*, (G) *Leptoxis dilatata*, and (H) *Pleurocera uncialis* in Virginia. Shading indicates counties and independent cities where the taxon has been found. Specific localities of occurrence, if known, are indicated by dots. Filled dots represent records collected during or after 1952. Unfilled circles indicate earlier records. The star in (B) indicates the location of a population resulting from an introduction by Dillon (1986). The star in (D) indicates the location of a population reestablished as a result of reintroduction efforts (Ahlstedt 1991). See figures 1-2 for names of rivers, counties, and independent cities.

spray zones of falls or springs (Fig. 4B, Tryon 1873, Burch 1950, Goodrich 1950, Dillon 1977, 1982, 1988, Dillon and Davis 1980, Dillon and Keferl 2000, FMNH 2002, VMNH). A population in Coyner Springs, Augusta County, consists entirely of descendants from snails introduced from tributaries of the Dan and New Rivers (Fig. 4B, Dillon 1986).

Elimia virginica (Say, 1817) (= *Goniobasis virginica*). This is the most abundant and widespread species of *Elimia* in large rivers of the Atlantic drainage (Fig. 4C, Burch 1950, Burch 1952, Clench and Boss 1967, Beetle 1973a, FMNH 2002, VDGIF 1998, VMNH). On rare occasions, it is recorded from small streams (Fig. 4C, VMNH). Based on its established range, we concluded that a report of *E. virginica* from Lee County is in error (Goodrich 1942, Burch 1989, FMNH 2002).

Io fluviialis (Say, 1825) (= *Fusus fluviialis*, *Io brevis* Anthony in Reeve, 1860, *Io clinchensis* Adams, 1914, *Io lyttonensis* Adams, 1914, *Io paulensis* Adams, 1914, *Io powellensis* Adams, 1914, *Io spinosa* Lea, 1837). The "spiny riversnail" occurs in some large tributaries of the Tennessee River, but only in flowing, well oxygenated habitats with abundant limestone (Fig. 4D, Say 1825, Tryon 1873, Adams 1900, Adams 1915, Goodrich 1913, Clench 1928, Lutz 1951, Dazo 1961, Beetle 1973a, Stansbery and Clench 1974a, Stansbery and Stein 1976, McLeod and Moore 1978, Ahlstedt 1979, Ahlstedt 1991, Neves *et al.* 1997, FMNH 2002, INHS 2003, VDGIF 1998, VMNH). Dramatic population declines of *I. fluviialis* from 1900 through the 1970s were documented through field surveys (Adams 1915, Lutz 1951, Stansbery and Stein 1976, McLeod and Moore 1978). Habitat degradation caused by deforestation and industrial pollution destroyed several Virginian populations during this time, including all of those in the North Fork Holston River south of Saltville, Smyth County (Adams 1915, Ahlstedt 1979, Ahlstedt 1991). Due to its small numbers, specific habitat requirements, and continuing threats to its survival, *I. fluviialis* is classified as "threatened" by the Virginia Department of Conservation and has been considered for protection under the federal Endangered Species Act (Neves *et al.* 1997, Roble 2001). Attention directed to *I. fluviialis* has had positive effects. Pol-

lution abatement programs in the 1970s enabled successful reestablishment of *I. fluviialis* in part of its historic range. Ahlstedt (1979) contributed to this recovery in 1978 by reintroducing this species to two sites on North Fork Holston River where it had been absent for almost 100 years. By 1986, Ahlstedt (1991) saw evidence of reproduction and increased population densities at downstream and upstream sites, including one site in Scott County (Fig. 4D).

Leptoxis praerosa (Say, 1821) (= *Anculosa praerosa*, *Anculosa subglobosa* Say, 1825, *Leptoxis subglobosa*, *Melania subglobosa*). This species also inhabits tributaries of the Tennessee River (Fig. 4E, Say 1825, Goodrich 1913, 1940, Stansbery 1972, Beetle, 1973a, Stansbery and Clench 1974a, 1974b, 1977, Goudreau *et al.* 1993, Reed-Judkins *et al.* 1998, FMNH 2002, VDGIF 1998, VMNH). *Leptoxis praerosa* is

often associated with *Io fluviialis* in large rivers, but *L. praerosa* also occurs in small tributaries that do not support *Io fluviialis* (Figs. 4D, E). Similar to *I. fluviialis*, *L. praerosa* suffered severe population declines during much of the 20th century (Ahlstedt 1979). However, populations of *L. praerosa* recovered more rapidly than *I. fluviialis* following water quality improvements.

Leptoxis carinata (Bruguière, 1792) (= *Anculosa carinata*, *Leptoxis nickliniana* Lea, 1839, *Melania nickliniana*, *Mudalia carinata*, *Nitrocris carinata*, *Spirodon carinata*). This is the most abundant and widespread pleurocerid in eastern and central Virginia; densities can reach 500 individuals/m² on rocky bottoms of rivers and small creeks (Fig. 4F, Tryon 1873, Pilsbry 1894, Goodrich 1942, Burch 1950, Burch 1989, Clench and Boss 1967, Beetle 1973a, Miller 1985, Dillon 1989, Stewart and Garcia 2002, FMNH 2002, VDGIF 1998, VMNH). *Leptoxis carinata* is restricted to the Atlantic drainage, so we did not plot records from Buchanan, Montgomery, Pulaski, and Wythe counties (Goodrich 1942, Beetle 1973a, FMNH 2002).

Leptoxis dilatata (Conrad, 1835) (= *Nitrocris dilatatus*, *Spirodon dilatata*). This species occurs in the New River drainage (Fig. 4G, Tryon 1873, Goodrich 1940, Beetle 1973a, Dillon 1977, Burch 1989, Farris *et al.* 1994, Reed-Judkins *et al.* 1998, FMNH 2002). Dillon (1977) found this species to be among the most common molluscs in the upper New River drainage and noted its occurrence in the main river and tributaries. We did not plot records from Alleghany, Amherst, Rockbridge, and Scott counties because these localities are within Atlantic and Tennessee drainages, where *L. dilatata* is replaced by *Leptoxis carinata* and *Leptoxis praerosa*, respectively (Goodrich 1940, Goodrich 1942, Beetle 1973a, FMNH 2002).

Pleurocera canaliculata (Say, 1821) (= *Pleurocera canaliculatum*). This species is restricted to the Tennessee River drainage. Beetle (1973a) reported this species from Lee, Scott, Smyth, Washington, and Wise counties.

Pleurocera gradata (Anthony, 1854) (= *Pleurocera gradatum*). This species has not been seen in Virginia in over 100 years. The only record was from the Holston River, Washington County (Tryon 1873). Despite its rarity, the species has not been granted statewide or federal protection (Roble 2001).

Pleurocera uncialis (Haldeman, 1841) (= *Goniobasis uncialis*, *Pleurocera "unciale"*). This species occurs in upper tributaries of the Tennessee River (Fig. 4H, Goodrich 1913, 1937, 1940, Beetle 1973a, Stansbery and Clench 1974a, 1974b 1977, Burch 1989, Goudreau *et al.* 1993, Reed-Judkins *et al.* 1998, FMNH 2002, VDGIF 1998). It is the most common species of *Pleurocera* in western Virginia, but pollution has caused declines in abundance (Goudreau *et al.* 1993).

Family Lymnaeidae

Fossaria spp. The taxonomy of the genus *Fossaria* is in a confused state, with species distinguished by minor differences in shell attributes that might be ecophenotypic in origin. Records occurred for the following *Fossaria* "species": *F. humilis* (Say, 1822), *F. dalli* (Baker, 1907), *F. galbana* (Say, 1825), *F. obrussa* (Say, 1825), and *F. parva* (Lea, 1841) (Fig. 5A, Goodrich 1913, Burch 1950, Beetle 1973a, Dillon 1977, Dillon and Benfield 1982, FMNH 2002). *Fossaria* spp. occur in lakes, ponds, and streams, and can thrive in waters with low levels of dissolved oxygen (Baker 1911, Goodrich 1913, Dillon 1977, Dillon 2000). These snails are often semiaquatic, inhabiting moist areas above the water line (Haldeman 1840-1845, Baker 1911, Baker 1928a).

Pseudosuccinea columella (Say, 1817) (= *Lymnaea columella*). This species is found in ponds, lakes, and stream pools across Virginia (Fig. 5B, Rehder 1949, Burch 1950, Burch 1952, Burch and Wood 1955, Beetle 1973a, Dillon 1977, Dillon and Benfield 1982, FMNH 2002). It withstands oxygen fluctuations characteristic of eutrophic habitats, and individuals often occur above the water line on mud and other substrates (Baker 1928a, Jokinen 1983).

Radix auricularia (Linnaeus, 1758). This Eurasian species invaded North America and now occurs at scattered locations (Burch 1989, Mills *et al.* 1993). Populations frequent eutrophic lentic habitats and can be found on mud or plants (Clarke 1979, 1981). In Virginia, *R. auricularia* has only been reported from Giles County (Beetle 1973a).

Stagnicola neopalustris (Baker, 1911). Baker (1911) described a new species of lymnaeid from Orange township, Orange County, Virginia. This is the only known record for this species.

Family Physidae

Physella gyrina (Say, 1821) (= *Physella ancillaria* [Say, 1825], *Physella aurea* [Lea, 1838], *Physella crocata* [Lea, 1864], *Physella elliptica* [Lea, 1831], *Physellaa inflata* [Lea, 1841], *Physella microstoma* [Haldeman, 1840]). Most populations of *Physella* (= *Physa*) show little reproductive isolation (R. T. Dillon, Jr. pers. comm.). Here we synonymize six nominal species reported from Virginia under the oldest veritable name, *P. gyrina*. This species can be found in almost any environment supporting freshwater snails (Clarke 1981, Dillon 2000). However, taxonomic uncertainties and lack of attention directed to pulmonates have resulted in few records for *P. gyrina* or its synonyms (Fig. 5C, Tryon 1865, Walker 1918, Baker 1928a, Burch 1950, Clench and Boss 1967, Beetle 1973a, Wethington *et al.* 2000, VMNH).

Physella acuta (Draparnaud, 1805) (= *Physella hender-soni* [Clench, 1925], *Physella heterostropha* [Say, 1817], *Physella pomilia* Conrad, 1833). After finding no evidence of reproductive isolation among three species of *Physella* (=

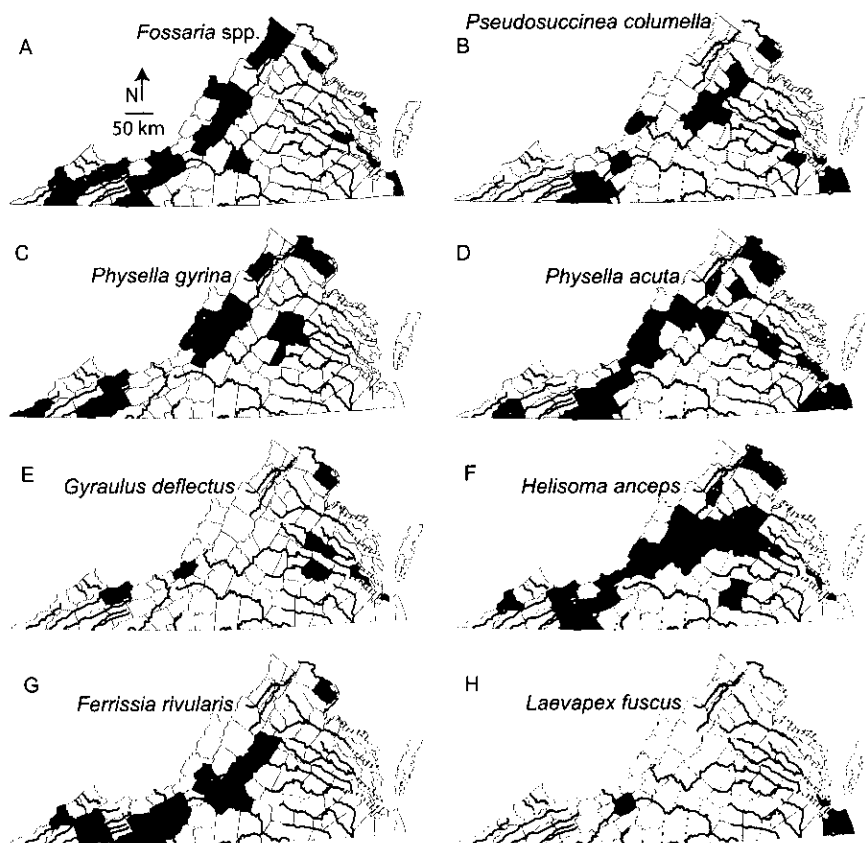


Figure 5. Distributions of (A) *Fossaria* spp., (B) *Pseudosuccinea columella*, (C) *Physella gyrina*, (D) *Physella acuta*, (E) *Gyraulus deflectus*, (F) *Helisoma anceps*, (G) *Ferrissia rivularis*, and (H) *Laevapex fuscus* in Virginia. Shading indicates counties and independent cities where the taxon has been found. Specific localities of occurrence, if known, are indicated by dots. Filled dots represent records collected during or after 1952. Unfilled circles indicate earlier records. See figures 1-2 for names of rivers, counties, and independent cities.

Physa) reported from Virginia, including *P. acuta*, *P. hendersoni*, and *P. heterostropha*, Dillon *et al.* (2002) assigned the name *P. acuta* to this entire group. *Physella acuta* could be the most abundant and cosmopolitan freshwater gastropod in the world (Dillon *et al.* 2002). The snail occurs in streams, rivers, brooks, ditches, permanent and temporary ponds and lakes and is found on hard and soft substrates (Clarke 1981, Jokinen 1983, Strayer 1987). It inhabits oligo-, meso-, and eutrophic waters (Clarke 1979). Taxonomic confusion and lack of attention directed to pulmonates resulted in few Virginian records for *P. acuta* and its synonyms, although this species probably occurs throughout the entire state (Fig. 5D, Pilsbry 1894, Goodrich 1913, Baker 1928a, Rehder 1949, Burch 1950, Burch 1952, Burch and Wood 1955, Beetle 1973a, 1973b, Dundee 1974, Dillon, 1977, Dillon and Benfield 1982, VDGIF 1998, FMNH 2002).

Aplexa elongata (Say, 1821) (= *Aplexa hypnorum* Linnaeus, 1758). This species is primarily an inhabitant of vernal freshwater habitats, including temporary woodland pools, but has been found in small streams (Baker 1928a, Clarke 1981). It is rare in Virginia (Beetle 1973a, Jokinen 1983, Burch 1989). Records exist from Greene and Surry counties (Beetle 1973a, FMNH 2002).

Family Planorbidae

Gyraulus deflectus (Say, 1824) (= *Gyraulus hirsutus*). This species reaches the southern limits of its geographic range in Virginia and adjacent states (Clarke 1981, Burch 1989). This small snail occurs in mesotrophic and eutrophic lakes, large ponds, and quiet areas of rivers (Fig. 5E, Baker 1928a, Burch 1950, Burch 1952, Burch and Wood 1955, Beetle 1973a, Clarke 1979, Strayer 1987, VDGIF 1998).

Gyraulus parvus (Say, 1817). This species is commonly found in heavily vegetated lakes and ponds, and occasionally lotic habitats (Baker 1928a, Strayer 1987). It has been recorded from Augusta, Frederick, Giles, Rockbridge, Shenandoah, Wythe, and York counties and the city of Newport News (Burch 1950, Beetle 1973a).

Helisoma anceps (Menke, 1830) (= *Helisoma antrosa* Conrad, 1834, *Planorbis bicarinatus* Say, 1819). This species is common throughout Virginia (Fig. 5F, Pilsbry 1894, Walker 1909, Goodrich

1913, Baker 1945, Burch, 1950, Burch 1952, Burch and Wood 1955, Clench and Boss 1967, Beetle 1973a, Dillon 1977, Dillon and Benfield 1982, Burch 1989, FMNH 2002, VDGIF 1998, VMNH). Among planorbids, this species is unusual in that it is most commonly found in lotic habitats, although it also inhabits ponds and lakes (Jokinen 1983, Dillon 2000).

Micromenetus brogniartianus (Lea, 1842) (= *Menetus brogniartianus*). Both global and Virginian distributions of this small planorbid are poorly known (Burch 1989). It was reported from Surry County and the city of Newport News (Beetle 1973a).

Micromenetus dilatatus (Gould, 1841) (= *Menetus dilatatus*). Baker (1945) recorded this species from the vicinity of Luray, Page County, Virginia. Additional records exist from Culpeper, Fairfax, New Kent, and Prince William

Counties and the cities of Hampton and Newport News (Beetle, 1973a). This species is encountered in vegetated lentic habitats and also in upland streams (Jokinen 1983, Strayer 1987).

Planorbella trivolvis (Say, 1817) (= *Helisoma trivolvis*). Although this large planorbid is distributed throughout the eastern and midwestern United States, we found few records (Baker 1928a, Burch 1989). It has been reported from the Holston River, near Marion in Smyth County, and from Fairfax County and the cities of Newport News and Norfolk (Beetle 1973a). *Planorbella trivolvis* occurs in lentic habitats and areas of slow flow in rivers and streams (Baker 1928a, Clarke 1981).

Planorbella armigera (Say, 1821). This snail is usually associated with vegetation in perennial, lentic habitats (Baker 1928a, Clarke 1981, Burch 1989). It has been reported from Fairfax County and the cities of Hampton, Newport News, and Virginia Beach (Beetle 1973a).

Promenetus exacuous (Say, 1821) (= *Menetus exacuous*). This species inhabits still areas of permanent and vernal freshwater habitats (Baker 1928a, Clarke 1979, Burch 1989). It has been recorded in Dinwiddie and Prince George counties (Beetle 1973a).

Family Ancyliidae

Ferrissia fragilis (Tryon, 1863) (= *Ancylus pumilus* Lea, 1845, *Ferrissia californica* [Rowell, 1863], *Ferrissia shimckii* [Pilsbry, 1890], *Gundlachia meekiana* Stimpson, 1863). This tiny gastropod occurs in lentic, eutrophic waters (Basch 1963, Clarke 1979, Burch 1989). Walker (1904b) recorded this species from Fairfax County near Alexandria, Virginia. Additional records occur from Hanover and Rockbridge counties (Burch 1952, Beetle 1973a).

Ferrissia parallela (Haldeman, 1841) (= *Ancylus parallelus*). This limpet reaches the southern extent of its range in northern Virginia (Basch 1963, Burch 1989). The only record we found was from Fairfax County (Beetle 1973a). *Ferrissia parallelus* inhabits lentic habitats where it is often found clinging to vegetation (Baker 1928a, Clarke 1981).

Ferrissia rivularis (Say, 1817) (= *Ancylus depressus* Haldeman, 1844, *Ancylus haldemani* Bourguignat, 1853, *Ancylus rivularis*, *Ancylus tardus* Say, 1830). This is the most commonly reported ancyliid in Virginia (Fig. 5G, Haldeman 1840-1845, Walker 1904b, Basch 1963, Beetle 1973a, Dillon 1977, Reed-Judkins *et al.* 1998, VDGIF 1998). *Ferrissia rivularis* lives in lotic habitats, where it occupies cobbles or other hard substrates in riffles (Baker 1928a, Jokinen 1983).

Laevapex fuscus (Adams, 1841) (= *Ancylus fuscus*, *Ferrissia fusca*). This species typically inhabits lakes and slow-flowing areas of streams and rivers, with occasional records of collections from rivulets (Fig. 5H, Rehder 1949, Beetle 1973a, Dillon 1977). *Laevapex fuscus* can be found attached

to vegetation, rocks, and man-made objects (Baker 1928a, Basch 1963).

CONCLUSIONS

A diverse group of freshwater gastropods inhabits Virginia, with more than 50 species occurring there historically or presently. However, the lack of recent records for several species is cause for concern, as is evidence that some species are found only at one or two locations. Because intensive survey efforts have been directed to them, it is clear that *Fontigens bottimeri*, *Fontigens morrisoni*, *Holsingeria unthan-kensis*, and *Holsingeria* sp. 1 are extremely rare and endangered. Other species with few records, including *Somatogyrys virginicus*, *Pomatiopsis cincinnatiensis*, *Elimia arachnoidea*, *Pleurocera gradata*, and *Stagnicola neopalustris* are also likely endangered or extirpated. However, field surveys are still needed to determine their statuses.

Other taxa and specific geographic regions should also be surveyed. Specifically, pulmonates (families Lymnaeidae, Physidae, Planorbidae, and Ancyliidae) have been undersurveyed, thus their maps underestimate their distributions. Additionally, we found no records from the Big Sandy drainage, including Buchanan and Dickenson counties and the Levisa and Russel Rivers, and only one record (*Littoridinops tenuipes*; Beetle 1973a) from the eastern shore (i. e., Accomack and Northampton Counties). Absence of records from these regions are in contrast to the Tennessee drainage in southwest Virginia, where detailed surveys of rivers revealed declines and subsequent recoveries of pleurocerid populations (Adams 1915, Ahlstedt 1979, 1991).

By summarizing survey data from different sources, we hope to stimulate research that will improve our understanding of the freshwater gastropod fauna of Virginia. We identified species and geographic regions that have been well surveyed, as well as those requiring additional study. Furthermore, we provide critical baseline data for measuring temporal changes in gastropod abundance and distributions. Comparisons of data from historic and future field surveys will facilitate legal protection of endangered species by providing evidence of restricted or shrinking geographic ranges. Consequently, effective management plans can be developed for species in need of assistance.

ACKNOWLEDGMENTS

We thank the American Malacological Society and staff at the College of Charleston for organizing the 2002 AM meeting. Special thanks to Amy Martin (Virginia Department of Game and Inland Fisheries) for access to the Vir

ginia Fish and Wildlife Information Service electronic database, Elizabeth Moore (Virginia Museum of Natural History) for museum records, and Christopher Register (Longwood University) for cartographic assistance. Comments by Eileen Jokinen, Janice Voltzow, and an anonymous reviewer improved the manuscript.

LITERATURE CITED

- Adams, C. C. 1900. Variation in *Io*. *Proceedings of the American Association for the Advancement of Science* 49: 208-225.
- Adams, C. C. 1915. The variations and ecological distribution of the snails of the genus *Io*. *Memoirs of the National Academy of Sciences* 12: 1-92.
- Ahlstedt, S. A. 1979. Recent mollusk transplants into the North Fork Holston River in southwestern Virginia. *Bulletin of the American Malacological Union* 1979: 21-23.
- Ahlstedt, S. A. 1991. Reintroduction of the spiny riversnail *Io fluviialis* (Say, 1825) (Gastropoda: Pleuroceridae) into the North Fork Holston River, Southwest Virginia and Northeast Tennessee. *American Malacological Bulletin* 8: 139-142.
- Baker, F. C. 1911. *The Lymnaeidae of North and Middle America, Recent and Fossil*. Chicago Academy of Sciences Special Publication No. 3., Chicago, Illinois.
- Baker, F. C. 1928a. *The Fresh Water Mollusca of Wisconsin. Part I. Gastropoda*. Wisconsin Academy of Sciences, Arts, and Letters, Madison, Wisconsin.
- Baker, F. C. 1928b. The American *Bithynia* not wholly an introduced species. *Transactions of the Illinois State Academy of Sciences* 20: 56-62.
- Baker, F. C. 1931. Ecological relationship of the genus *Pomatiopsis* with special reference to *Pomatiopsis lapidaria*. *Ecology* 12: 489-496.
- Baker, F. C. 1945. *The Molluscan Family Planorbidae*. The University of Illinois Press. Urbana, Illinois.
- Basch, P. F. 1963. A review of the recent freshwater limpet snails of North America (Mollusca: Pulmonata). *Bulletin of the Museum of Comparative Zoology* 129: 399-461.
- Batie, R. 1991. Unthanks cave snail. In: K. Terwilliger, ed., *Virginia's Endangered Species, Proceedings of a Symposium*, McDonald and Woodward Publishing Company, Blacksburg, Virginia. Pp. 307.
- Beetle, D. E. 1973a. A checklist of the land and freshwater mollusks of Virginia. *Sterkiana* 49: 21-35.
- Beetle, D. E. 1973b. *Physa acuta* in Virginia. *Nautilus* 87: 28.
- Berry, E. G. 1943. The Amnicolidae of Michigan: Distribution, ecology, and taxonomy. *University of Michigan Museum of Zoology Miscellaneous Publications* 57: 1-68.
- Bogan, A. E. 1998. Freshwater molluscan conservation in North America: Problems and practices. *Journal of Conchology Special Publication* 2: 223-230.
- Burch, J. B. 1952. A preliminary list of Mollusca of Hanover County, Virginia. *Nautilus* 66: 60-63.
- Burch, J. B. 1989. *North American Freshwater Snails*. Malacological Publications, Hamburg, Michigan.
- Burch, P. R. 1950. Mollusks. In: James River Project Committee of the Virginia Academy of Science, ed., *The James River Basin. Past, Present and Future.*, Virginia Academy of Science, Richmond, Virginia. Pp. 129-137.
- Burch, P. R. and J. T. Wood. 1955. The salamander *Siren lacertina* feeding on clams and snails. *Copeia* 3: 255-256.
- Clarke, A. H. 1979. Gastropods as indicators of trophic lake stages. *Nautilus* 93: 138-142.
- Clarke, A. H. 1981. *The Freshwater Mollusks of Canada*. National Museums of Canada, Ottawa, Ontario, Canada.
- Clench, W. J. 1928. *Io fluviialis turrita* Anthony. *Nautilus* 42: 36.
- Clench, W. J. 1962. A catalogue of the Viviparidae of North America with notes on the distribution of *Viviparus georgianus* Lea. *Occasional Papers on Mollusks* 2: 261-287.
- Clench, W. J. and K. J. Boss. 1967. Freshwater Mollusca from James River, VA and a new name for *Mudalia* of authors. *Nautilus* 80: 99-102.
- Clench, W. J. and S. L. H. Fuller. 1965. The genus *Viviparus* (Viviparidae) in North America. *Occasional Papers on Mollusks* 2: 385-412.
- Clench, W. J. and R. D. Turner. 1955. The North American genus *Lioplax* in the family Viviparidae. *Occasional Papers on Mollusks* 2: 1-20.
- Dazo, B. C. 1961. Some studies on the genus *Io*. *Bulletin of the American Malacological Union* 1961: 6.
- Dillon, R. T., Jr. 1977. *Factors in the Distributional Ecology of Upper New River Mollusks (Virginia/North Carolina)*. Undergraduate Honors Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Dillon, R. T., Jr. 1982. *The Correlates of Divergence in Isolated Populations of the Freshwater Snail, Goniobasis proxima*. Ph.D. Dissertation, University of Pennsylvania, Philadelphia, Pennsylvania.
- Dillon, R. T., Jr. 1986. Inheritance of isozyme phenotype at three loci in the freshwater snail, *Goniobasis proxima*: Mother-offspring analysis and artificial introduction. *Biochemical Genetics* 24: 281-290.
- Dillon, R. T., Jr. 1988. Evolution of transplants between genetically distinct populations of freshwater snails. *Genetica* 76: 111-119.
- Dillon, R. T., Jr. 1989. Karyotypic evolution in pleurocerid snails. I. Genomic DNA estimated by flow cytometry. *Malacologia* 31: 197-203.
- Dillon, R. T., Jr. 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press. Cambridge, United Kingdom.
- Dillon, R. T., Jr. and E. F. Benfield. 1982. Distribution of pulmonate snails in the New River of Virginia and North Carolina, U.S.A.: Interaction between alkalinity and stream drainage area. *Freshwater Biology* 12: 179-186.
- Dillon, R. T., Jr. and G. M. Davis. 1980. The *Goniobasis* of southern Virginia and northwestern North Carolina: Genetic and shell morphometric relationships. *Malacologia* 20: 83-98.
- Dillon, R. T., Jr. and E. P. Keferl. 2000. A survey of the pleurocerid gastropods of South Carolina. In: P. D. Johnson and R. S. Butler, eds., *Proceedings of the First Freshwater Mollusk Con-*

- ervation Society Symposium, 1999*, Ohio Biological Survey, Columbus, Ohio. Pp. 153-160.
- Dillon, R. T., Jr., A. R. Wethington, J. M. Rhett, and T. P. Smith. 2002. Populations of the freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra*. *Invertebrate Biology* 121: 226-234.
- Dundee, D. S. 1974. Catalog of introduced molluscs of eastern North America (north of Mexico). *Sterkiana* 55: 1-37.
- Farris, J. L., J. L. Grudzien, S. E. Belanger, D. S. Cherry, and J. Cairns, Jr. 1994. Molluscan cellulolytic responses to zinc exposure in laboratory and field stream comparisons. *Hydrobiologia* 287: 161-178.
- FMNH 2002. Florida Museum of Natural History Invertebrate Zoology: Malacology and marine invertebrates. Available at: <http://www.flmnh.ufl.edu/malacology> February 2004.
- Goodrich, C. 1913. Spring collecting in southwest Virginia. *Nautilus* 27: 81-82, 91-95.
- Goodrich, C. 1937. Studies of the gastropod family Pleuroceridae-VI. *Occasional Papers of the Museum of Zoology, University of Michigan* 347: 1-12.
- Goodrich, C. 1940. The Pleuroceridae of the Ohio River drainage system. *Occasional Papers of the Museum of Zoology, University of Michigan* 417: 1-21.
- Goodrich, C. 1942. The Pleuroceridae of the Atlantic Coastal Plain. *Occasional Papers of the Museum of Zoology, University of Michigan* 456: 1-6.
- Goodrich, C. 1950. *Goniobasis proxima* (Say). *Nautilus* 63: 78-80.
- Goudreau, S. E., R. J. Neves, and R. J. Sheehan. 1993. Effects of wastewater treatment plant effluents on freshwater mollusks in the upper Clinch River, Virginia, USA. *Hydrobiologia* 252: 211-230.
- Haldeman, S. S. 1840-1845. *A Monograph of the Limniades and Other Fresh Water Univalve Shells of North America*. Parts I-VIII. J. Dobson, Philadelphia, Pennsylvania.
- Haldeman, S. S. 1842. Description of five new species of American freshwater shells. *Journal of the Academy of Natural Sciences of Philadelphia* 8: 200-202.
- Hershler, R. 1989. *Holsingeria unthankensis*, a new genus and species of aquatic cavesnail from eastern North America. *Malacological Review* 22: 93-100.
- Hershler, R., J. R. Holsinger, and L. Hubricht. 1990. A revision of the North American freshwater snail genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* 509: 1-49.
- Hershler, R. and F. G. Thompson. 1988. Notes on morphology of *Ammicola limosa* (Say, 1817) (Gastropoda: Hydrobiidae) with comments on status of the subfamily Amnicolinae. *Malacological Review* 21: 81-92.
- Hershler, R. and F. G. Thompson. 1992. A review of the aquatic gastropod subfamily Cochliopinae (Prosobranchia: Hydrobiidae). *Malacological Review, Supplement* 5: 1-140.
- Holsinger, J. R. 1964. The biology of Virginia caves. In: H. H. Douglas, ed., *Caves of Virginia*, Virginia Region of the National Speleological Society, Virginia Cave Survey, Falls Church, Virginia. Pp. 57-74.
- Holsinger, J. R. and D. C. Culver. 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: Zoogeography and ecology. *Brimleyana* 14: 1-162.
- Hubricht, L. 1957. New species of *Fontigens* from Shenandoah National Park. *Nautilus* 71: 9-10.
- Hubricht, L. 1976. The genus *Fontigens* from Appalachian caves (Hydrobiidae: Mesogastropoda). *Nautilus* 90: 86-88.
- INHS 2003. The Illinois Natural History Survey Mollusk Collection. Available at: <http://www.inhs.uiuc.edu/cbd/collections/mollusk.html> February 2004.
- Jokinen, E. H. 1982. *Cipangopaludina chinensis* (Gastropoda: Viviparidae) in North America, review and update. *Nautilus* 96: 89-95.
- Jokinen, E. H. 1983. *The Freshwater Snails of Connecticut*. State Geological and Natural History Survey of Connecticut, Department of Environmental Protection Bulletin 109, Hartford, Connecticut.
- Kabat, A. R. and R. Hershler. 1993. The prosobranch snail family Hydrobiidae (Gastropoda: Rissooidea): A review of classification of supraspecific taxa. *Smithsonian Contributions to Zoology* 547: 1-94.
- Lutz, L. 1951. Variation in *Io*, fifty years later. *Proceedings of the Oklahoma Academy of Science* 32: 11-13.
- Marshall, W. B. 1933. *Bulimus tentaculatus* (L.) (*Bithynia tentaculata*) living in the Potomac River. *Nautilus* 47: 141-142.
- Martin, S. M. 1999. Freshwater snails (Mollusca: Gastropoda) of Maine. *Northeastern Naturalist* 6: 39-88.
- McLeod, M. J. and J. D. Moore. 1978. Change in the gastropod *Io spinosa* (Pleuroceridae; Mollusca) in 70 years. *American Midland Naturalist* 99: 198-205.
- Miller, C. 1985. Correlates of habitat favourability for benthic macroinvertebrates at five stream sites in an Appalachian Mountain drainage basin, U.S.A. *Freshwater Biology* 15: 709-733.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19: 1-54.
- Neves, R. J. 1991. Mollusks. In: K. Terwilliger, ed. *Virginia's Endangered Species, Proceedings of a Symposium*, The McDonald and Woodward Publishing Company, Blacksburg, Virginia. Pp. 251-263.
- Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of the aquatic mollusks in the southeastern United States: A downward spiral of diversity. In: G. W. Benz and D. E. Collins, eds., *Aquatic Fauna in Peril*, Southeast Aquatic Research Institute Special Publication 1, Lenz Design and Communications, Decatur, Georgia. Pp. 43-85.
- Palmer, S. 1985. Some extinct molluscs of the U.S.A. *Atala* 13: 1-7.
- Pilsbry, H. A. 1894. Critical list of mollusks collected in the Potomac Valley. *Proceedings of the Academy of Natural Sciences of Philadelphia* 46: 11-31.
- Pilsbry, H. A. 1932. *Bithynia tentaculata* in the Potomac. *Nautilus* 46: 69.
- Pilsbry, H. A. 1952. *Littoridinops tenuipes*. *Nautilus* 66: 50-54.
- Reed-Judkins, D. K., J. L. Farris, D. S. Cherry, and J. Cairns, Jr.

1998. Foodborne uptake and sublethal effects of copper and zinc to freshwater snails. *Hydrobiologia* **364**: 105-118.
- Rehder, H. A. 1949. Some land and freshwater mollusks from the coastal region of Virginia and North and South Carolina. *Nautilus* **62**: 121-126.
- Richardson, C. L., R. Robertson, G. M. Davis, and E. E. Spamer. 1991. Catalog of the types of neontological Mollusca of the Academy of Natural Sciences of Philadelphia. 6: Gastropoda. Mesogastropoda: Viviparacea, Valvatacea, Littorinacea, Rissoacea (Pt. 1: Adeorbidae, Amnicolidae, Anabathridae, Assimineidae, Barleidae, Bithyniidae, Caecidae, Cingulopsidae, Elachisinidae, Falsicingulidae). *Tryonia* **23**: 1-243.
- Roble, S. M. 2001. *Natural Heritage Resources of Virginia: Rare Animal Species*. Natural Heritage Technical Report 01-16, Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Say, T. 1817. Descriptions of new species of land and fresh water shells. *Journal of the Academy of Natural Sciences of Philadelphia* **1**: 123-126.
- Say, T. 1825. Descriptions of some new species of fresh water and land shells of the United States. *Journal of the Academy of the Natural Sciences of Philadelphia* **5**: 119-131.
- Stansbery, D. H. 1972. The mollusk fauna of the North Fork Holston River at Saltville, Virginia. *Bulletin of the American Malacological Union* **1971**: 45-46.
- Stansbery, D. H. and W. J. Clench. 1974a. The Pleuroceridae and Unionidae of the North Fork Holston River above Saltville, Virginia. *Bulletin of the American Malacological Union* **1974**: 33-36.
- Stansbery, D. H. and W. J. Clench. 1974b. The Pleuroceridae and Unionidae of the Middle Fork Holston River in Virginia. *Bulletin of the American Malacological Union* **1974**: 51-54.
- Stansbery, D. H. and W. J. Clench. 1977. The Pleuroceridae and Unionidae of the upper South Fork Holston River in Virginia. *Bulletin of the American Malacological Union* **1977**: 75-79.
- Stansbery, D. H., and C. B. Stein. 1976. Changes in the distribution of *Io fluviatilis* (Say, 1825) in the upper Tennessee River system (Mollusca, Gastropoda, Pleuroceridae). *Bulletin of the American Malacological Union* **1976**: 28-33.
- Stewart, T. W. and J. E. Garcia. 2002. Environmental factors causing local variation in densities and biomass of the snail *Lep toxis carinata*, in Fishpond Creek, Virginia. *American Midland Naturalist* **148**: 172-180.
- Strayer, D. 1987. Ecology and zoogeography of the freshwater mollusks of the Hudson River basin. *Malacological Review* **20**: 1-68.
- Thompson, F. G. 1977. The hydrobiid snail genus *Marstonia*. *Bulletin of the Florida State Museum, Biological Sciences* **21**: 113-158.
- Thompson, F. G. 1984. North American snail genera of the hydrobiid subfamily Lithoglyphinae. *Malacologia* **25**: 109-141.
- Tryon, G. W. 1865. Catalogue of the species of *Lymnaea* inhabiting the United States. *American Journal of Conchology* **1**: 247-258.
- Tryon, G. W. 1873. Land and fresh-water shells of North America. Part IV. Streptomatidae (American Melanians). *Smithsonian Miscellaneous Collections* **16**: 1-435.
- Turgeon, D. D., J. F. Quinn, A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada*. American Fisheries Society Special Publication 26, Bethesda, Maryland.
- van der Schalie, H. and D. S. Dundee. 1955. The distribution, ecology, and life history of *Pomatiopsis cincinnatiensis* (Lea), an amphibious, operculate snail. *Transactions of the American Microscopical Society* **74**: 119-133.
- van der Schalie, H. and L. L. Getz. 1962. Distribution and natural history of the snail *Pomatiopsis cincinnatiensis* (Lea). *American Midland Naturalist* **68**: 203-231.
- VDFIF 1998. Virginia Fish and Wildlife Information Service. Available at: <http://vafwis.org> February 2002.
- Walker, B. 1904a. New species of *Somatogyrus*. *Nautilus* **17**: 133-142.
- Walker, B. 1904b. Notes on American Ancyli. III. *Nautilus* **18**: 75-83.
- Walker, B. 1909. Notes on *Planorbis* II: *P. bicarinatus*. *Nautilus* **23**: 21-32.
- Walker, B. 1918. A synopsis of the classification of the freshwater 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**: 1-213.
- Wethington, A. R., E. R. Eastman, and R. T. Dillon, Jr. 2000. No premating reproductive isolation among populations of a simultaneous hermaphrodite, the freshwater snail *Physa*. In: P. D. Johnson and R. S. Butler, eds., *Proceedings of the First Freshwater Mollusk Conservation Society Symposium, 1999*, Ohio Biological Survey, Columbus, Ohio. Pp. 245-251.
- Woodward, S. L. and R. L. Hoffman. 1991. The Nature of Virginia. In: K. Terwilliger, ed., *Virginia's Endangered Species, Proceedings of a Symposium*, The McDonald and Woodward Publishing Company, Blacksburg, Virginia. Pp. 23-48.

Accepted: 2 March 2004