FRESHWATER SNAILS (MOLLUSCA: GASTROPODA) OF MAINE

SCOTT M. MARTIN [1]

ABSTRACT - Forty-five freshwater gastropod species have been reported from Maine. The taxonomic status of seven of these mollusks is questionable. These snails represent three prosobranch (Viviparidae, Valvatidae, Hydrobiidae) and four pulmonate (Lymnaeidae, Physidae, Planorbidae, Ancylidae) families. Nine species and varieties have their type localities in Maine. Only one of the state's freshwater gastropods, *Cipangopaludina chinensis malleata*, is an alien species. Thirty-four freshwater snail species have been reported from Aroostook County. *Campeloma decisum* has been found in all 16 of Maine's counties.

The purpose of this paper is to (1) present a species list (Table 1) and distributional analysis (Table 2) of Maine's freshwater snails from widely scattered historical records; (2) highlight features of the biology, ecology, and importance of these animals; (3) describe the history of freshwater gastropod research in Maine, including a discussion of type species (Table 3); (4) introduce the families of Maine's freshwater snails; (5) discuss methods for working with the animals; and (6) suggest topics for future studies. While this paper is largely written for a general readership, specialists should find the collation of historical material to be useful.

INTRODUCTION

> Mud is my delight in fresh or salt water. It is swarming with life. ... Dip and sift dry and examine with a lens; the tiny chaps are easily overlooked. [Winkley (1909)]

It is reputed (Lytle 1948) that a Chicago professor once gave a test of 15 questions to his students with the declaration that they were not truly educated unless they could answer "yes" to each query. Two of the questions were: Can you be high-minded and happy in the meaner drudgeries of life? Can you look into a mud puddle by the wayside and see anything in the puddle but mud? The Rev. Henry W. Winkley (1858-1918) (Fig. 1), an Episcopalian minister and amateur conchologist, no doubt could have aced the test easily. Winkley took delight at perusing Nature in a jar of muddy water or among the aquatic debris enmeshed on his collecting sieve. He readily discerned the minute freshwater snails among his begrimed samples and often collected thousands of them after a few hours of sloshing through some pond or stream.

[1] 712 Harley Drive, Columbus, Ohio 43202

In 1896, Winkley discovered a tiny hydrobiid snail in Goose Fair Brook at Saco (York County), Maine. Specimens were later sent to Henry Augustus Pilsbry, a professional malacologist at the Philadelphia Academy of Natural Sciences, who described the snail as a new species and dubbed it *Amnicola* (now *Cincinnatia*) *winkleyi* (Pilsbry 1912, Winkley 1896) (Tables 1 and 3). While this animal tolerates freshwater, apparently it prefers oligohaline [from the Greek *oligos* (few) and *hals* (salt)] conditions. Thus, it has also been found in the brackish waters of some of Maine's salt marshes (Davis and Mazurkiewicz 1985, Davis et al. 1982). At Old Orchard (also York County), Maine, and at Danvers, Massachusetts, Winkley found a freshwater fingernail clam which was described as *Musculium winkleyi* by Victor Sterki (1909) (this clam has since been synonymized with *Musculium lacustre*). A rare species of marine pyramidellid snail was named *Odostomia winkleyi* in Winkley's honor by Paul Bartsch (1909). Bartsch (1909) named two other pyramidellids after Winkley: *Pyramidella winkleyi* and *Turbonilla winkleyi*. These snails have now been equated with *Sayella fusca* and *Turbonilla interrupta*, respectively, but *O. winkleyi* is still considered to be a valid species.

The first descriptions of freshwater gastropods by a naturalist in the United States were by Thomas Say (1787-1834), the father of American malacology, in his article on conchology in the 1817 edition of William Nicholson's *American Edition of the British Encyclopedia or Dictio-*

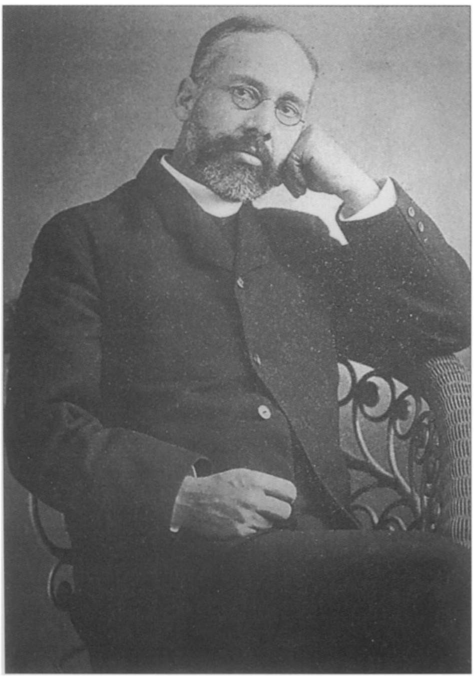


Figure 1. Rev. Henry W. Winkley (1858-1918). This amateur conchologist is immortalized in *Cincinnatia winkleyi*, an aquatic gastropod discovered by him in Maine's York County. [from *Nautilus*, volume 31 (1918)]

Table 1. Freshwater snails reported from Maine.

Scientific Name	Common Name
Subclass Prosobranchia	
Order Mesogastropoda	
Family Viviparidae	
Campeloma decisum (Say, 1817)	Pointed campeloma
* *Campeloma rufum* (Haldeman, 1841)	——
## *Cipangopaludina chinensis malleata* (Reeve, 1863)	Chinese mysterysnail
Family Valvatidae	
Valvata lewisi Currier, 1868	Fringed valvata
Valvata sincera Say, 1824	Mossy valvata
Valvata tricarinata (Say, 1817)	Threeridge valvata
Family Hydrobiidae	
* *Amnicola decisa* Haldeman, 1845	——
Amnicola limosa (Say, 1817)	Mud amnicola
Lyogyrus pupoideus (Gould, 1841)	Pupa duskysnail
** *Cincinnatia winkleyi* (Pilsbry, 1912)	Winkley hydrobiid
Subclass Pulmonata	
Order Basommatophora	
Family Lymnaeidae	
* *Fossaria exigua* (Lea, 1841)	——
Fossaria galbana (Say, 1825)	Boreal fossaria
Fossaria humilis (Say, 1822)	Marsh fossaria
Fossaria modicella (Say, 1825)	Rock fossaria
Fossaria obrussa (Say, 1825)	Golden fossaria
Fossaria parva (Lea, 1841)	Pygmy fossaria
* *Fossaria peninsulae* (Walker, 1908)	——
* *Fossaria rustica* (Lea, 1841)	——
Lymnaea stagnalis Linnaeus, 1758	Swamp lymnaea
Pseudosuccinea columella (Say, 1817)	Mimic lymnaea
Stagnicola caperata (Say, 1829)	Wrinkled marshsnail
Stagnicola catascopium (Say, 1817)	Woodland pondsnail
Stagnicola elodes (Say, 1821)	Marsh pondsnail
Stagnicola emarginata (Say, 1821)	St. Lawrence pondsnail
Stagnicola mighelsi (Binney, 1865)	Bigmouth pondsnail
Stagnicola oronoensis (Baker, 1904)	Obese pondsnail
Family Physidae	
Aplexa elongata (Say, 1821)	Lance aplexa
Physella ancillaria (Say, 1825)	Pumpkin physa
Physella gyrina (Say, 1821)	Tadpole physa
Physella heterostropha (Say, 1817)	Pewter physa
Physella magnalacustris (Walker, 1901)	Great Lakes physa
Family Planorbidae	
Gyraulus crista (Linnaeus, 1758)	Star gyro
Gyraulus deflectus (Say, 1824)	Flexed gyro
Gyraulus parvus (Say, 1817)	Ash gyro
Helisoma anceps (Menke, 1830)	Two-ridge rams-horn
Micromenetus dilatatus (Gould, 1841)	Bugle sprite
Planorbella campanulata (Say, 1821)	Bellmouth rams-horn
Planorbella trivolvis (Say, 1817)	Marsh rams-horn
Planorbula armigera (Say, 1821)	Thicklip rams-horn
Promenetus exacuous (Say, 1821)	Sharp sprite
Family Ancylidae	
* *Ancylus borealis* Morse, 1864	——
* *Ancylus ovalis* Morse, 1864	——
Ferrissia fragilis (Tryon, 1863)	Fragile ancylid
Ferrissia parallela (Haldeman, 1841)	Oblong ancylid
Ferrissia rivularis (Say, 1817)	Creeping ancylid

The above classification is based on Vaught (1989). Scientific and common names are taken from Turgeon et al. (1998). Maine is the type locality for several of the gastropods (Table 3). * Classification uncertain (Turgeon et al. 1998). ** Oligohaline/freshwater species. ## Exotic species introduced from the Orient. If in a scientific name the author and date are in parentheses, then the author originally described the species in another genus.

nary of Arts and Sciences. Many taxonomic epithets (e.g., *Sayella*) of mollusks and other animals have been named after Say. From 1817 to 1826, Say published 10 articles about freshwater, terrestrial, and marine mollusks in the journal of the Philadelphia Academy of Natural Sciences, of which he was a founding member. Additional descriptions of land and aquatic shells were published in 1829-1831 in *The Disseminator of Useful Knowledge*, a weekly newspaper at New Harmony, Indiana, where Say and others attempted to establish a utopian society which stressed unanimity, education, industry, and ethical conduct (the coterie quickly failed!). Also published at New Harmony was Say's seven-part *American Conchology*, which contained beautiful colored figures of the shells of North America. Say died at New Harmony, and his stately gravestone can still be viewed there.

Another landmark publication on freshwater snails was the eight-part *Monograph of the Freshwater Univalve Mollusca of the United States* (1840-45) by Samuel S. Haldeman (1816-1880). Haldeman was a college professor who served several years as the state geologist of New Jersey. Recognition was paid Haldeman by Charles Darwin in the preface of his *Origin of Species*:

> In 1843-44, Professor Haldeman (Boston Journal of Nat. Hist. U. States, vol. iv, p. 468) has ably given the arguments for and against the hypothesis of the development and modification of species: he seems to lean towards the side of change.

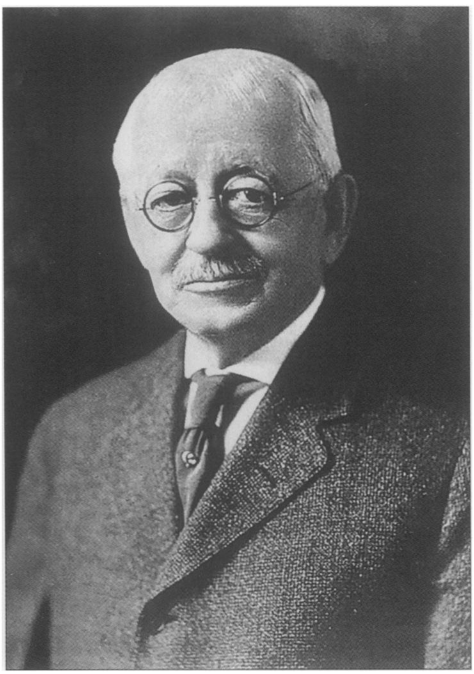


Figure 2. Bryant Walker (1856-1936). This Detroit lawyer and amateur malacologist studied the freshwater Mollusca of North America, including specimens from Maine. [from *Nautilus*, volume 50 (1936)]

Additional pioneer works on aquatic snails were published by the Smithsonian Institution. These were *Land and Fresh Water Shells of North America*, Part I (in 1869, by William Greene Binney and Thomas Bland) and Parts II and III (in 1865, by Binney alone). Most of the molluscan figures in these three historic monographs were drawn by native Mainer and naturalist Edward Sylvester Morse. Morse (1870) was among the first to write about freshwater snails for a general readership. More recent popular articles have been contributed by Barr (1988) and McElaney (1997).

Later workers in the field of freshwater snails included Bryant Walker (Fig. 2) and Frank Collins Baker (Fig. 3). Walker (1856-1936) was a Detroit lawyer and amateur malacologist. He believed that as a youth he was the first to observe the advent of the pestiferous house sparrow into eastern Michigan when he killed a specimen with a shotgun in his family's chicken yard. His interest in snails was whetted by a copy of *American Naturalist*, volume 1 (1867-68), which contained a series of articles by Edward S. Morse entitled "The Land Shells of New England." Walker's enthusiasm for mollusks for nearly 70 years would generate 155 publications and proposals of 143 new taxa! His *A Synopsis of the Classification of the Freshwater Mollusca of North America, North of Mexico*, published in two parts in 1918 by the University of Michigan's Museum of Zoology (which would later acquire Walker's extensive collection of land and freshwater shells), listed four freshwa-

Figure 3. Frank Collins Baker (1867-1942). This professional scientist wrote several classic monographs on freshwater snails of North America that included species from Maine. [from *Nautilus*, volume 56 (1943)]

ter gastropods with type localities in Maine. The malacological journal *Walkerana* is named after Walker.

Frank C. Baker (1867-1942) was a professional scientist with interests in malacology, ecology, paleontology, archaeology, and museum administration. His career included curatorships at the Chicago Academy of Sciences (1894-1915) and the Museum of Natural History at the University of Illinois, Urbana (1918-1939). He often remarked that shells were the favorite childhood toys brought to him from distant places by a seafaring grandfather. An advancing deafness in his later years afforded Baker an opportunity to "tune out" distractions and immerse himself uninterruptedly in his studies. His pen yielded nearly 400 publications, of which about two-thirds were on the Mollusca. Two of Baker's classic works dealt specifically with the freshwater gastropods. These were *The Lymnæidae of North and Middle America, Recent and Fossil* (published in 1911 by the Chicago Academy of Sciences) and *The Molluscan Family Planorbidae* (published posthumously in 1945 by the University of Illinois Press). The former book described 11 lymnaeids from Maine, while the latter depicted 3 planorbids from the state. At the 1941 convention of the American Malacological Union held in Rockland/Thomaston, Maine, Baker was elected incoming president of the organization, but he died before completing his tenure.

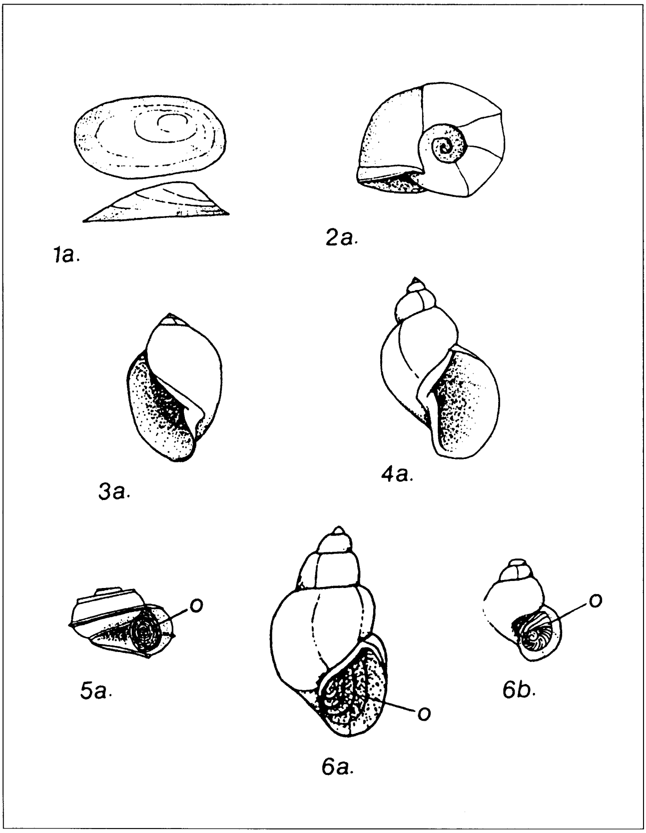
BIOLOGY OF FRESHWATER SNAILS (GASTROPODA)

Classification

Freshwater snails belong to the molluscan class Gastropoda. The term is etymologically derived from the Greek *gaster* ("belly") and *podos* ("foot"). Thus, gastropods are the "belly-footed" animals, i.e., having a ventral muscular surface adapted for creeping. In their usual habitats, freshwater gastropods can be seen crawling on the bottom substrate, along the stems of aquatic macrophytes or among debris, and even ventral side up just beneath the water's surface.

Freshwater gastropods are extremely easy to assign to families (Fig. 4) but can be notoriously difficult to classify to species, even for the specialist. Taxonomic identifications are complicated by the small size of some snails (e.g., Valvatidae, Hydrobiidae) and by subtle morphological differences among species that are confounded by genetic and environmental variation. Indeed, the same freshwater snail may vary morphologically from one riffle to another! This natural variation has led to a proliferation of varietal names for the same mollusk, especially for *Helisoma anceps* (Burch 1989). Environmental variables that affect phenotypic plasticity in freshwater snails include food supply, population density, water temperature, dissolved oxygen, calcium concentration, and current velocity (Brown and Richardson 1992). Variable gastropod shell morphology has been studied in such diverse species as *Stagnicola elodes* (Hunter 1975),

Figure 4. Illustrations and key to living shells of Maine's freshwater snail families.



1a. Shell cone-shaped .... Ancylidae
1b. Shell whorled 2

2a. Whorls in one plane .... Planorbidae
2b. Whorls in more than one plane.. 3

3a. Whorls sinistral (see text) .... Physidae
3b. Whorls dextral (see text) 4

4a. No operculum (see Fig. 5) .... Lymnaeidae
4b. With operculum (see Fig. 5) ....,........................ 5

5a. Spire (see Fig. 5) only slightly elevated .... Valvatidae
5b. Spire (see Fig. 5) moderately to greatly elevated 6

6a. Adults ≥ 15 mm high ....,...... Viviparidae
6b. Adults ≤ 15 mm high .... Hydrobiidae

Key and figures adapted from Harman and Berg (1971). o, operculum.

Physella spp. (Burnside and McMahon 1997, True 1869), and *Ferrissia rivularis* (Nickerson 1972, Russell-Hunter et al. 1970). Burnside and McMahon (1997) reported that shell morphology in *Physella* is so highly ecophenotypic that the number of North American species in this genus can probably be reduced. For certain freshwater snails (e.g., Hydrobiidae, Physidae), meticulous dissections of soft parts are necessary to confirm identifications. Thus, an aquatic snail cannot always be identified solely from an empty shell.

Eight families of freshwater gastropods have been reported from New England (Strayer 1990) but only seven from Maine (Table 1, Fig. 4). The family Pleuroceridae does not occur in the state (Clench 1929). The only pleurocerid reported from New England, exclusive of Lake Champlain, is *Goniobasis virginica* in Connecticut and Massachusetts (Anonymous 1892, Strayer 1990, Winkley 1901). Smith (1995) related that this species has not been seen in Massachusetts in recent years, but it still occurs in northern Connecticut (Jokinen, personal communication; Smith 1980).

Three of Maine's freshwater snail families belong to the subclass Prosobranchia, while the remaining four are in the subclass Pulmonata (Vaught 1989) (Table 1). Distinctive features of the calciferous shells of Maine's prosobranch and pulmonate snails are shown in Fig. 5 and additionally depicted in Jokinen (1983).

A different taxonomy, based on cladistics, i.e., a method of classification which attempts to reconstruct phylogeny in terms of branching sequences of ancestor-descendant lineages, places Maine's non-pulmonates in the subclass Streptoneura, with the viviparids in the order Archaeogastropoda and the valvatids and hydrobiids in the order Apogastropoda (Haszprunar 1988, Salvini-Plawen and Haszprunar 1987). Turgeon et al. (1998) present yet another classification scheme.

One evolutionary scenario is that the freshwater prosobranchs are derived from marine species, whereas aquatic pulmonates are descended from land snails that have returned to the water (Barr 1988, Calow 1978, McMahon 1983, Russell-Hunter 1952, Strayer 1990).

Burch (1960) determined the chromosome numbers of numerous pulmonate snails, including 21 species known from Maine. The diploid number for most of the snails was 36, except that it was 60 for the limpet *Ferrissia parallela*. Since most terrestrial pulmonates belong to the order Stylommatophora and have diploid numbers >36, it is difficult to visualize these animals as being ancestral to aquatic pulmonates, since this transition would have involved a chromosome gain with land specialization followed by a subsequent loss in chromosomes with adaptation to freshwater (Burch 1960).

The taxonomy and pylogeny of the lymnaeid pulmonates (Table 1) are especially problematical (Bargues and Mas-Coma 1997, Remigio and Blair 1997a,b; Swiderski 1990). Bargues and Mas-Coma (1997) used the sequences of 18 S ribosomal RNA genes of six lymnaeids to differentiate them into four subgenera: *Radix*, *Galba*, *Leptolimnaea*, and *Lymnaea*. They placed *Lymnaea stagnalis* in the subgenus *Lymnaea*. The DNA sequence of the nuclear ribosomal internal transcribed spacer (ITS) region showed that *Stagnicola caperata* of the subgenus *Hinkleyia* could be easily distinguished from three species of stagnicoline snails in the subgenus *Stagnicola*: *Stagnicola catascopium*, *Stagnicola elodes*, and *Stagnicola emarginata* (Remigia and Blair 1997a). The similarity of the ITS sequences of the latter three snails suggested that they may not be separate species. Sequences of the mitochondrial large subunit ribosomal RNA gene also demonstrated the close similarity among these three taxa (Remigia and Blair 1997b). Additional molecular genetic studies may someday prompt systematists to synonymize several of the aquatic gastropod species reported from Maine.

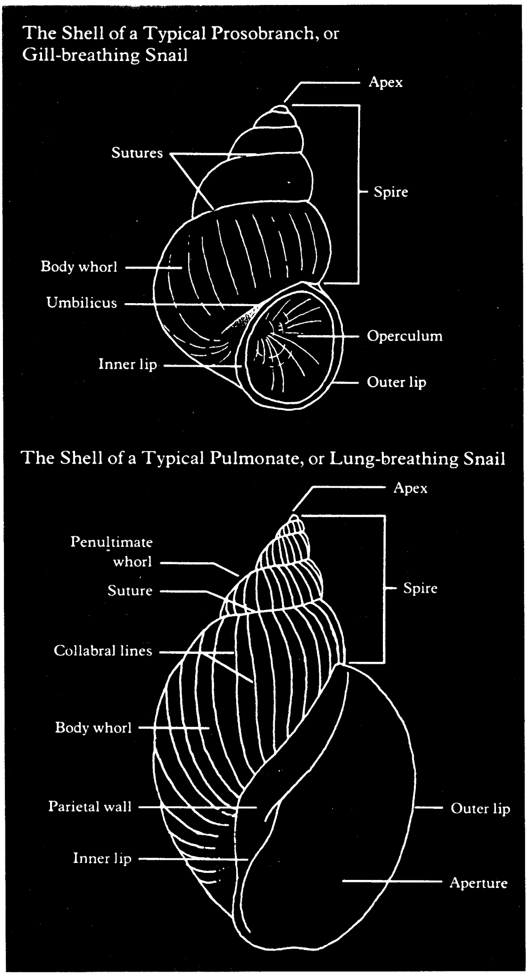


Figure 5. Freshwater gastropod shell morphologies. From Clarke (1981). Reprinted with permission of Canadian Museum of Nature, Ottawa, Ontario.

Prosobranchs

In traditional taxonomy, Maine's prosobranchs belong to the order Mesogastropoda (Vaught 1989). The Greek *mesos* means "middle." Thus, of the three orders of Prosobranchia (Archaegastropoda, Mesogastropoda, and Neogastropoda), the Mesogastropoda is the "middle" one. Snails in this order have traits that are neither the most primitive nor the most advanced in terms of phylogeny (Boss 1982, Hyman 1967). This distinguishes them from the archaegastropods (Greek *archaios* = "ancient") and the neogastropods (Greek *neos* = "new"). Prosobranchia is derived from the Greek *pros* ("forward") and *branchia* ("gills"). The name denotes that the gills of these animals are "forward" in the body; i.e., in the mantle cavity in front of the heart (Brown 1991, Burch and Jung 1992). Prosobranchs are gill-breathing snails whose dependence on dissolved oxygen for respiration makes them intolerant of polluted waters (Harman 1974, Strayer 1990). Prosobranchs are rarely found in stagnant water bodies, such as roadside ditches and shallow ponds, where oxygen levels are low at night or when temperatures are high (Jokinen 1983). These snails are most common in fast-flowing streams and lake littoral zones, where they rarely experience hypoxia (Brown 1991).

All prosobranchs possess an operculum, a corneous or calcareous plate borne on the dorsal surface of the foot (Figs. 4-6). The operculum closes the aperture when the snail withdraws into its shell. Many operculated snails can seal up in dried substrata until aqueous conditions are restored (Solem 1974). The opercular morphology of Maine's prosobranchs is multispiral, concentric, or paucispiral (Walter and Burch 1957) (Fig. 6). Sometimes a paucispiral operculum has a multispiral center (Pennak 1989). Other morphological features of the Prosobranchia are shown in Fig. 7.

Pulmonates

Maine's four families of pulmonate snails are in the order Basommatophora. This term is derived from the Greek *basis* ("base"),

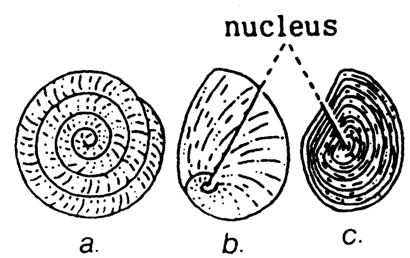


Figure 6. Operculum morphology of Maine's freshwater prosobranchs. a. multispiral; b. paucispiral; c. concentric. Sketches from Burch (1962).

ommatos ("eye"), and *phoros* ("bearing"). These mollusks bear their eyes at the base of a single pair of noninvaginable tentacles (Fig. 8A). All pulmonates lack an operculum (Fig. 5). Other distinctive pulmonate features are shown in Fig. 8. Pulmonata is etymologically derived from the Latin *pulmo*, meaning "lung." Pulmonates have a single vascular "lung" and obtain oxygen directly from the air (Cheatum 1934, McMahon 1983, Russell-Hunter 1978). Having the flexibility to breathe air frees these snails from a dependence on dissolved oxygen, enabling pulmonates to tolerate more polluted waters than prosobranchs

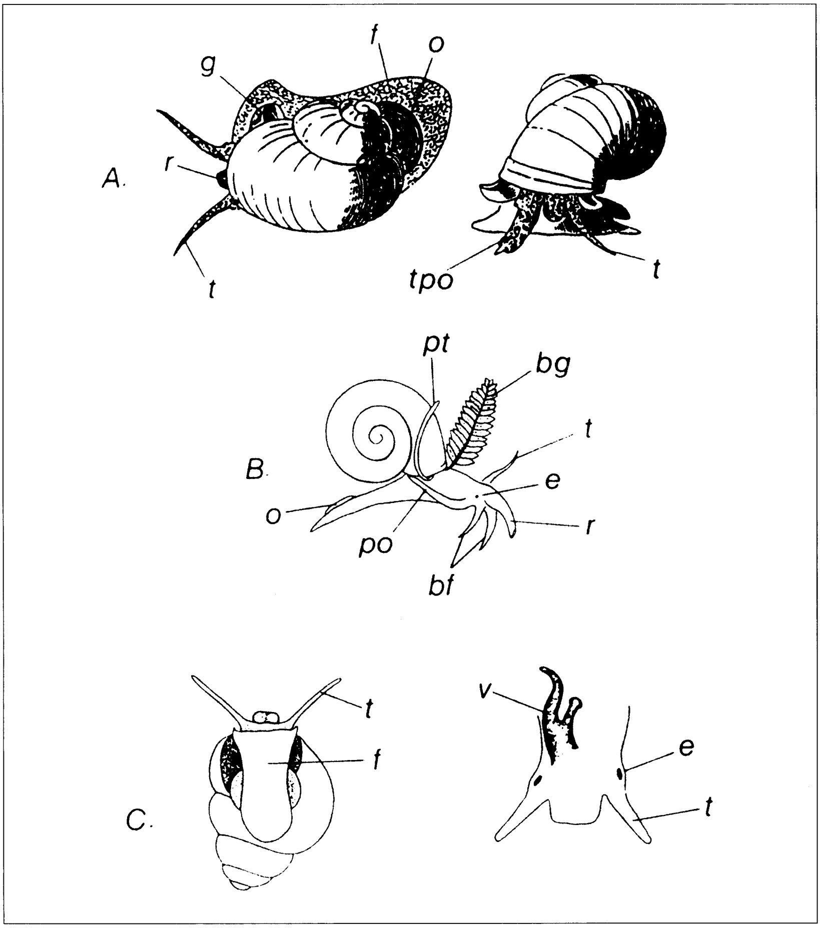


Figure 7. Representative Prosobranchia, showing selected soft parts of active animals. A. Viviparidae. B. Valvatidae. C. Hydrobiidae. Sketches adapted from Baker (1928), Binney (1865b), and Morse (1870). bf, bilobed foot; bg, bipectinate gill; e, eye; f, foot; g, gill cavity entrance; o, operculum; pt, pallial tentacle; po, penile organ; r, rostrum; t, tentacle; tpo, tentacle modified as penile organ; v, verge.

(Clarke 1981, Strayer 1990). Air breathing generally necessitates coming to the water's surface to breathe, but some pulmonates pick up air bubbles underwater, thus precluding their ascension to the surface (Baker 1911, Cheatum 1934). In some lymnaeids, the highly vascularized lung can be filled with water and used as a gill (Pennak 1989, Strayer 1990). Other pulmonates possess "secondary gills" that enable them to stay submerged indefinitely (Pennak 1989, Strayer 1990). Maine's freshwater limpets (Table 1) have a vestigial lung; they obtain oxygen through the skin and by means of an accessory gill called the pseudobranch (Fig. 8) (McMahon 1983, Pennak 1989, Russell-Hunter

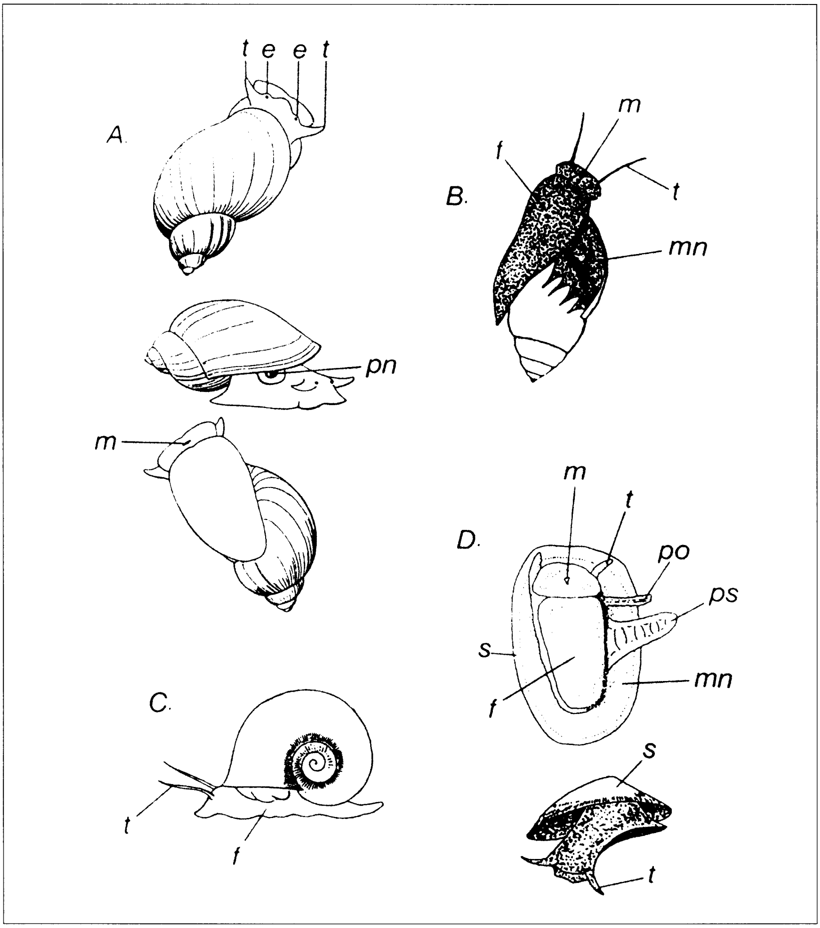


Figure 8. Representative Pulmonata, showing selected soft parts of active animals. A. Lymnaeidae. B. Physidae. C. Planorbidae. D. Ancylidae. Sketches adapted from Baker (1902, 1928), Basch (1963), Binney (1865a), and Morse (1887). e, eye; f, foot; m, mouth; mn, mantle; pn, pneumostome (breathing orifice); po, penile organ; ps, pseudobranch; s, shell; t, tentacle;

1978). Respiration in limpets has been studied in some detail by Berg (1951, 1952).

Keys and General References

An invaluable reference on the systematics of freshwater snails is that by Burch (1989). This book provides detailed keys and is a comprehensive source for synonymies and descriptions of apparent subspecies. It is an invaluable sourcebook for the specialist or serious amateur. Other keys to freshwater gastropods can be found in Burch and Jung (1992), Emerson et al. (1976), Harman and Berg (1971), Jokinen (1983, 1992), Mackie et al. (1980), and Strayer (1990). None of these keys covers all of the species reported from Maine (Table 1), however. A key specifically for prosobranch species can be found in Smith (1995). Generic keys only are provided by Burch (1991), Pennak (1989), and Walter and Burch (1957). The simplified picture key by Walter and Burch (1957) covers most of the genera known from Maine and is especially useful because it depicts natural sizes of the snails.

Individual discussions about many, but not all, of the species in Table 1 are given in Burch and Jung (1992), Clarke (1981), Emerson et al. (1976), Jokinen (1983, 1992), Morris (1939), and Wu et al. (1997).

The biology of freshwater gastropods is discussed at length by Brown (1991, Burch (1989), Janus (1982), and Pennak (1989)). Treatises specifically about pulmonate snails are provided by Fretter and Peake (1975), Geraerts and Joosse (1984), and Hubendick (1978). Scanning electron micrographs of the radular teeth (used for rasping food) of selected Planorbidae were taken by Burch and Jeong (1984), including those for two of Maine's snails, *Helisoma anceps* and *Planorbella trivolvis*.

Morphology

Members of six of the freshwater gastropod families shown in Figure 4 have a spiral shell. In four of these familes, the shell whorls are dextral. If one holds the shell's apex upward, the opening, called the aperture, will be on the righthand side (Latin *dexter* = "right") (Fig. 4). In the Physidae, the whorls are sinistral. If a physid shell is held with the apex up, the aperture opens on the lefthand side (Latin *sinister* = "left") (Fig. 4). Occasionally, a dextral snail will produce a sinistral shell (or vice versa), but such variants are rare, possibly because the reversed condition is unfavorable for maturation (Pilsbry 1897). Nylander (1900a) related that he removed four sinistral young from a normal dextral female *Campeloma decisum* that he had collected in Maine's Portage Lake (Aroostook County). In the Planorbidae, the whorls are so depressed that the animals have a discoidal shell (Fig. 4). In the Ancylidae (the limpets), the shell is in the form of a very low cone (Fig. 4).

Reproduction and Genetics

Maine's prosobranch snails differ greatly in their reproductive strategies (Aldridge 1983). The viviparids and hydrobiids are dioecious (i.e., having separate sexes) (Brown 1991). The viviparids are ovoviviparous; i.e., the young hatch from eggs, partially develop in the mantle cavity of the female, and thus are "born alive" (Pennak 1989, Strayer 1990). Maine's freshwater hydrobiids (Table 1) lay eggs (oviparous) that are attached to hard substrates (Berry 1943, Jokinen 1983, Strayer 1990). The Valvatidae are hermaphroditic (i.e., monoecious, with male and female sex organs in one individual) (Brown 1991, Burch 1989, Burch and Jung 1992, Jokinen 1983, Pennak 1989) and oviparous (Jokinen 1983).

Maine's pulmonate snails are also hermaphroditic and oviparous (Bondesen 1950, Brown 1991, Burch 1989, Burch and Jung 1992, Duncan 1975, Jokinen 1983, Pennak 1989). Bondesen (1950) provided information about the egg capsules of pulmonates, including those of 11 taxa found in Maine. Depending on the species, hermaphroditic snails may (1) cross-fertilize (also called outcrossing) by exchanging sperm with another individual, each animal acting as both male and female during the process; (2) self-fertilize; or (3) exhibit protandry (Geraerts and Joosse 1984, Jarne and Delay 1991, Pennak 1989). In the latter case, the single gonad (ovotestis) produces sperm at one time and eggs at another (but not both, as in cross-fertilization) (Pennak 1989). Cross-fertilization is thought to be the usual means of reproduction in hermaphroditic snails (Pennak 1989, Solem 1974). But some monoecious snails tolerate the inbreeding effected by self-fertilization quite well, producing generation after generation until the investigators grow tired of the experiment (Solem 1974)! Deleteriousness caused by inbreeding is thought to be a major selective force for outcrossing, whereas selfing may be favored in situations of low population density or adaptation to local environmental conditions (Jarne and Delay 1991).

Self-fertilization in *Pseudosuccinea columella* was studied by Colton (1912, 1918, 1922) and Colton and Pennypacker (1934). By isolating newly hatched snails to prevent them from mating, it was possible to maintain for 20 years a viable, highly inbred line of *P. columella* strictly by self-fertilization (Colton and Pennypacker 1934)! Using the same procedure, Colton (1918) demonstrated self-fertilization in *Fossaria modicella*, *Stagnicola catascopium*, *Stagnicola elodes*, *Physella heterostropha*, *Gyraulus parvus*, *Promenetus exacuous*, and *Ferrissia rivularis*. Self-fertilization was additionally studied in *S. elodes* by Crabb (1928) and in *P. heterostropha* by Wethington and Dillon (1997). *Physella heterostropha* also outcrosses (Wethington and Dillon 1997). Paraense and Corrêa (1988) studied selfing in *Planorbella trivolvis*, and Cain (1956) studied both cross- and self-fertilization in *Lymnaea stagnalis*.

Some prosobranchs are long-lived (i.e., having lifespans of 3-5 years), while many pulmonates are short-lived and complete their life cycles in 1 year or less (Comfort 1957, Duncan 1975, Strayer 1990).

Adaptive radiation is defined as the evolutionary divergence of many new taxa from a common ancestor to fill diverse ecological niches. The evolutionary events involve (1) acquisition of new adaptive characters, (2) immigration into unoccupied sites, and (3) speciation in these new areas (Clarke 1969). According to Clarke (1969), the adaptive characters in lymnaeids and planorbids include self-fertilization and the ability to be passively transported, whereas those for viviparids include the dioecious habit and brood protection afforded by ovoviviparity. Calow (1978) has discussed in greater detail the possible scenarios for the evolution of life cycle strategies in freshwater gastropods.

Learning

Aquatic snails exhibit adaptive changes in behavior as a result of individual experiences; i.e., they can "learn" (Carew and Sahley 1986, Willows 1973). The freshwater snails most commonly used in learning studies have been *Physella* spp. (Thompson 1917, Wells and Buckley 1972, Wells and Wells 1971) and *Lymnaea stagnalis* (Alexander et al. 1984, Cook 1971, Kemenes and Benjamin 1989, Whelan and McCrohan 1996). Alexander et al. (1984) reported that with sufficient food deprivation, *L. stagnalis* can form an association between a novel non-food chemostimulus (amyl acetate) and food after a single pairing, and that this non-aversive learning persists for at least 19 days. Kemenes and Benjamin (1989) showed that *L. stagnalis* could be rapidly conditioned to produce a feeding reponse to a neutral tactile stimulus (i.e., touching a tentacle) that, during training, had been repeatedly paired with food as a positive reinforcement. They claimed that this conditioned response exhibited many of the same characteristics seen in appetitive learning in vertebrates. Wells and Buckley (1972) became frustrated in their attempts to teach a physid snail to choose which arm of a Y tube to follow to the water's surface because the animal effectively "cheated" by laying down a "trail" in a previous run that it could follow over and over!

ECOLOGY OF FRESHWATER SNAILS

The ecology of freshwater snails in general has been discussed by Aldridge (1983), Baker (1901a, 1911, 1945), Boycott (1936), Brown (1991), Harman and Berg (1971), Lodge et al. (1987), Mozley (1954), and Pennak (1989). The ecology of freshwater pulmonates is covered by Cheatum (1934), McMahon (1983), and Russell-Hunter (1978). Basch (1963) discussed the ecology of freshwater limpets.

The ecology of aquatic gastropods in southern New England and

New York has been studied by Jokinen (1983, 1987, 1991, 1992), and her work should be consulted by anyone contemplating such studies in Maine, which possesses a similar molluscan fauna.

Factors which govern the distribution, abundance, and reproductive success of freshwater snails include pH, water temperature, calcium concentration (for making calciferous shells), food availability, substrate type, interspecific competition, predation, and environmental disturbance (Bendell and McNicol 1993; Brown 1979, 1997; Jokinen 1987, Kershner and Lodge 1990; Lassen 1975; Lodge et al. 1977; Økland 1983; Servos et al. 1985; Young 1975). Stewart and Haynes (1994) reported that as zebra and quagga mussels (*Dreissena* spp.) colonized natural cobble and artificial reef substrates in southwestern Lake Ontario, they enhanced population increases of other invertebrates, including five of the freshwater snails also found in Maine. They hypothesized that the mussel colonies provided additional habitat for other invertebrate taxa and facilitated energy transfer to the benthos via pseudofecal/fecal deposition. On the other hand, Wisenden and Bailey (1995) observed that as zebra mussels colonized rocks in Lake St. Clair, they excluded several other invertebrates, including physid snails.

Feeding

Snails function primarily in freshwater habitats as herbivores (including the consumption of algae) and detritivores (Aldridge 1983; Baker 1911, 1945; Barnese et al. 1990; Bovbjerg 1968, 1975; Boycott 1936; Brönmark 1989; Brown 1982, 1991; Doremus and Harman 1977; Kehde and Wilhm 1972; Lodge 1985, 1986; Osenberg 1989; Pennak 1989; Smith 1989; Strayer 1990; Weber and Lodge 1990). Smith (1989) tediously examined the stomach contents of *Planorbella trivolvis* from five field sites in New York state. He identified to genus 10,00 diatoms, representing 88 species from 9 families, that had been consumed by this snail species! Brown (1982) observed that the high overlap in habitat and dietary preference of *Stagnicola elodes* and *Physella gyrina* resulted in competition that decreased the fecundity of *P. gyrina*. Lodge (1985, 1986) determined that the choice of freshwater snails for certain aquatic plants was related to the snails' predilection for the periphyton (i.e., attached food, principally algae) and detritus associated with these macrophytes. In laboratory and field tests, Weber and Lodge (1990) demonstrated the preference of aquatic snails for periphyton-covered rocks if the risk of their being preyed upon were low.

Predators and Parasites

Important predators of freshwater snails include fishes, aquatic birds, crayfishes, leeches, beetle larvae, water bugs, and dragonfly nymphs (Alexander and Covich 1991; Baker 1928; Brönmark 1989, 1992; Brown 1991; Brown and DeVries 1985; Brown and Strouse 1988;

Chilton and Margraf 1990; Covich et al. 1994; Crowl 1990; Eyerdam 1968; French and Morgan 1995; Hanson et al. 1990; Kesler and Munns 1989; Klosiewski 1991; Lodge et al. 1987; Michelson 1957; Moser and Willis 1994; Olsen et al. 1991; Osenberg and Mittelbach 1989; Pennak 1989; Strayer 1990; Turner 1996; Weber and Lodge 1990; Young and Procter 1986). Larvae of the fly family Sciomyzidae prey on freshwater gastropods to such an extent that they are called "snail killers" (Berg 1953, Berg and Knutson 1978, Foote 1959, Knutson and Berg 1964). When Covich et al. (1994) exposed aquatic snails to extreme crayfish predation, *Campeloma decisum* responded by burying itself in the sand, whereas *Stagnicola emarginata* and *Physella gyrinia* simply crawled out of the water, especially when they were young; as shell size and strength increased with age, the latter two snails engaged less in this evasive behavior. Several possibilities for the coevolution of freshwater gastropods and their predators are discussed by Vermeij and Covich (1978).

Aquatic gastropods serve as intermediate hosts to many species of larval digenetic (i.e., having successive sexual and asexual stages) trematode worms whose infectivity can be extremely deleterious to the snails (Baker 1945, Brown 1978, Michelson 1957). The prevalence of parasites in *Stagnicola emarginata* from three northern Michigan lakes was monitored over a >50 year period (Keas and Blankespoor 1997). This one snail species could be infested by at least 14 taxa of trematodes whose definitive (vertebrate) hosts included turtles, aquatic birds, voles, bats, and the muskrat! In their capacity as intermediate hosts, freshwater snails can spread parasites to even more definitive hosts, including man (see below).

Dispersal

A fascinating aspect of the ecology of freshwater gastropods is their dispersal to new habitats. The multiple means of molluscan dispersal have been reviewed by Jokinen (1983), Kew (1893), Rees (1965), and Russell-Hunter (1978). According to Jokinen (1983), a snail's migratory success depends on (1) local abundance of the species, (2) size of the animal, (3) life history pattern, (4) microhabitat specificity, and (5) reproductive biology.

Presumably, it is possible for a snail species to migrate slowly on its own throughout an entire, connected drainage system provided that it does not encounter unfavorable environmental conditions (Pennak 1989). Floodwaters and normal currents may transport snail eggs or rafting adults to distant locales (Pennak 1989). Snails can be carried on the feathers or in mud on the feet or legs of aquatic birds (Crandall 1901, Malone 1965a, Pennak 1989, Rees 1965). Boag (1986) demonstrated experimentally that juvenile aquatic snails may be attracted to feathers by surface tension and that a substantial fraction of the attached mollusks can survive several minutes of simulated flight. A duck flying for 15 min at

41 km/h was deemed capable of carrying at least three surviving individuals of *Lymnaea stagnalis*, *Stagnicola elodes*, or *Planorbella trivolvis* over a distance of about 10 km (Boag 1986). The upland sandpiper (*Bartramia longicauda*), on its northward migration from the Caribbean, apparently stashes physid snails among its feathers and feeds on them enroute (McAttee 1914, Rees 1965)! Gastropods may also be dispersed via the gastrointestinal tract of birds (Malone 1965b). Limpets may adhere to water beetles and thus "hitch a ride" (Johnson 1904, Rees 1965, Rosewater 1970). *Helisoma anceps* was observed to be transported by a giant water bug (Owen 1962). Hitchhiking on the back of an aquatic turtle is another possible means of travel. The wind-borne dispersal of mollusks has been discussed by Rees (1965). This aerial transport is primarily by hurricanes or tornadoes, the mollusks in a water body actually being sucked into the air and deposited elsewhere.

Several alien freshwater snails have entered the United States by anthropogenic means. *Cipangopaludina chinensis malleata* (Table 1) was brought to this country from Japan as a foodsource for man. Smith (1995) suggested that the animal might also have been passively attached to ornamental lotus plants or even been brought into this country as pets. The snail's odyssey has been traced by Abbott (1950), Clench and Fuller (1965), Emerson et al. (1976), and Jokinen (1982). The mollusk was first noticed in 1892 in San Francisco, where it was being sold at a Chinese food market. In 1914, the snail was discovered in the Muddy River of Boston's Fenway, and in 1925 it was found in Philadelphia's Fairmount Park. By the 1940s, it had reached New York City. By 1965, *C. chinensis malleata* had traversed the country and had also colonized Hawaii.

IMPORTANCE OF FRESHWATER SNAILS

Olof Olsson Nylander (1943a) related the following about *Stagnicola caperata*, an aquatic snail that he collected in Maine's Aroostook County:

> This small shell used to be common along the roads in ditches and in damp springy places in pastures and meadows. ... [It] sometimes crawls out of the water on plant stems and browsing sheep eat the plants and swallow the snails. The snails often are the hosts of different species of trematodes. The common liver fluke, very destructive to sheep, is carried into their systems by eating plants.

The sheep liver fluke (*Fasciola hepatica)* also infests cattle, goats, pigs, horses, rabbits, deer, and occasionally people (Brown 1978, Mozley 1957, Pantelouris 1965, Price 1953). Its association with a lymnaeid snail as intermediate host was first reported in 1881 by the German parasitologist Rudolf Leuckart (Reinhard 1957, Taylor 1937). The life cycle of *F. hepatica* was completely worked out by an Englishman, Algernon Phillips Withiel Thomas (1883). A fluke life stage called the cercaria may leave the snail host, encyst as a metacercaria on aquatic vegetation at the water's edge, and subsequently be ingested by herbivorous mammals. Pantelouris (1965) documented that, because of the presence of potential molluscan hosts, fascioliasis could indeed occur in Maine. In addition to Nylander's *Stagnicola caperata*, lymnaeid snails reported from Maine that can potentially serve as hosts for *F. hepatica* include *Fossaria modicella* (Krull 1933a), *Lymnaea stagnalis* (Brown 1978, Kendall 1949), and *Pseudosuccinea columella* (Batte et al. 1951, Krull 1933b).

Thousands of people die each year, primarily in Africa and Asia, from blood fluke (*Schistosoma* spp.) infestations spread by freshwater pulmonates (Baker 1945, Gonzalez 1989). The Allied invasion of the Phillippines during World War II was stymied until the snail vector of *Schistosoma japonicum*, which fatally infected the troops, was discovered and steps taken to control it (Abbott 1947). Maine's *Stagnicola emarginata* has been studied as a possible biological control for the schistosome snail host *Biomphalaria glabrata*, because the lymnaeid ingests the egg masses of *B. glabrata* (Michelson and Du Bois 1974).

The irritating condition called "swimmer's itch" is a schistosome dermatitis caused by the incomplete penetration into human skin by the cercariae, i.e., the parasitic stages released from infected snails (Fig. 9), of a non-human blood fluke (Blankespoor and Reimink 1991, Hoeffler 1974, Mulvihill and Burnett 1990, Rapp et al. 1972, Wall 1976, Williamson 1969). Swimmer's itch was first studied by W. W. Cort at the University of Michigan's Biological Station at Douglas Lake, Michigan (Blankespoor and Reimik 1991). Cort (1928) demonstrated that water which contained cercariae that had issued from infected *Stagnicola emarginata*, when placed on his own wrist, promoted formation of the pustular lesions of swimmer's itch. Normal hosts for the dermatitis-causing trematodes include ducks, songbirds, mice, voles, the muskrat, and deer (Hoeffler 1974, Rapp et al. 1972, Wall 1976). Swimmer's itch has been reported from Maine (Jarcho and van Burkalow 1952). It also occurs in the Canadian Maritimes (Farley 1967, Scott and Burt 1976) and Rhode Island (Kravitz and Lewis 1977). In New Brunswick, *Stagnicola catascopium* and *Physella gyrina*, two freshwater snails native to Maine, were found to act as intermediate hosts for the causative fluke (Scott and Burt 1976). Four aquatic snails which serve as intermediate hosts for swimmer's itch in the Great Lakes region have also been reported from Maine. In addition to *S. emarginata*, these are *Lymnaea stagnalis*, *Stagnicola elodes*, and *P. gyrina* (Cort 1928, Hoeffler 1974, Wall 1976). "Clam digger's itch" along the Maine coast is caused by an avian dermatitis-producing schistosome whose intermediate host is the intertidal marine snail *Ilyanassa obsoleta* (Sindermann 1960, Sindermann and Gibbs 1953).

Freshwater gastropods are important as indicators of water pollution (Goodrich 1940, Harman 1974, Jokinen 1983, Wurtz 1955). Lymnaeid and planorbid snails have even been used to monitor the radionuclide pollution associated with the Chernobyl nuclear power plant outburst in the Ukraine (Frantsevich et al. 1996).

Aquatic snails can be used as monitors of water acidification (Bendell and McNicol 1993, Eilers et al. 1984, Økland 1983). Hunter (1990) determined that the periostracum (i.e., the proteinaceous outer layer) protected the shell of *Helisoma anceps* from dissolution by acidic waters, presumably prolonging the life of individuals located in water bodies subjected to gradual acidification. Since aquatic snails are a potentially important source of calcium for breeding waterfowl (Bendell and McNicol 1993) as well as food for fishes, their demise in acidic waters will adversely affect these organisms. Snails are more sensitive to low pH than fishes, so they will disappear before the fishes are extirpated (Økland 1983). A number of Maine's freshwater gastropods fare best when the aquatic pH is 6.5-7.5 (Jokinen 1991).

Aquatic snails have also been used as indicators of trophic lake stages (Clarke 1979, Costil and Clement 1996, Jokinen 1983). Trophic stages are delineated on the basis of nutrient levels (the Greek *trophe* means "nourishment"), with oligotrophic lakes being nutrient poor and eutrophic lakes nutrient rich (and often filled with fast-growing algae as a consequence). Clarke (1979) determined that *Stagnicola catascopium* was primarily found in oligotrophic and mesotrophic lakes, while *Amnicola limosa*, *Lymnaea stagnalis*, and *Planorbula armigera* mainly occurred in eutrophic lakes. Costil and Clement (1996) reported that *Stagnicola elodes* was characteristic of mesotrophic conditions, while *L. stagnalis* occurred in meso-eutrophic conditions.

Perfused neurons of *Lymnaea stagnalis* have been used in studies of nerve function (Byerly and Moody 1984, Byerly et al. 1984). Indeed, this snail has become a favorite subject for neurophysiology experiments (Carew and Sahley 1986).

Freshwater snails have been utilized to study ancient environments (Evans 1969, Sparks 1970). Aquatic gastropods associated with the remains of Pleistocene Epoch mastodons discovered in Randolph County, Indiana, and Berrien County, Michigan, were so similar to modern forms that they could be readily identified to species (Smith 1899, Walker 1898). Nylander (1901a, 1909, 1941, 1943a) delighted in collecting fossils of freshwater snails from marl deposits in Maine's Aroostook County. Again the fossils were little changed from modern snails. In Madison County, Ohio, mastodon remains were unearthed from a grayish clay marl that was overlain with a black muck. The snail shell assemblage in both the gray and black layers suggested that the mastodon had died in a Pleistocene pond or lake that later became swampy (La Rocque 1952). The shelled remains of snails and sphaeriid clams discovered in the Humboldt Deposit in Ross County, Ohio, were indicative of a shallow Pleistocene lake in this region (Reynolds 1959).

EARLY FRESHWATER SNAIL STUDIES IN MAINE

A thorough search of historical records revealed that 45 species of freshwater gastropods, representing three families of prosobranchs and four of pulmonates, have been reported from Maine (Table 1). Illustrations of many of these mollusks are presented in Burch and Jung (1992), Clarke (1981), and Harman and Berg (1971). The provisional county distribution of Maine's freshwater snails is listed in Table 2. These data provide a baseline for future research and likely do not represent an actual distribution of Maine's aquatic snails. In only a few counties (e.g., Aroostook, Cumberland, Knox, Penobscot, and York) have freshwater gastropods been actively collected in the past, since it was here that most of the early conchologists lived or frequented. Seven of the snails have been reported from only one county in Maine (Table 2). Burch (1989) and Burch and Tottenham (1980) reported *Physella magnalacustris* from Maine, but they did not specify a county locale (Table 2). This snail was first described by Bryant Walker (1901) as a variant of *Physella ancillaria*, but a few months later it was treated as a separate species by Crandall (1901). Nine freshwater gastropods have their type localities in Maine (Table 3). Three of these represent questionable subspecies. The taxonomy of freshwater gastropods has changed frequently, making it problematical to search the historical literature for scientific names currently in vogue. Archaic synonyms of the freshwater snails can be found in Burch (1989), Burch and Jung (1992), Johnson (1915), and Lermond (1908).

In Nicholson's *British Encyclopedia*, Thomas Say (1817) first described nine of the freshwater gastropods known from Maine (Table 1), including *Campeloma decisum*, which has been reported from each of the state's 16 counties (Table 2). A few years later, Say described seven other freshwater snails that occur in Maine (Say 1821). Indeed, of the 45 freshwater gastropods reported from Maine, 24 were first described by Say (Table 1). Two, *Lymnaea stagnalis* and *Gyraulus crista*, both of which also occur in Europe, were first described in 1758 by the Swedish systematist Carolus Linnaeus (1707-1778) in the tenth edition of his *Systema Naturae* (Table 1).

In 1837, the earliest printed list of Maine shells appeared in the appendix of the *First Report on the Geology of the State of Maine*, by Charles Thomas Jackson. It contained four freshwater snails, all of which had been described by Say. These species were *Pseudosuccinea columella*, *Physella heterostropha*, *Planorbella campanulata*, and *Planorbella trivolvis*. The shells were identified by Augustus Addison Gould, a physician whose serious malacological avocation culminated in the publication in 1841 of his classic work, *Report on the Invertebrata of Massachusetts* (the second, enlarged edition was published posthumously in 1870 and contained the artwork of Edward S. Morse). Jackson, also a physician by training (he did pioneering work in anesthesiology), served as the state geologist of Maine and New Hampshire from 1837 to 1844.

In 1841, another physician, Jesse Wedgwood Mighels, along with Charles Baker Adams reported two new snails from Maine. These were described as *Lymnœa decollata*, discovered by a Dr. Milliken at Unity Lake (Waldo County), and *Physa fragilis*, discovered by Dr. N. T. True in a mill stream at Monmouth (Kennebec County) (Mighels and Adams 1841, 1842). Samuel Haldeman, in his *Monograph of the Freshwater Univalve Mollusca of the United States* (1840-45), listed seven freshwater snails from Maine. He equated the *L. decollata* of Mighels and Adams (1841, 1842) with *Lymnaea* (now *Stagnicola*) *catascopium*, with which Edward S. Morse fully concurred in his classic 1864 treatise about

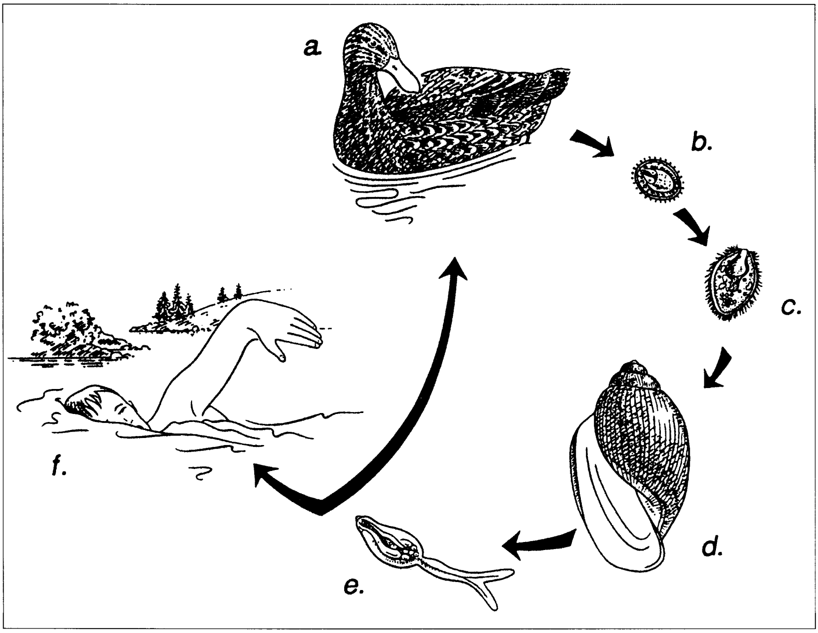


Figure 9. Life cycle of swimmer's itch. Adapted from Blankespoor and Reimink (1991). a. Adult schistosomes usually reside in the mesenteric veins of their host, often an aquatic bird. b. Fully embryonated eggs are released in the feces and hatch in the water to produce miracidia. c. A non-feeding miracidium actively swims in the water until it dies (in about one day) or else penetrates a suitable aquatic snail. d. Inside the snail, the miracidium elongates to form two successive generations of sporocysts. The second generation of sporocysts produces many cercariae daily as long as the snail lives. e. The cercariae are released back into the water. If a cercaria enters a suitable host, e.g., another susceptible bird, it develops into an adult, and the cycle is repeated. f. If the cercaria accidentally enters a person's skin, a pustule forms at the site of entry and may itch intensely for several days before healing.

Maine's non-marine mollusks. Samuel Stillman Berry, who would become prominent as an expert on the cephalopods of the Pacific Ocean, collected freshwater snails at his hometown of Unity, Maine (Berry 1910). He found *S. catascopium* in Unity Lake where Dr. Milliken had collected it for Mighels and Adams (1841, 1842) nearly 70 years before. Morse (1864) later synonymized the *P. fragilis* of Mighels and and Adams (1841, 1842) with *Physa* (now *Physella*) *ancillaria*. He reasoned thusly:

> *Physa fragilis*...was found in a mill stream charged with wood dust from a neighboring saw mill. In the waters above the mill, *P. ancillaria* occurred in abundance, with no trace of *P. fragilis*. This mill was afterward destroyed, and nearly synchronous with this event was the entire obliteration of *P. fragilis* and the recurrence of the normal form *P. ancillaria*; nothing approaching this abnormal form has elsewhere been observed in the state.

Apparently, the snail described by Mighels and Adams (1841, 1842) represented a distortion effected by water pollution (True 1869). Rev. Edwin Cortland Bolles, a friend of Morse, collected at Cape Elizabeth (Cumberland County) specimens of a distorted *Physella heterostropha* which had an enlarged whorl near the aperture (Anonymous 1865). Whether this was a genetic anomaly or an environmental variant is not known.

In 1843, Mighels published the first catalog of Maine's marine, freshwater, and terrestrial shells. It listed 20 freshwater gastropods. In 1854, Rev. John White Chickering, Jr., privately printed a list of marine, freshwater, and land shells of the Portland (Cumberland County) area. It contained 17 freshwater snails. More complete catalogs of Maine's mollusks, including freshwater gastropods, were produced by Edward S. Morse (1864), Norman Wallace Lermond (1908), and Charles Willison Johnson (1915). Although outdated, these three catalogs are still useful to malacologists today because of the meticulous detail which they provide.

FRESHWATER SNAILS WITH TYPE LOCALITIES IN MAINE

In 1821, Say described *Lymneus emarginatus* and designated the type locality as "lakes of Maine" (Table 3). This snail had been discovered in the state by Aaron Stone (Say 1821). The type specimen of *L. emarginatus* (now called *Stagnicola emarginata*) became lost, and the name of the lakes was not provided by Say (Nylander 1921). Nearly 75 years later, Olof O. Nylander, a tireless amateur naturalist from Aroostook County, sampled many of Maine's northern lakes, from Moosehead Lake (Piscataquis County) northward even to Lake Temiscouata in Quebec. Only one locale had specimens of *S. emarginata* that seemed to compare with Say's description. This was Mud Lake, located between Cross Lake and Long Lake in northeastern Aroostook County, which was visited by Nylander in 1901 (Nylander

Table 2. County Distribution of Maine's Freshwater Snails as Compiled from Historical Records.

	AN	AR	CU	FR	HA	KE	KN	LI	OX	PE	PI	SA	SO	WL	WS	YO
VIVIPARIDAE																
C. decisum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
C. rufum	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
C. c. malleatus	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
VALVATIDAE																
V. lewisi	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-
V. sincera	-	X	-	-	-	-	X	-	-	-	-	-	X	-	-	-
V. tricarinata	X	X	X	-	-	-	X	-	-	X	-	X	-	X	-	-
HYDROBIIDAE																
A. decisa	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
A. limosa	-	X	-	-	-	X	X	X	-	X	X	-	X	X	O	X
A. pupoidea	-	-	X	-	-	X	-	-	-	X	-	-	-	-	-	-
C. winkleyi	-	X	X	-	-	-	-	-	-	-	-	X	-	-	-	X
LYMNAEIDAE																
F. exigua	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. galbana	-	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-
F. humilis	-	X	X	-	-	-	X	-	-	-	-	-	-	-	-	-
F. modicella	-	X	-	-	-	-	X	-	-	-	-	-	-	X	-	-
F. obrussa	-	X	X	-	-	-	X	-	X	X	-	-	-	X	-	X
F. parva	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-
F. peninsulae	-	X	-	-	-	-	X	-	-	-	-	-	-	X	-	-
F. rustica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
L. stagnalis	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. columella	-	-	X	-	-	-	X	-	X	X	-	-	-	-	-	X
S. caperata	X	X	-	-	X	-	X	-	X	X	-	-	-	-	-	X
S. catascopium	-	X	X	-	-	X	X	-	-	X	-	X	-	X	-	-
S. elodes	-	X	X	-	-	X	X	-	-	-	-	-	X	X	-	-
S. emarginata	-	X	X	-	-	-	-	-	-	X	X	-	-	-	-	-
S. mighelsi	-	X	X	-	-	-	-	-	-	-	-	-	X	-	-	-
S. oronoensis	X	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-
PHYSIDAE																
A. elongata	-	X	X	-	-	X	X	-	X	X	-	-	-	X	-	X
P. ancillaria	X	X	X	-	-	X	X	-	X	X	-	-	-	X	-	X
P. gyrina	-	X	-	-	-	X	X	-	-	-	-	-	-	-	-	X
P. heterostropha	X	X	X	X	-	-	X	-	-	X	X	-	-	X	X	X
P. magnalacustris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PLANORBIDAE																
G. crista	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G. deflectus	-	X	-	-	-	-	X	-	X	X	-	-	-	X	-	-
G. parvus	-	X	X	-	-	-	X	-	-	-	-	-	-	X	O	-
H. anceps	-	X	X	-	X	-	X	-	-	X	X	-	X	X	-	-
M. dilatatus	-	-	X	-	-	-	X	-	X	-	-	-	-	-	-	-
P. campanulata	-	X	-	-	O	-	-	-	-	-	-	-	X	X	O	-
P. trivolvis	-	X	X	-	-	-	-	-	X	-	-	-	-	X	O	-
P. armigera	-	-	-	-	X	X	X	X	-	X	-	-	-	X	-	X
P. exacuous	-	X	-	-	-	-	X	-	X	-	-	-	-	X	-	-
ANCYLIDAE																
A. borealis	-	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-
A. ovalis	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-
F. fragilis	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
F. parallela	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
F. rivularis	-	X	X	-	-	-	X	X	-	X	-	-	-	-	-	X

See Table 1 for the complete scientific names. The data marked X were assembled from literature records and from catalogued specimens in Harvard University's Museum of Comparative Zoology. Burch (1989) and Burch and Tottenham (1980) listed *Physella magnalacustris* as occurring in Maine but gave no county locale. Species marked O have been collected by students and staff of the Humboldt Field Research Institute, Steuben, Maine, since 1990. County acronyms are as follows: AN, Androscoggin; AR, Aroostook; CU, Cumberland; FR, Franklin; HA, Hancock; KE, Kennebec; KN, Knox; LI, Lincoln; OX, Oxford; PE, Penobscot; PI, Piscataquis; SA, Sagadahoc; SO, Somerset; WL, Waldo; WS, Washington; YO, York.

1902). Frank C. Baker (1911) examined a large series of specimens from Mud Lake (sent to him by Nylander) and concluded that the true type of *S. emarginata* resided here. Nylander (1921) resolved, "If students of shells will agree with me, let us call this the type locality of Say's *Lymnæus emarginatus*."

In a series of publications, Nylander (1901b, 1902, 1921, 1922, 1936b, 1943b) related the curious saga of *Stagnicola mighelsi* from this same region of Maine. During 1841-42, the civil engineer Alexander Longfellow (brother of the poet Henry Wadsworth Longfellow) was surveying the northeastern boundary of Maine. While in this region, he discovered a large lymnaeid snail, which was very abundant, along with *Physella ancillaria*, at the inlet to Square Lake (called Second Eagle Lake) which connects with Cross Lake. Longfellow collected only four specimens of this large snail and gave them to Jesse W. Mighels, who described the animal as a new species, *Limnea ampla* (Mighels 1843b). For many years, this mollusk was regarded as a subspecies of *Stagnicola emarginata*, but today it is considered to be a separate species, *S. mighelsi* (Tables 1,3). It was William G. Binney (1865a) who proposed naming the snail after Mighels. Mighels' extensive shell collection, including his types of *S. mighelsi*, was eventually sold to the Portland [Maine] Society of Natural History and was lost in the city fire of 1854 which destroyed most of the Society's holdings (Martin 1995).

In June, 1859, Edward S. Morse and his friend John M. Gould attempted to locate the original type locality of *Stagnicola mighelsi*. They believed it to be Mud Lake [this confusion over lake names was finally deciphered by Nylander (1921)]. They made the long journey

Table 3. Freshwater Snails with Type Localities in Maine

Scientific Name	Type Locality	Reference
VALVATIDAE		
Valvata sincera nylanderi	Portage Lake, Aroostook Co.	Dall (1905:122)
HYDROBIIDAE		
Cincinnatia winkleyi	Saco, York Co.	Pilsbry (1912:1)
LYMNAEIDAE		
Stagnicola emarginata	"Lakes of Maine"	Say (1821:170)
Stagnicola mighelsi	Square Lake inlet, Aroostook Co.	Binney (1865a:31)
Stagnicola oronoensis	Orono, Penobscot Co.	Baker (1904:62)
PLANORBIDAE		
Helisoma anceps aroostookensis	Woodland, Aroostook Co.	Pilsbry (1895:115)
Helisoma anceps portagensis	Portage Lake, Aroostook Co.	Baker (1908:45)
ANCYLIDAE		
Ancylus borealis	Patten, Penobscot Co.	Morse (1864:45)
Ancylus ovalis	Bethel, Oxford Co.	Morse (1864:44)

See the bibliographic section entitled "Maine's Freshwater Gastropods" for the complete references.

from Portland, Maine, to Fort Kent (Aroostook County) by stagecoach, thence down the St. John River by boat to Madawaska, and finally traveled by road to Long Lake. Here they hired a boat to take them over to Mud Lake, where they set up camp. That first night was quite chilly and as they were alone and fearful of robbers, the two youthful adventurers (Morse was a few days shy of his twenty-first birthday) spent an unpleasant, sleepless night with revolvers clutched in their hands. The next day, a local Frenchman charitably gave them a catch of trout to eat, and they now felt safe. Morse and Gould spent several days in the region but found only a few empty shells of *S. mighelsi*. Morse (1865) later discovered living specimens of this snail in Seabass Lake (Cumberland County), only 15 miles from Portland and nearly 200 miles from its presumed type locality.

In summer, 1894, Nylander spent several weeks shell collecting in northeastern Maine. He chanced upon the Square Lake inlet, where he found large quantities of both *Stagnicola mighelsi* and *Physella ancillaria*, as had Longfellow in 1842. These snails were identified by Henry A. Pilsbry, to whom Nylander sent specimens. Nylander visited the Square Lake inlet again in 1899 and 1900, making large collections each time, including living specimens which were sent to Frank C. Baker. Baker (1900a) published a meticulous study of this material and of the related *Stagnicola emarginata*. Since on three different occasions Nylander had found *S. mighelsi* and *P. ancillaria* together at the Square Lake inlet, he reasoned that this must have been the original type locality where Longfellow had discovered *S. mighelsi* in 1842 (Nylander 1902, 1921, 1922).

About 1900, a Mr. Cumming built a fishing and hunting camp at the Square Lake inlet. Cumming's wife made a large collection of shells from the inlet. In 1914, Nylander returned to this region. A thorough search of the inlet revealed no living specimens of *Stagnicola mighelsi* (Nylander 1914c). Apparently, the heavy traffic of sportsmen through this area over the years had completely extirpated the colony of snails (Nylander 1936b, 1943b).

Two species of limpets with Maine type localities were first described in the monograph by Morse (1864). These were *Ancylus borealis* and *Ancylus ovalis* (Table 3). In 1854, John M. Gould had found *A. borealis* in the Androscoggin River at Bethel (Oxford County), and in 1859 during his trip to Maine's North Country with Morse, he discovered *A. ovalis* at Patten (Penobscot County). Nylander later collected *A. borealis* in the St. John River at Fort Kent and sent specimens to Morse and to Bryant Walker (Nylander 1900a, 1936a).

Sometime in the late nineteenth century, the amateur naturalist Anson Allen found a new snail in the Penobscot River at Orono (Penobscot County). Twelve specimens were sent to Bryant Walker and one specimen thence to Baker, who subsequently described the animal as *Lymnæa decollata oronoensis* (Baker 1904). Today, the snail has been raised to a species rank as *Stagnicola oronoensis* (Tables 1,3). Allen also found the snail at nearby Pushaw Lake, as did Professor F. H. Steinmitz of the University of Maine in September, 1941 (Nylander 1943b). The next month, Steinmitz also found the snail along the Penobscot River at Orono [a photo in Nylander (1943b) shows Steinmitz collecting *S. oronoensis* at this location]. Nylander (1912) discovered a large colony of *S. oronoensis* near the confluence of Caribou Stream with the Aroostook River and concluded that the snail was growing on the refuse of a nearby potato starch factory. In November, 1941, Nylander (1943b) rediscovered *S. oronoensis* in the Penobscot River at Orono and sent additional specimens to Baker.

Olof O. Nylander compiled extensive lists of the freshwater gastropods that he collected in Maine's Aroostook County (e.g., Nylander 1895, 1900a,b, 1936a). He especially focused on the lymnaeid snails of this region (Nylander 1943b), studying them for over 50 years. Nylander sent thousands of specimens of freshwater gastropods for identification to such malacological luminaries as Henry A. Pilsbry, Arnold Edward Ortmann (of the Carnegie Museum, Pittsburgh), William Healey Dall (of the Smithsonian Institution), Victor Sterki of New Philadelphia, Ohio (a specialist in the Valvatidae and the freshwater sphaeriid clams), as well as to Walker and Baker. Pilsbry (1895) described *Helisoma anceps aroostookensis* (Table 3) from snails which Nylander found in Salmon Brook near his home at Woodland, Maine, while Baker (1908) described *Helisoma anceps portagensis* (Table 3) from specimens which Nylander collected from Aroostook County's Portage Lake.

In summer, 1899, the railroad tycoon Edward Henry Harriman took a vacation cruise to Alaska with his family, which included Harriman's 7-year-old son W. Averell, future governor of New York. Thirty professionals from academia and government were invited along to study the zoology, botany, geology, and glaciology of the territory. This august group included the naturalists John Burroughs and John Muir, as well as the Smithsonian's Alaska expert, William H. Dall. The Harriman Expedition lasted two months, covered 9000 miles, accumulated countless specimens of flora and fauna (including many new genera and species), and generated several volumes of scientific discourse. In volume 13 of the expedition's memoirs, Dall described the land and freshwater mollusks of Alaska. In this same text, he named *Valvata sincera nylanderi* (Table 3) from shells which Nylander had sent to him from Aroostook County and compared it with related shells from Alaska (Dall 1905). Dall (1905) also discussed the subtleties between *Stagnicola emarginata* and *Stagnicola mighelsi*.

MAINE'S FRESHWATER SNAIL FAMILIES

Viviparidae

This family has a worldwide distribution, but in North America the animals are found principally in the eastern United States and Canada (Burch and Jung 1992). Only three viviparids have been reported from Maine (Table 1). While the classification of *Campeloma rufum* is listed as uncertain by Turgeon et al. (1998), other malacologists, e.g., Burch and Jung (1992), equate this snail with *Campeloma decisum*. In only one instance has *C. rufum* been reported from Maine (Table 2). According to Lermond (1908), John Alpheus Allen collected it in South Pond at Buckfield (Oxford County).

The family name means "live-bearing" and is derived from the Latin *vivus* ("alive") and *parere* ("to beget"). The name refers to the ovoviviparous nature of these mollusks. Viviparids are sometimes called "mystery snails." This name may allude to the "mystery" of how a single snail suddenly gives rise to a multitude of tiny juveniles! In male viviparids, the noticeably thickened right tentacle functions as a modified penile organ (Fig. 7). The operculum of Maine's viviparids is concentric (Fig. 6).

Campeloma decisum is noteworthy in that it can reproduce by parthenogenesis (i.e., development from an unfertilized egg). Entire populations of this snail may consist only of females (Chamberlain 1958, van der Schalie 1965). Among 470 specimens of *C. decisum* collected in Kansas and Missouri, there were about two females to every male, as verified by dissection (Branson 1963). A study of genetic variation among northern and southern populations of *C. decisum* suggested a dual origin for parthenogenesis in this snail. Thus, parthenogenesis arose (1) spontaneously and was maintained by the castration of male snails effected by infection with a digenetic trematode, and (2) by hybridization between genetically distinct sexual ancestors (Johnson 1992a,b, 1994; Johnson et al. 1995).

Maine's viviparids are medium- to large-sized snails. *Campeloma decisum* is 20-40 mm high, while the Oriental snail *Cipangopaludina chinensis malleata* may attain a a height of 63 mm (Burch and Jung 1992, Clarke 1981). The latter animal is the only alien freshwater gastropod reported from Maine (Table 1). The generic name is derived from Cipango, a Far Eastern island (probably Japan) described by the adventurer Marco Polo (Emerson et al. 1976).

Valvatidae

Most snails in the Valvatidae belong to the genus *Valvata*. The name comes from the Latin *valvatus*, meaning "having folding doors." Apparently, the name refers to the "valve," or operculum, that can close the rather prominent aperture. Species of this genus occur in North

America, Eurasia, the Near East, and northeastern Africa (Burch and Jung 1992).

Three valvatids have been found in Maine (Table 1). All three have been reported only from Aroostook and Knox counties (Table 2). These snails possess a multispiral operculum (Fig. 6). Valvatids have several distinctive morphological features (Fig. 7). The external male penile organ is located at the base of the right tentacle. Posterior to this structure and also on the right side is a cleaning organ called the pallial tentacle; this structure apparently represents a rudimentary gill. Opposite the pallial tentacle, and on the left side, is the single functional gill that often is extruded from the shell. This gill is said to be bipectinate, because it has comb-like projections on both sides of a central rachis (Latin *pectin* = "comb"). The anterior portion of the ventral foot is bilobed. Maine's valvatids are small snails, about 3-5 mm high and 5-6 mm wide (Burch and Jung 1992, Clarke 1981).

Hydrobiidae

This large family of snails contains freshwater, brackish, and marine species that are distributed worldwide in temperate, subtropical, and tropical regions (Burch and Jung 1992). The family name is derived from the Greek *hydor* ("water") and *bios* ("life").

In Maine, the Hydrobiidae comprises three species of freshwater mollusks (the classification of one is uncertain) and one oligohaline/freshwater snail (*Cincinnatia winkleyi*) (Table 1). Three salt marsh (i.e., marine) hydrobiids have been reported from Maine: *Hydrobia totteni*, *Hydrobia truncata*, and *Spurwinkia salsa* (Davis et al. 1982, Johnson 1915, Lermond 1908). In the marine species, but not the others, the eggs hatch into free-swimming veliger larvae (Davis et al. 1982, Mazurkiewicz 1972). The most ubiquitous hydrobiid in Maine's freshwaters is *Amnicola limosa* (Table 2). The anatomy and systematics of *C. winkleyi* were studied by Davis and Mazurkiewicz (1985), using specimens collected in Maine. A monograph by Berry (1943) about Michigan's Hydrobiidae contains much information applicable to Maine's forms. Depending on the species, the operculum of hydrobiids is either multispiral or paucispiral (Fig. 6).

Adult hydrobiids are diminutive in size (< 5 mm high) (Clarke 1981, Jokinen 1983). The shells of Maine's species are so similar morphologically that careful examination of external male soft parts is necessary to confirm examinations. The male copulatory organ is called the verge, which emerges over the right tentacle (Fig. 7). Morphological features of the verge are species specific (Berry 1943, Smith 1995). Microscopic examination of the verge requires that the snail's body be narcotized in an expanded condition. Live snails in the water from the collection locality can be narcotized by sprinkling a few menthol crystals on the water's surface (Berry 1943, Smith 1995). Tobacco from mentholated cigarettes will also act as a narcotizing agent when scattered on top of the water (Jokinen 1983). Narcotization procedures for freshwater snails are additionally described by Araujo et al. (1995), Pennak (1989), and Thompson (1984).

Lymnaeidae

The lymnaeids occur worldwide, but their greatest diversity is in the northern United States and central Canada (Baker 1911, Burch and Jung 1992). Some lymnaeids live in high mountain lakes, while a few can even tolerate hot springs (Baker 1919). Members of this family are sometimes called pond snails. The familial name is derived from the Greek *limne*, meaning "pond."

Sixteen lymnaeids have been identified from Maine (Table 1). Nylander (1936a, 1943b) found a white-colored *Stagnicola elodes* in Aroostook County which he called var. *albida*. Nylander (1941, 1943a) also discovered shells of *Lymnaea stagnalis* in marl deposits at Houlton, Maine. They were little changed from modern forms. Apparently, the only reference to *L. stagnalis* as actually living in Maine is by Tryon (1865b). *Lymnaea stagnalis* has been a favorite subject for biological studies.

This is a difficult group taxonomically, as shells of both *Fossaria* and *Stagnicola* species exhibit subtle morphological differences. The snails are small, medium, or large in size, depending on the species. Maine's smallest lymnaeids are in the genus *Fossaria*, whose members are ≤ 13 mm high. (Clarke 1981). The largest lymnaeid reported from Maine is *Lymnaea stagnalis*, which can attain a height of 56 mm (Clarke 1981). The tentacles of lymnaeids are characteristically short, flat, and triangular (Fig. 8).

Bourns and Scott (1964) creatively marked living specimens of *Lymnaea stagnalis* with numbered plastic bird bands for recapture during field studies.

Inaba (1969) studied the chromosome complements of 16 species of lymnaeids from 22 localities. All of the four genera of lymnaeids found in Maine (Table 1) contain 18 pairs of chromosomes, suggesting their close phylogenetic affinity (Burch 1960, Inaba 1969). Inaba (1969) speculated that these four genera emerged during the Cenozoic Era. Crabb (1927) attempted to hybridize several species of *Lymnaea*. Each pair copulated, and all the acting females deposited egg masses, but the hatchlings resembled the mother in each instance. Among the speculations rendered was that the foreign sperm had induced parthenogenesis. Burch and Ayers (1973) obtained similar results in breeding experiments with *Stagnicola* spp.

Physidae

The Physidae is another worldwide family, but most of its members are confined to the New World (Burch and Jung 1992). In North

America, the Physidae constitutes the most widespread and abundant group of freshwater gastropods (Burch and Jung 1992). Physids are sometimes called "tadpole snails." Some of these snails are quite resistant to water pollution (Harman 1974). The family name is derived from the Greek *physa*, which means "air bubble." Physids come to the surface for a bubble of air that is carried in the lung as they submerge. Not only does this air bubble serve as a portable supply of oxygen (analogous to a scuba diver with his tank of air!), but it makes the snail more buoyant (McMahon 1983, Russell-Hunter 1978). According to Wells and Buckley (1972), *Physella* spp. lay down "trails" and follow these in successive runs to the water's surface.

Four species of physids have been reported from Maine (Table 1). Because of a highly variable shell structure and general similarity among species, the three *Physella* spp. can be difficult to differentiate. Baker (1902) and Crandall (1901) reported a difference in surface morphology among the shells of *Physella gyrina* and *Physella heterostropha*, and Baker (1901b) noted a difference in the digitations of the mantle between the two species. The mantle is the soft, thin organ which secretes the shell. It can partially be seen outside the shell in living physids (Fig. 8B). Microdissections of the male reproductive system are required to identify with certainty the three species of *Physella* that occur in Maine. The procedures are discussed by Anderson (1996) and Jokinen (1983, 1992).

Maine's *Physella* spp. are of medium size, 18-24 mm high and 16-18 mm wide (Clarke 1981). The state's thinnest physid is *Aplexa elongata*, which grows to 18 mm high and 7.5 mm wide (Clarke 1981). The biology of physids was studied by Dawson (1911). This is still a useful monograph. A systematic study of the Physidae was conducted by Te (1978, 1980).

Augustus A. Gould was quite enamored with the physids:

> It is quite interesting to keep a number of them in a vessel of water and to observe their motions and habits. The manner in which they open their mouths and display their lingual organ, the manner in which they rise to the surface and open the air cavity, into which its structure permits no water to enter, and above all, the beautiful and unaccountable manner in which it glides along, will never fail to excite astonishment. [quoted in Emerson et al. (1976)]

Planorbidae

The Planorbidae also has a worldwide distribution (Baker 1945). These are called the "rams-horn snails." Indeed, the discoidal shells (Figs. 4, 8) of some of these animals bear a striking resemblance to a curled ram's horn. The family name is derived from the Latin *planus* and *orbis* and literally means "flat orb." Typically, planorbid shells are coiled in one plane.

Nine species of planorbids have been reported from Maine (Table 1). These are small- to large-sized snails. The diminutive *Gyraulus crista* is only 3 mm in diameter, whereas *Planorbella trivolvis* may be as wide as 32 mm (Clarke 1981). One of the most easily recognizable freshwater snails in Maine is the planorbid *Planorbella campanulata,* which has a distinctive flared lip. A common planorbid in Maine is *Helisoma anceps* (Table 2).

The spire of many planorbid shells is telescoped down to the level of the body whorl. If one holds a shell of *Helisoma anceps* such that the telescoped spire is up, then the aperture falls to the left, meaning that the shell is sinistral. For the other four genera of Maine's planorbids (*Gyraulus, Micromenetus, Planorbella, and Promenetus)* (Table 1), the shell appears to be dextral. According to Emerson et al. (1976), in these animals the telescoped spire is actually pushed so far down that it comes out on the other side. Thus, the shells are "pseudodextral" or "ultrasinistral." Internally, the soft parts of these animals exhibit a sinistral arrangement, with their respiratory, excretory, and reproductive openings being on the left side.

Planorbid snails may possess a pseudobranch as an accessory breathing organ (Baker 1945, Pennak 1989). This external structure is on the left side and functions as a gill when atmospheric air is unavailable. In planorbids, the respiratory pigment is hemoglobin, whereas it is hemocyanin in other freshwater snails (McMahon 1983). The increased oxygen affinity of hemoglobin over hemocyanin enables planorbids to remain submerged longer and to extend to greater depths than either lymnaeids or physids, as well as to consume oxygen cutaneously during long periods of burrowing in hypoxic bottom sediments (McMahon 1983).

Sometimes planorbids form a mating chain of copulating individuals. In such instances, since each of the hermaphroditic snails has separate male and female orifices, a single animal simultaneously serves as a male for one animal and a female for another (Emerson et al. 1976)!

Ancylidae

Also worldwide in scope (Burch and Jung 1992), this family comprises the freshwater limpets. In the Ancylidae, the shell consists of a thin, low cone which in some species is hooked (Greek *ankylis* = "hook"). The shell exhibits both concentric and radial sculpturing (Burch and LoVerde 1974). The apex of the shell is behind center and on the right side or tilted toward the right (Fig. 4). Basch (1963) prepared a useful monograph on North American limpets. This treatise includes directions for dissecting the animals.

Five freshwater limpets have been reported from Maine (Table 1). These are small gastropods, 5-7.6 mm long (Clarke 1981). Basch (1963) considered the two limpets described by Morse (1864) (Tables

1,3) to be variants of the common *Ferrissia rivularis*. The generic name of this limpet is an eponym for the amateur conchologist James H. Ferriss, who avidly collected land snails in the southern and western United States. Ferriss discovered more new species of terrestrial snails than any American since Thomas Say.

The low conical shape of *Ferrisia rivularis* adapts it to withstand the stress of a turbulent riffle environment, where it can be seen adhering to stream obstructions, such as rocks, logs, or other hard objects. By contrast, *Ferrissia fragilis* and *Ferrisia parallela* occur primarily in lentic habitats (Jokinen 1978, 1983).

The soft parts of limpets are sinistrally arranged (Burch and Jung 1992). The pseudobranch, used in breathing, is located on the left side of the animal (Fig. 8D), as are the openings for the excretory and reproductive systems.

COLLECTING AND STUDYING FRESHWATER SNAILS

Methods for collecting freshwater gastropods have been detailed by Athearn (1969), Baker (1902, 1974), Clarke (1981), Dall (1892), Jokinen (1983), Lewis (1868), Sterki (1916), Walker (1902), and Wetherby (1882). A procedure designed especially to collect snails of the genus *Campeloma* was described by Allison (1942). Aquatic snails can be found in a variety of habitats: lakes, ponds, and streams of various sizes; vernal pools; sloughs; even roadside ditches. Pulmonates most commonly inhabit the shallows near shore, especially in regions rich in plant or animal detritus. The stems and leaves of aquatic plants are also favorite sites for aquatic snails.

The preservation of freshwater snails (both shells and soft parts) is treated by Burch and Jung (1992), Jokinen (1983), Lewis (1868), and Pennak (1989). A general purpose preservative for intact animals is 70% isopropyl alcohol, obtainable at most drugstores. Field data should accompany those specimens that are collected. As a minimum, these data should include the species' scientific name, date and place of collection (including county and state), and the collector's name. Early lots (a lot = one species per place per date) in the finest museums sometimes lack these essentials, thereby hindering future research.

The rearing and maintenance of living aquatic snails is discussed by Cheatum (1937), Janus (1982), and Krull (1937). The methods are comparatively simple and consist of keeping the snails in some type of aquarium and feeding them lettuce or leaves. A source of calcium carbonate (for making shells) is also essential. Colton (1908) reported that *Pseudosuccinea columella* had a "muscular gizzard" which contained sand grains used to break up the food. Without this fine sand, the animal would starve amid abundance. Therefore, it was recommended that a pinch of soil be added to the culture container (Colton and Pennypacker 1934).

The preparation of aquatic gastropods for anatomical studies (e.g., to observe the genitalia for species identifications) is described by Baker (1911), Burch and Jung (1992), Jokinen (1983), and Pennak (1989).

SUGGESTIONS FOR FUTURE STUDIES

Ample opportunities exist for the study of freshwater snails in Maine. Distributional data are incomplete, and the presence of species in their old habitats needs to be verified. Have some snails expanded their ranges in the state, while others have retracted them? Does *Physella magnalacustris* really exist in Maine, and if so where? How has water pollution affected aquatic gastropod distributions? Nylander (1914a) believed that sawmill wastes dumped in the water adversely affected the molluscan life in the St. John River. According to Stauffer (1990), the alkalinities of Maine lakes between 1938-1944 and 1985 have actually *increased* (not decreased due to acid rain), so attendant changes in aquatic snail taxa might be expected.

While the precarious status of many freshwater mussels, largely due to human activities, has raised the public consciousness, fewer people seem alarmed that freshwater snails represent another endangered fauna in this country. According to Watters (1997), 118 species of aquatic snails once lived in the Mobile River system of the southern United States. Largely because of impoundments, 38 of these species are possibly extinct and another 70 are candidates for federal endangered status. As of November, 1994, 210 of the 516 taxa of aquatic gastropods in the United States were on the federal list of candidate species (Neves et al. 1997). According to McCollough (1996), no aquatic snails in Maine are considered to be rare or endangered, but future surveys might reveal otherwise. Likely possibilities could be *Stagnicola mighelsi* and *Stagnicola oronoensis*.

Do those aquatic gastropods with type localities in Maine (Table 3) still exist in their old haunts? Nylander (1936b, 1943b) believed that *Stagnicola mighelsi* had been extirpated from its type locality at the Square Lake inlet (Aroostook County) by 1914. Has this lymnaeid made a comeback since then? Can viable populations of *Lymnaea stagnalis* be found in Maine today? In summer, 1997, G. Keel Kemper of Maine's Inland Fisheries and Wildlife collected living specimens of *Cipangopaludina chinensis malleata* from the Messalonskee River at Waterville (Kennebec County), where it was first reported by Clench and Fuller (1965), and in nearby Tyler Pond (these specimens have been deposited in the Museum of Biological Diversity, Ohio State University). Has this exotic snail invaded other water bodies in Maine? Is it accompanied by the related alien species, *Cipangopaludina japonica*, which is sometimes the case (this author has collected both snails together in Lake Erie)? Future survey efforts may discover freshwater gastropods new to Maine, alien or otherwise. Clarke (1981), Dundee (1974), and Smith

(1995) mention several snails extralimital to the state which might now reside in Maine. These mollusks may have been overlooked by the early conchologists, or they could have entered the state in recent years.

Some cursory survey work of Maine's freshwater gastropods has been conducted by staff and students of the Humboldt Field Research Institute at Steuben, Maine (Table 2). In summer, 1990, Joerg-Henner Lotze found *Planorbella campanulata* in Deer Lake (Hancock County), and the following summer he discovered this snail and *Helisoma anceps* at Green Lake (also Hancock County). In summer, 1995, the freshwater malacology class of Arthur E. Bogan, of which this writer was a member, discovered *Campeloma decisum* in Spring River Lake and Fox Pond (both Hancock County) as well as in the Narraguagus River at Cherryfield (Washington County). At the latter site, *Physella heterostropha* and *Planorbella trivolvis* were also present. *Amnicola limosa* was collected from the Pleasant River at Columbia Falls (Washington County). Also in summer, 1995, Lotze collected *C. decisum*, *H. anceps*, and *P. campanulata* in Long Pond (Hancock County). Lewis Boobar, following in the footsteps of Nylander, collected several freshwater snails in Aroostook County, mostly in beaver flowages. These included *Physella gyrina*, *Gyraulus crista*, *Gyraulus parvus*, *H. anceps*, *P. trivolvis*, and *Promenetus exacuous*. All of these species had previously been found in the county by Nylander (1936a). In summer, 1996, Loretta Stillman discovered *A. limosa*, *G. parvus*, and *P. campanulata* in Beddington Lake (Washington County).

Much remains to be learned about the ecology and life history of the freshwater snails of Maine. Only limited studies have been conducted on these mollusks in the past. The life cycles of many freshwater snails have not been studied at all. Many discoveries about Maine's aquatic gastropods can yet be made both by professional scientists and dedicated amateurs.

> We need, if possible, to look at the world from the molluscs' point of view and it is unlikely that their categories correspond with our own. (from Boycott, 1936).

ACKNOWLEDGEMENTS

Thanks are extended to Richard I. Johnson of Harvard University's Museum of Comparative Zoology who provided the author with data about catalogued specimens of freshwater snails from Maine in the holdings of this museum. Thanks are also accorded Eileen H. Jokinen, Associate Director of the Connecticut Institute of Water Resources, who directed the peer review of this paper. Special thanks should go to the staff of Ohio State University's Interlibrary Loan Department who located many of the references cited here. The reproductive photography for Figures 1-3 was performed by ONC Inc. of Columbus, Ohio. Figure 9 was illustrated by Scott Rawlins.

BIBLIOGRAPHY

General

Note: The following general references are cited within the text.

ABBOTT, R.T. 1947. Mollusks and medicine in World War II. Annual Report of the Board of Regents of the Smithsonian Institution, pp. 325-338.

ABBOTT, R.T. 1950. Snail invaders. Natural History, 59(2):80-85.

ALDRIDGE, D.W. 1983. Physiological ecology of freshwater prosobranchs, pp. 329-358. *In* The Mollusca, vol. 6 (W.D. Russell-Hunter, Ed.). Academic Press, Orlando, FL.

ALEXANDER, J.E., Jr., and A.P. COVICH. 1991. Predation risk and avoidance behavior in two freshwater snails. Biological Bulletin, 180(3):387-393.

ALEXANDER, J., Jr., T.E. AUDESIRK, and G.J. AUDESIRK. 1984. One-trial reward learning in the snail *Lymnea stagnalis*. Journal of Neurobiology, 15(1):67-72.

ALLISON, L.N. 1942. Trapping snails of the genus *Campeloma*. Science, 95(247):131-132.

ANDERSON, R. 1996. *Physa gyrina* (Say), a North American freshwater gastropod new to Ireland, with a key to the British Isles Physidae. Irish Naturalists' Journal, 25(7):237-272.

ANONYMOUS. 1892. *Goniobasis virginica* in Conn. Nautilus, 6(3):36.

ARAUJO, R., J.M. REMÓN, D. MORENO, and M.A. RAMOS. 1995. Relaxing techniques for freshwater molluscs: trials for evaluation of different methods. Malacologia, 36(1-2):29-41.

ATHEARN, H.D. 1969. How to find freshwater mollusks in creek-size streams. American Malacological Union Annual Reports, pp. 31-33.

BAKER, F.C. 1901a. Snails of pond, river and brook. Birds and Nature, 9:128-133.

BAKER, F.C. 1901b. The digitations of the mantle in *Physa*. Bulletin of the Chicago Academy of Sciences, 2(4):225-228. Plates I-II.

BAKER, F.C. 1919. The ecology of North American Lymnæidae. Science (New Series), 49(1274):519-521.

BAKER, F.C. 1974. Fresh water snails, pp 56-59. *In* How to Study & Collect Shells (M.K. Jacobson, Ed.). 4th Ed. Amer. Malacol. Union, Wrightsville Beach, NC.

BARNESE, L. E., R.L. LOWE, and R.D. HUNTER. 1990. Comparative grazing efficiency of pulmonate and prosobranch snails. Journal of the North American Benthological Society, 9(1):35-44.

BARGUES, M.D., and S. MAS-COMA. 1997. Phylogenetic analysis of lymnaeid snails based on 18S rDNA sequences. Molecular Biology and Evolution, 14(5):569-577.

BARR, D. 1988. Not always to the swift. Seasons, 28(1):18-21. [*Seasons* is the quarterly publication of the Federation of Ontario Naturalists.]

BARTSCH, P. 1909. Pyramidellidae of New England and the adjacent region. Proceedings of the Boston Society of Natural History, 34:67-113.

BATTE, E.G., L.E. SWANSON, and J.B. MURPHY. 1951. Control of fresh water snails (intermediate hosts of liver flukes) in Florida. Journal of the American Veterinary Medical Association, 118(888):139-141.

BENDELL, B.E., and D.K. McNICOL. 1993. Gastropods from small northeastern Ontario lakes: their value as indicators of acidification. Canadian Field-Naturalist, 107(3):267-272.

BERG, C.O. 1953. Sciomyzid larvae (Diptera) that feed on snails. Journal of Parasitology, 39(6): 630-636.

BERG, C.O., and L. KNUTSON. 1978. Biology and systematics of the Sciomyzidae. Annual Review of Entomology, 23:239-258.

BERG, K. 1951. On the respiration of some molluscs from running and stagnant water. L'Année Biologique, 27(7):329-335.

BERG, K. 1952. On the oxygen consumption of Ancylidae (Gastropoda) from an ecological point of view. Hydrobiologia, 4:225-267.

BERRY, E.G. 1943. The Amnicolidae of Michigan: Distribution, Ecology, and Taxonomy. Miscellaneous Publications No. 57. University of Michigan Press, Ann Arbor, MI. 68 pp. Plates I-IX.

BLANKESPOOR, H.D., and R.L. REIMINK. 1991. The control of swimmer's itch in Michigan: past, present, and future. Michigan Academician, 24(1):7-23.

BOAG, D.A. 1986. Dispersal in pond snails: potential role of waterfowl. Canadian Journal of Zoology, 64(4):904-909.

BONDESEN, P. 1950. A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. Natura Jutlandica, 3:1-208. Plates I-IX.

BOSS, K.J. 1982. Mollusca, pp. 945-1166. *In* Synopsis and Classification of Living Organisms, vol. 1 (S.P. Parker, Ed.). McGraw-Hill Book Company, New York, NY.

BOURNS, T.K.R., and D.M. SCOTT. 1964. Plastic bird bands for marking lymnaeid snails. Journal of Parasitology, 50(1):59.

BOVBJERG, R.V. 1968. Responses to food in lymnaeid snails. Physiological Zoölogy, 41(4):412-423.

BOVBJERG, R.V. 1975. Dispersal and dispersion of pond snails in an experimental environment varying to three factors, singly and in combination. Physiological Zoölogy, 48(3):203-215.

BOYCOTT, A.E. 1936. The habitats of fresh-water Mollusca in Britain. Journal of Animal Ecology, 5(1):116-186.

BRANSON, B.A. 1963. Additions to and distributional annotations on the Kansas gastropod fauna. Transactions of the Kansas Academy of Science,66(1):72-75.

BRÖNMARK, C. 1989. Interactions between epiphytes, macrophytes and freshwater snails: a review. Journal of Molluscan Studies, 55(2):299-311.

BRÖNMARK, C. 1992. Leech predation on juvenile freshwater snails: effects of size, species and substrate. Oecologia, 91(4):526-529.

BROWN, D.S. 1978. Pulmonate molluscs as intermediate hosts for digenetic trematodes, pp. 287-333. *In* Pulmonates, vol. 2A (V. Fretter and J. Peake, Eds.). Academic Press, New York, NY.

BROWN, K.M. 1979. The adaptive demography of four freshwater pulmonate snails. Evolution, 33(1):417-432.

BROWN, K.M. 1982. Resource overlap and competition in pond snails: an experimental analysis. Ecology, 63(2):412-422.

BROWN, K.M. 1991. Mollusca: Gastropoda, pp. 285-314. *In* Ecology and Classification of North American Freshwater Invertebrates (J.H. Thorp and A.P. Covich, Eds.). Academic Press, New York, NY.

BROWN, K.M. 1997. Temporal and spatial patterns of abundance in the gastropod assemblage of a macrophyte bed. American Malacological Bulletin, 14(1):27-33.

BROWN, K.M., and D.R. DeVRIES. 1985. Predation and the distribution and abundance of a pulmonate pond snail. Oecologia, 66(1):93-99.

BROWN, K.M., and T.D. RICHARDSON. 1992. Phenotypic plasticity in the life histories and production of two warm-temperate viviparid prosobranchs. Veliger, 35(1):1-11.

BROWN, K.M., and B.H. STROUSE. 1988. Relative vulnerability of six freshwater gastropods to the leech *Nephelopsis obscura*. Freshwater Biology, 19(2):157-165.

BURCH, J.B. 1960. Chromosome studies of aquatic pulmonate snails. Nucleus 3(2):177-208.

BURCH, J.B. 1962. How to Know the Eastern Land Snails. Wm. C. Brown Company, Dubuque, IA. 214 pp.

BURCH, J.B. 1991. Malacology in Michigan. Michigan Academician, 24(1):115-170.

BURCH, J.B., and P.A. AYERS. 1973. Breeding experiments with *Stagnicola elodes* and *S. emarginata*. Malacological Review, 6:51-52.

BURCH, J.B., and K. JEONG. 1984. The radular teeth of selected Planorbidae. Malacological Review, 17:67-84.

BURCH, J.B., and Y. JUNG. 1992. Freshwater snails of the University of Michigan Biological Station Area. Walkerana, 6(15):1-218.

BURCH, J.B., and P.T. LoVERDE. 1974. Apical shell sculpture of some North American freshwater limpets (Gastropoda: Basommatophora). Occasional Papers on Mollusks, 4(50):39-44. Plates 5-9.

BURNSIDE, C.A., and R.F. McMAHON. 1997. Interpopulation, ecophenotypic shell-shape variation in the aquatic pulmonate genus *Physella*. Journal of the North American Benthological Society, 14(1):149.

BYERLY, L., and W.J. MOODY. 1984. Intracellular calcium ions and calcium currents in perfused neurones of the snail, *Lymnaea stagnalis*. Journal of Physiology, 352:637-652.

BYERLY, L., R. MEECH, and W. MOODY, Jr. 1984. Rapidly activating hydrogen ion currents in perfused neurones of the snail, *Lymnaea stagnalis*. Journal of Physiology, 351:199-216.

CAIN, G.L. 1956. Studies on cross-fertilization and self-fertilization in *Lymnaea stagnalis appressa* Say. Biological Bulletin, 111(1):45-52.

CALOW, P. 1978. The evolution of life-cycle strategies in fresh-water gastropods. Malacologia, 17(2):351-364.

CAREW, T.J., and C.L. SAHLEY. 1986. Invertebrate learning and memory: from behavior to molecules. Annual Review of Neuroscience, 6:435-487.

CHAMBERLAIN, N.A. 1958. Life history studies of *Campeloma decisum*. Nautilus, 72(1):22-29. Plate 3.

CHEATUM, E.P. 1934. Limnological investigations on respiration, annual migratory cycle, and other related phenomena in fresh-water pulmonate snails. Transactions of the American Microscopical Society, 53(4):348-407.

CHEATUM, E.P. 1937. Rearing aquatic pulmonate snails, p. 522. *In* Culture Methods for Invertebrate Animals (P.S. Galtsoff, F.E. Lutz, P.S. Welch, and J.G. Needham, Eds.). Comstock Publishing Company, Ithaca, NY.

CHILTON, E.W., and F.J. MARGRAF. 1990. Effects of fish predation on invertebrates associated with a macrophyte in Lake Onalaska, Wisconsin. Journal of Freshwater Ecology, 5(3):289-296.

CLARKE, A.H. 1969. Some aspects of adaptive radiation in recent freshwater molluscs. Malacologia, 9(1):263.

CLARKE, A.H. 1979. Gastropods as indicators of trophic lake stages. Nautilus, 94(4):138-142.

CLARKE, A.H. 1981. The Freshwater Molluscs of Canada. Canadian Museum of Nature, Ottawa, Ontario. 446 pp.

CLENCH, W.J. 1929. Freshwater shells of New England. Bulletin of Boston Society of Natural History, 52:3-8.

COLTON, H.S. 1908. Some effects of the environment on the growth of *Lymnæa columella* Say. Proceedings of the Academy of Natural Sciences of Philadelphia, 60:410-448.

COLTON, H.S. 1912. *Lymnæa columella*, and self-fertilization. Proceedings of the Academy of Natural Sciences of Philadelphia, 64:173-183.

COLTON, H.S. 1918. Self fertilization in the air-breathing pondsnails. Biological Bulletin, 35(1):48-49.

COLTON, H.S. 1922. Ten years with the self-fertilized line of *Lymnaea columella*, Say. Anatomical Record, 23:97.

COLTON, H.S., and M. PENNYPACKER. 1934. The results of twenty years of self-fertilization in the pond snail *Lymnaea columella*. American Naturalist, 68(715):129-136.

COMFORT, A. 1957. The duration of life in mollusks. Proceedings of the Malacological Society of London [England], 32:219-241.

COOK, A. 1971. Habituation in a freshwater snail *(Limnaea stagnalis)*. Animal Behaviour, 19(3):463-474.

CORT, W.W. 1928. Schistosome dermatitis in the United States (Michigan). Journal of the American Medical Association, 90(13):1027-1029.

COSTIL, K., and B. CLEMENT. 1996. Relationship between freshwater gastropods and plant communities reflecting various trophic levels. Hydrobiologia, 321(1):7-16.

COVICH, A.P., T.A. CROWL, J.E. ALEXANDER, Jr., and C.C. VAUGHN. 1994. Predator-avoidance responses in freshwater decapod-gastropod interactions mediated by chemical stimuli. J. of the North American Benthological Society, 13(2):283-290.

CRABB, E.D. 1927. Genetic experiments with pond snails *Lymnaea* and *Physa*. American Naturalist, 61(672):54-67.

CRABB, E.D. 1928. Self-fertilization in the pond snail *Lymnaea palustris*. Transactions of the American Microscopical Society, 47(l):82-88. Plate XII.
CRANDALL, O.A. 1901. The American Physæ. Nautilus, 15(3:25-30; 15(4):42-45; 15(5):54-58.
CROWL, T.A. 1990. Life-history strategies of a freshwater snail in response to stream permanence and predation: balancing conflicting demands. Oecologia, 84(2):238-243.
DALL, W.H. 1892. Instructions for collecting mollusks, and other useful hints for the conchologist. Bulletin of the United States National Museum No. 39, Part G. Smithsonian Institution, Washington, D.C. 56 pp.
DAWSON, J. 1911. The biology of *Physa*. Behavior Monographs, 1(4):1-120.
DOREMUS, C.M., and W.N. HARMAN. 1977. The effects of grazing by physid and planorbid freshwater snails on periphyton. Nautilus, 91(3):92-96.
DUNCAN, C.J. 1975. Reproduction, pp. 309-365. *In* Pulmonates, Vol. 1 (Functional Anatomy and Physiology) (V. Fretter and J. Peake, Eds.). Academic Press, NY, NY.
EILERS, J.M., G.J. LIEN, and R.G. BERG. 1984. Aquatic Organisms in Acidic Environments: A Literature Review. Technical Bulletin No. 150. Department of Natural Resources, Madison, WI. 18 pp.
EVANS, J.G. 1969. Land and freshwater Mollusca in archaeology: chronological aspects. World Archaeology, 1(2):170-183.
EYERDAM, W.J. 1968. Fresh-water mollusks eaten by trout and other fish. Nautilus, 81(3):103-104.
FARLEY, J. 1967. Schistosome dermatitis in the Maritime provinces. Canadian Journal of Zoology, 45(6):1300-1302.
FOOTE, B.A. 1959. Biology and life history of the snail-killing flies belonging to the genus *Sciomyza* Fallen (Diptera: Sciomyzidae). Annals of the Entomological Society of America, 52(1):31-43.
FRANTSEVICH, L., A. KORNIUSHIN, I. PANKOV, A. ERMAKOV, and T. ZAKHARCHUK. 1996. Application of molluscs for radioecological monitoring of the Chernobyl outburst. Environmental Pollution, 94(1):91-100.
FRENCH, J.R.P., III, and M.N. MORGAN. 1995. Preference of redear sunfish on zebra mussels and rams-horn snails. Journal of Freshwater Ecology, 10(1):49-55.
FRETTER, V., and J. PEAKE (Eds.) 1975. Pulmonates, Vol. 1 (Functional Anatomy and Physiology). Academic Press, New York, NY. 417 pp.
GERAERTS, W.P.M., and J. JOOSSE. 1984. Freshwater snails (Basommatophora), pp. 141-207. *In* The Mollusca, vol. 7 (A.S. Tompa, N.H. Verdonk, and J.A.M. Van den Biggelaar, Eds.). Academic Press, New York, NY.
GONZALEZ, E. 1989. Schistosomiasis, cercarial dermatitis, and marine dermatitis. Dermatologic Clinics, 7(2):291-300.
GOODRICH, C. 1940. Civilization and aquatic mollusks. Nautilus, 54(1):6-10.
HANSON, J.M., P.A. CHAMBERS, and E.E. PREPAS. 1990. Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. Freshwater Biology, 24(1):69-80.
HARMAN, W.N. 1974. Snails (Mollusca: Gastropoda), pp. 275-312. *In* Pollution Ecology of Freshwater Invertebrates (C.W. Hart, Jr., and S.L.H. Fuller, Eds.). Academic Press, New York, NY.
HARMAN, W.N., and C.O. BERG. 1971. The Freshwater Snails of Central New York with Illustrated Keys to the Genera and Species. Search (Cornell University Agricultural Experiment Station), 1(4):1-68.
HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies, 54(4):367-441.
HOEFFLER, D.F. 1974. Cercarial dermatitis: its etiology, epidemiology, and clinical aspects. Archives of Environmental Health, 29(4):225-229.
HUBENDICK, B. 1978. Systematics and comparative morphology of the Basommatophora, pp. 1-47. *In* Pulmonates, vol. 2A (V. Fretter and J. Peake, Eds.). Academic Press, New York, NY.
HUNTER, R.D. 1975. Variation in populations of *Lymnaea palustris* in upstate New York. American Midland Naturalist, 94(2):401-420.

HUNTER, R.D. 1990. Shell dissolution rate in freshwater pulmonate snails: influence of periostracum and water chemistry. Nautilus, 104(3):87-91.
HYMAN, L.H. 1967. The Invertebrates: Mollusca I. Vol. 6. McGraw-Hill Book Company, New York, NY. 792 pp.
INABA, A.. 1969. Cytotaxonomic studies of lymnaeid snails. Malacologia, 7(2-3):143-168.
JANUS, H. 1982. The Illustrated Guide to Molluscs. Harold Starke Limited, London, England. 180 pp.
JARCHO, S., and A. VAN BURKALOW. 1952. A geographical study of "swimmers' itch" in the United States and Canada. Geographical Review, 42(2):212-226.
JARNE, P., and B. DELAY. 1991. Population genetics of freshwater snails. Trends in Ecology and Evolution, 6(12):383-386.
JOHNSON, C.W. 1904. Ancyli adhering to water beetles. Nautilus, 17(10):120.
JOHNSON, S.G. 1992a. Spontaneous and hybrid origins of parthenogenesis in *Campeloma decisum* (freshwater prosobranch snail). Heredity, 68(3):253-261.
JOHNSON, S.G. 1992b. Parasite-induced parthenogenesis in a freshwater snail: stable, persistent patterns of parasitism. Oecologia, 89(4):533-541.
JOHNSON, S.G. 1994. Parasitism, reproductive assurance and the evolution of reproductive mode in a freshwater snail. Proceedings of the Royal Society of London [England], 255B(1344):209-213.
JOHNSON, S.G., C.M. LIVELY, and S.J. SCHRAG. 1995. Evolution and ecological correlates of uniparental reproduction in freshwater snails. Experientia, 51(5):498-509.
JOKINEN, E.H. 1978. Habitats of two species of freshwater limpets *(Ferrissia*: Ancylidae) from New England. Nautilus, 92(4):156-160.
JOKINEN, E.H. 1983. The Freshwater Snails of Connecticut. Bulletin 109. State Geological and Natural History Survey of Connecticut, Hartford, CT. 83 pp.
JOKINEN, E.H. 1987. Structure of freshwater snail communities: species-area relationships and incidence categories. American Malacological Bulletin, 5(1):9-19.
JOKINEN, E.H. 1991. The malacofauna of the acid and non-acid lakes and rivers of the Adirondak Mountains and surrounding lowlands, New York state, USA. Internationalale Vereinigung für Theoretische und Angewandte Limnologie, 24(5):2940-2946.
JOKINEN, E.H. 1992. The Freshwater Snails (Mollusca: Gastropoda) of New York State. Bulletin 482. New York State Museum Biological Survey, Albany, NY. 112 pp.
KEAS, B.E., and H.D. BLANKESPOOR. 1997. The prevalence of cercariae from *Stagnicola emarginata* (Lymnaeidae) over 50 years in northern Michigan. Journal of Parasitology, 83(3):536-540.
KEHDE, P.M., and J.L. WILHM. 1972. The effects of grazing by snails on community structure of periphyton in laboratory streams. American Midland Naturalist, 87(1):8-24.
KEMENES, G., and P.R. BENJAMIN. 1989. Appetitive learning in snails shows characteristics of conditioning in vertebrates. Brain Research, 489(1):163-166.
KENDALL, S.B. 1949. *Lymnaea stagnalis* as an intermediate host of *Fasciola hepatica.* Nature, 163(4153):880-881.
KERSHNER, M.W., and D.M. LODGE. 1990. Effect of substrate architecture on aquatic gastropod-substrate associations. Journal of the North American Benthological Society, 9(4):319-326.
KESLER, D.H., and W.R. MUNNS, Jr. 1989. Predation by *Belostoma flumineum* (Hemiptera): an important cause of mortality in freshwater snails. Journal of the North American Benthological Society, 8(4):342-350.
KEW, H.W. 1893. The Dispersal of Shells: An Inquiry Into the Means of Dispersal Possessed by Fresh-water and Land Mollusca. Kegan Paul, Trench, Trübner & Co., London, England. 291 pp.
KLOSIEWSKI, S.P. 1991. The Role of Pumpkinseed Sunfish in Structuring Snail Assemblages in Northern Wisconsin Lakes. Doctor of Philosophy Dissertation. Ohio State University, Columbus, Ohio. 159 pp.
KNUTSON, L.V., and C.O. BERG. 1964. Biology and immature stages of snail-killing flies: the genus *Elgiva* (Diptera: Sciomyzidae). Annals of the Entomological Society of America, 57(2):173-192.

KRAVITZ, P., and M. LEWIS. 1977. Swimmer's itch - a Rhode Island malady. Rhode Island Medical Journal, 60(8):382-383.

KRULL, W.H. 1933a. A new snail and rabbit hosts for *Fasciola hepatica* L. Journal of Parasitiology, 20(1):49-52.

KRULL, W.H. 1933b. The snail *Pseudosuccinea columella* (Say) as a potentially important intermediate host in extending the range of *Fasciola hepatica* Linn. Journal of the Washington [D.C.] Academy of Sciences, 23(8):389-391.

KRULL, W. 1937. Rearing aquatic snails, pp. 523-526. *In* Culture Methods for Invertebrate Animals (P.S. Galtsoff, F.E. Lutz, P.S. Welch, and J.G. Needham, Eds.). Comstock Publishing Company, Ithaca, NY.

LA ROCQUE, A. 1952. Molluscan faunas of the Orleton mastodon site, Madison County, Ohio. Ohio Journal of Science, 52(1):10-27.

LASSEN, H.H. 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. Oecologia, 19(1):1-8.

LEWIS, J. 1868. Directions for collecting land and fresh-water shells. American Naturalist, 2(8):410-420.

LODGE, D.M. 1985. Macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshwater Biology, 15(6):695-708.

LODGE, D.M. 1986. Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions. Freshwater Biology, 16(6):831-841.

LODGE, D.M., K.M. BROWN, S.P. KLOSIEWSKI, R.A. STEIN, A.P. COVICH, B.K. LEATHERS, and C. BRÖNMARK. 1987. Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. American Malacological Bulletin 5(1): 73-84.

LYTLE, C.F., ED. 1948. Leaves of Gold. Coslett Publishing Co., Williamsport, PA. 200 pp.

MACKIE, G.L., D.S. WHITE, and T.W. ZDEBA. 1980. A Guide to Freshwater Mollusks of the Laurentian Great Lakes with Special Emphasis on the Genus *Pisidium*. United States Environmental Protection Agency, Duluth, MN. 143 pp.

MALONE, C.R. 1965a. Killdeer *(Charadrius vociferus* Linnaeus) as a means of dispersal for aquatic gastropods. Ecology, 46(4):551-552.

MALONE, C.R. 1965b. Dispersal of aquatic gastropods via the intestinal tract of water birds. Nautilus, 78(4):135-139.

MARTIN, S.M. 1995. Maine's early malacological history. Maine Naturalist, 3(1):1-34.

MAZURKIEWICZ, M. 1972. Reproduction and development of estuarine hydrobiid gastropods. American Zoologist, 12(4):726.

McATEE, W.L. 1914. Birds transporting food supplies. Auk, 31(3):404-405.

McCOLLOUGH, M. 1996. Non-marine mollusk diversity in Maine, pp. 87-96. *In* Biological Diversity in Maine: Appendices (S.C. Gawler et al., Eds.). Maine Natural Areas Program, Augusta, ME.

McELANEY, B.L. 1997. Freshwater shells - the excitement of discovery. American Conchologist, 25(1):3-5.

McMAHON, R.F. 1983. Physiological ecology of freshwater pulmonates, pp. 359-430. *In* The Mollusca, vol. 6 (W. D. Russell-Hunter, Ed.). Academic Press, Orlando, FL.

MICHELSON, E.H. 1957. Studies on the biological control of schistosome-bearing snails. Predators and parasites of fresh-water Mollusca: a review of the literature. Parasitology, 47(3-4):413-426.

MICHELSON, E.H., and L. DU BOIS. 1974. *Lymnaea emarginata*, a possible agent for the control of the schistosome snail host, *Biomphalaria glabrata*. Nautilus, 88(4):101-108.

MORRIS, P.A. 1939. What Shell Is That? A Guide to the Shell-bearing Mollusks of Eastern North America. D. Appleton-Century Company, New York, NY. 198 pp.

MORSE, E.S. 1887. First Book of Zoölogy. 2nd Ed. D. Appleton and Company, New York, NY. 190 pp.

MOSER, W.E., and M.S. WILLIS. 1994. Predation on gastropods by *Placobdella* spp. (Clitellata: Rhynchobdellida). American Midland Naturalist, 132(2):399-400.

MOZLEY, A. 1954. An Introduction to Molluscan Ecology: Distribution and Population Studies of Fresh-water Molluscs. H. K. Lewis & Co., London, England. 71 pp.

MOZLEY, A. 1957. Liver-fluke snails in Britain. H. K. Lewis & Co., London, England. 55 pp.

MULVIHILL, C.A., and J.W. BURNETT. 1990. Swimmer's itch: a cercarial dermatitis. Cutis, 46(2):211-213.

NEVES, R.J., A.E. BOGAN, J.D. WILLIAMS, S.A. AHLSTEDT, and P.W. HARTFIELD. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity, pp. 43-85. *In* Aquatic Fauna in Peril: The Southeastern Perspective (G.W. Benz and D.E. Collins, Eds.). Southeast Aquatic Research Institute Special Publication 1.

NICKERSON, R.P. 1972. A Survey of Enzyme and Shell Variation in 16 Populations of the Stream Limpet, *Ferrissia rivularis*. Doctor of Philosophy Dissertation. Syracuse University, Syracuse, NY. 164 pp.

ØKLAND, JAN. 1983. Factors regulating the distribution of fresh-water snails (Gastropoda) in Norway. Malacologia, 24(1-2):277-288.

OLSEN, T.M., D.M. LODGE, G.M. CAPELLI, and R.J. HOULIHAN. 1991. Mechanisms of impact of an introduced crayfish *(Orconectes rusticus* on littoral congeners, snails, and macrophytes. Canadian J. of Fisheries and Aquatic Sciences, 48(10):1853-1861.

OSENBERG, C.W. 1989. Resource limitation, competition and the influence of life history in a freshwater snail community. Oecologia, 79(4):512-519.

OSENBERG, C.W., and G.G. MITTELBACH. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. Ecological Monographs, 59(4):405-432.

OWEN, D.F. 1962. *Helisoma anceps* transported by a giant water bug. Nautilus, 75(3):124-125.

PANTELOURIS, E.M. 1965. The Common Liver Fluke *Fasciola hepatica* L. Pergamon Press, Oxford, England. 259 pp.

PARAENSE, W.L., and L.R. CORRÉA. 1988. Self-fertilization in the freshwater snails *Helisoma duryi* and *Helisoma triviolvis*. Memórias do Instituto Oswaldo Cruz, 83(4):405-409.

PENNAK, R.W. 1989. Fresh-water Invertebrates of the United States: Protozoa to Mollusca. 3rd Ed. John Wiley & Sons, New York, NY. 628 pp.

PILSBRY, H.A. 1897. *Campeloma decisum* Say, reversed. Nautilus, 10(10):118.

PRICE, E.W. 1953. The fluke situation in American ruminants. Journal of Parasitology, 39(2):119-134.

RAPP, W.F., E.W. JOHNSON, and H.D. SMITH. 1972. Schistosome dermatitis or swimmer's itch. Nebraska Medical Journal (June, 1972):210-213.

REES, W.J. 1965. The aerial dispersal of Mollusca. Proceedings of the Malacological Society of London [England], 36:269-282.

REINHARD, E.G. 1957. Landmarks of parasitology. I. Discovery of the life cycle of liver fluke. Experimental Parasitology, 6(2):208-232.

REMIGIO, E.A., and D. BLAIR. 1997a. Relationships among problematic North American stagnicoline snails (Pulmonata: Lymnaeidae) reinvestigated using ribosomal DNA internal transcribed spacer sequences. Canadian Journal of Zoology, 75(9):1540-1545.

REMIGIO, E.A., and D. BLAIR. 1997b. Molecular systematics of the freshwater snail family Lymnaeidae (Pulmonata: Basommatophora) utilising mitochondrial ribosomal DNA sequences. Journal of Molluscan Studies, 63(2):173-185.

REYNOLDS, M.B. 1959. Pleistocene molluscan faunas of the Humboldt Deposit, Ross County, Ohio. Ohio Journal of Science, 59(3):152-166.

ROSEWATER, J. 1970. Another record of insect dispersal of an ancylid snail. Nautilus, 83(4):144-145.

RUSSELL-HUNTER, W. 1952. The adaptations of freshwater Gastropoda. Glasgow [Scotland] Naturalist, 16(2):84-85.

RUSSELL-HUNTER, W.D. 1978. Ecology of freshwater pulmonates, pp. 335-383. *In* Pulmonates, Vol. 2A (V. Fretter and J. Peake, Eds.). Academic Press, New York, NY.

RUSSELL-HUNTER, W.D., A.J. BURKY, and R.D. HUNTER. 1970. Interpopulation variation in shell components in the stream limpet, *Ferrissia rivularis*. Biological Bulletin, 139(2):402.

SALVINI-PLAWEN, L.V., and G. HASZPRUNAR. 1987. The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). Journal of Zoology (London, [England]), 211(4):747-770.

SAY, T. 1817. Conchology (15 pp., 4 pls.). *In* American Edition of the British Encyclopedia or Dictionary of Arts and Sciences (W. Nicholson, Ed.). Volume II (B-E). S.A. Mitchell and H. Ames, Philadelphia, PA. [no pagination]

SCOTT, M.E., and M.D.B. BURT. 1976. Swimmers' itch in New Brunswick: distribution and description of the causative agent *Cercaria catascopii* n. sp. Canadian Journal of Zoology, 54(12):2200-2207.

SERVOS, M.R., J.B. ROOKE, and G.L. MACKIE. 1985. Reproduction of selected Mollusca in some low alkalinity lakes in south-central Ontario. Canadian Journal of Zoology, 63(3):511-515.

SINDERMANN, C.J. 1960. Ecological studies of marine dermatitis-producing schistosome larvae in northern New England. Ecology, 41(4):678-684.

SINDERMANN, C.J., and R.F. GIBBS. 1953. A Dermatitis-producing Schistosome Which Causes "Clam Diggers Itch" Along the Central Maine Coast. Research Bulletin No. 12. Department of Sea and Shore Fisheries. Augusta, ME. 20 pp.

SMITH, D.A. 1989. Tests of feeding selectivity in *Helisoma trivolvis* (Gastropoda: Pulmonata). Transactions of the American Microscopical Society, 108(4):394-402.

SMITH, D.G. 1980. *Goniobasis virginica* (Gastropoda: Pleuroceridae) in the Connecticut River. Nautilus, 94(2):50-54.

SMITH, D.G. 1995. Keys to the Freshwater Macroinvertebrates of Massachusetts. 2nd Ed. Privately published by the author, Amherst, MA. 243 pp.

SMITH, W.H. 1899. Shells and mastodon. Nautilus, 13(3):34-35.

SOLEM, A. 1974. The Shell Makers: Introducing Mollusks. John Wiley & Sons, New York, NY. 289 pp.

SPARKS, B.W. 1970. Non-marine Mollusca and archaeology, pp. 395-406. *In* Science in Archaeology: A Survey of Progress and Research (D. Brothwell and E. Higgs, Eds.). Rev. Ed. Praeger Publishers, New York, NY.

STAUFFER, R.E. 1990. Alkalinities of Maine lakes: are they really changing? Limnology and Oceanography, 35(6):1238-1257.

STERKI, V. 1909. Descriptions of two new species of *Musculium*. Nautilus, 23(5):66-67.

STERKI, V. 1916. Some directions and suggestions for collecting the Sphaeriidae and aquatic gastropods. Annals of the Carnegie [Pittsburgh] Museum, 10(3-4):478-486.

STEWART, T.W., and J.M. HAYNES. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. Journal of Great Lakes Research, 20(2):479-493.

STRAYER, D. 1990. Freshwater Mollusca, pp. 335-372. *In* Freshwater Macroinvertebrates of Northeastern North America (B.L. Peckarsky, P.R. Frassinet, M.A. Penton, and D.J. Conklin, Jr., Eds.). Cornell University Press, Ithaca, NY.

SWIDERSKI, D.L. 1990. Analysis of Lymnaeacean relationships using phylogenetic systematics. Malacologia, 31(2):249-257.

TAYLOR, E.L. 1937. The revelation of the life-history of the liver fluke as an illustration of the process of scientific discovery. Veterinary Record, 49(3):53-58.

TE, G.A. 1978. A Systematic Study of the Family Physidae (Basommatophora: Pulmonata). Doctor of Philosophy Dissertation. University of Michigan, Ann Arbor, MI. 336 pp.

TE, G.A. 1980. New classification system for the family Physidae (Pulmonata: Basommatophora). Archiv für Molluskenkunde, 110 (4-6):179-184.

THOMAS, A.P. 1883. The life history of the liver-fluke *(Fasciola heptica)*. Quarterly Journal of Microscopical Science, 23:99-133. Plates II-III.

THOMPSON, E.L. 1917. An analysis of the learning process in the snail, *Physa gyrina* Say. Behavior Monographs, 3(3):1-88. Plates I-VIII.

THOMPSON, F.G. 1984. The Freshwater Snails of Florida: A Manual for Identification. University of Florida Press, Gainesville, FL. 94 pp.

TURGEON, D.D., J.F. QUINN, Jr., 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: Mollusks. 2nd Ed. American Fisheries Society Special Publication No. 26. 526 pp.

TURNER, A.M. 1996. Freshwater snails alter habitat use in response to predation. Animal Behaviour, 51(4):747-756.

VAN DER SCHALIE, H. 1965. Observations on the sex of *Campeloma* (Gastropoda: Viviparidae). Occasional Papers of the University of Michigan Museum of Zoology, (641):1-15. Plates I-V.

VAUGHT, K.C. 1989. A Classification of the Living Mollusca. American Malacologists, Melbourne, FL. 189 pp.

VERMEIJ, G.J., and A.P. COVICH. 1978. Coevolution of freshwater gastropods and their predators. American Naturalist, 112(987):833-843.

WALKER, B. 1898. Mollusca contemporaneous with the mastodon. Nautilus, 11(11):121-122.

WALKER, B. 1901. New varieties of *Physa ancillaria* Say. Nautilus, 14(9):97-99.

WALKER, B. 1902. Hints on collecting land and fresh-water Mollusca. Journal of Applied Microscopy and Laboratory Methods, 5(9):1954-1961.

WALL, R.C. 1976. An analysis of the current status of the schistosome dermatitis problem in Michigan. Sterkiana, (63/64):1-64.

WALTER, H.J., and J.B. BURCH. 1957. Key to the Genera of Freshwater Gastropods (Snails and Limpets) Occurring in Michigan. University of Michigan Museum of Zoology Circular No. 3. 8 pp.

WATTERS, T. 1997. Freshwater snails - an overlooked endangered fauna. BioOhio, 5(1):4-5. [*BioOhio* is the newsletter of the Ohio Biological Survey.]

WEBER, L.M., and D.M. LODGE. 1990. Periphytic food and predatory crayfish: relative roles in determining snail distribution. Oecologia, 82(1):33-39.

WELLS, M.J. and S.K.I. BUCKLEY. 1972. Snails and trails. Animal Behaviour, 20(2):345-355.

WELLS, M.J., and J. WELLS. 1971. Conditioning and sensitization in snails. Animal Behaviour, 19(2):305-312.

WETHERBY, A.G. 1882. Directions for collecting and preparing land and fresh water shells. Journal of the Cincinnati [Ohio] Society of Natural History, 5:44-51.

WETHINGTON, A.R., and R.T. DILLON, Jr. 1997. Selfing, outcrossing, and mixed mating in the freshwater snail *Physa heterostropha*: lifetime fitness and inbreeding depression. Invertebrate Biology, 116(3):192-199.

WHELAN, H.A., and C.R. McCROHAN. 1996. Food-related conditioning and neuronal correlates in the freshwater snail *Lymnaea stagnalis*. Journal of Molluscan Studies, 62(4):483-494.

WILLIAMSON, J. 1969. Swimmer's itch. Ontario Fish and Wildlife Review, 8(1):17-19.

WILLOWS, A.O.D. 1973. Learning in gastropod mollusks, pp. 187-274. *In* Invertebrate Learning, Vol. 2 (Arthropods and Gastropod Mollusks) (W.C. Corning, J.A. Dyal, and A.O.D. Willows, Eds.). Plenum Press, New York, NY.

WINKLEY, H.W. 1901. *Goniobasis* in Massachusetts. Nautilus, 15(7):83.

WINKLEY, H.W. 1909. On collecting. Nautilus, 23(5):68-69.

WISENDEN, P.A., and R.C. BAILEY. 1995. Development of macroinvertebrate community structure associated with zebra mussel (*Dreissena polymorpha*) colonization of artificial substrates. Canadian Journal of Zoology, 73(8):1438-1443.

WU, S., R.D. OESCH, and M.E. GORDON. 1997. Missouri Aquatic Snails. Missouri Department of Conservation, Jefferson City, MO. 97 pp.

WURTZ, C.B. 1955. Fresh-water mollusks and stream pollution. Nautilus, 69(3):96-100.

YOUNG, J.O. 1975. Preliminary field and laboratory studies on the survival and spawning of several species of Gastropoda in calcium-poor and calcium-rich waters. Proceedings of the Malacological Society of London [England], 41(5):429-437.

YOUNG, J.O., and R.M. PROCTER. 1986. Are the lake-dwelling leeches, *Glossiphonia complanata* (L.) and *Helobdella stagnalis* (L.), opportunistic predators on molluscs and do they partition this food resource? Freshwater Biology, 16(4):561-566.

Maine's Freshwater Gastropods

Note: The following literature records were used in compiling the provisional county distribution of Maine's freshwater gastropods (Table 2).

ANONYMOUS. 1865. Curious distortion in the shell of *Physa heterostropha*. American Journal of Conchology, 1(2):181-182. [abnormal specimens of this snail from Cumberland County, Maine]

ANONYMOUS. 1871. Field meeting at East Gloucester, Thursday, June 29th, 1871. Bulletin of the Essex Institute, 3(9):113-116. [*Pseudosuccinea columella* from Cumberland County, Maine]

BAKER, F.C. 1900a. The gross anatomy of *Limnæa emarginata*, Say, var. *mighelsi*, Binney. Bulletin of the Chicago Academy of Sciences, 2(3):191-211. Plates I-VI. [*Stagnicola emarginata* and *Stagnicola mighelsi* from Aroostook County, Maine]

BAKER, F.C. 1900b. A revision of the Physæ of northeastern Illinois. Nautilus, 14(2):16-24. [*Physella heterostropha* also from Maine]

BAKER, F.C. 1902. The Mollusca of the Chicago Area. Part II. The Gastropoda. 410 pp. Plates XXVIII-XXXVI. [three snails also from Maine; *Stagnicola mighelsi* depicted in plate 33]

BAKER, F.C. 1904. New American Lymnaeas. II. Nautilus, 18(6):62-63. [*Stagnicola oronoensis* from Penobscot County, Maine]]

BAKER, F.C. 1905. Critical notes on the smaller lymnaeas. Nautilus, 18(11):125-127. [*Fossaria humilis* and *Fossaria parva* from Maine]

BAKER, F.C. 1908. A new American *Planorbis*. Nautilus, 22(4-5):45. [*Helisoma anceps portagensis* from Aroostook County, Maine]

BAKER, F.C. 1909. Range of *Lymnæa umbilicata*. Nautilus, 23(6):80. [*Stagnicola caperata* from three Maine counties]

BAKER, F.C. 1911. The Lymnæidæ of North and Middle America, Recent and Fossil. Chicago Academy of Sciences Special Publication No. 3. 539 pp. Plates I-LVIII. [11 species from Maine]

BAKER, F.C. 1920. A new form of *Amnicola* from the Ohio Pleistocene deposits with notes on a *Physa* from the same formation. Nautilus, 33(4):125-127. [*Cincinnatia winkleyi* from Saco, Maine]

BAKER, F.C. 1928. The Fresh Water Mollusca of Wisconsin. Part I. Gastropoda. Wisconsin Academy of Sciences, Arts, and Letters, Madison, WI. 507 pp. Plates I-XXVII. [seven snails also from Maine]

BAKER, F.C. 1945. The Molluscan Family Planorbidae. University of Illinois Press, Urbana, IL. 530 pp. Plates 1-141. [two *Helisoma* variants and one *Planorbella* variant from Maine depicted in plates 83, 85, and 87, respectively]

BASCH, P.F. 1963. A review of the recent freshwater limpet snails of North America. Bulletin of the Museum of Comparative Zoology at Harvard College, 129(8):401-461. [three *Ferrissia* species from Maine]

BERRY, S.S. 1910. Mollusks of Unity, Maine. Nautilus, 24(6):61-63. [17 freshwater snails from Waldo County]

BINNEY, W.G. 1865a. Land and Fresh-water Shells of North America. Part II. Pulmonata, Limnophila and Thalassophila. Smithsonian Miscellaneous Collections No. 143. 161 pp. [five freshwater snails from Maine]

BINNEY, W.G. 1865b. Land and Fresh-water Shells of North America. Part III. Ampullariidæ, Valvatidæ, Viviparidæ, Fresh-water Rissoidæ, Cyclophoridæ, Truncatellidæ, Fresh-water Neritidæ, Helicinidæ Smithsonian Miscellaneous Collections No. 144. 120 pp. [*Lyrogyrus pupoideus* from Maine]

BISHOP, S.C., and N.T. CLARKE. 1922. A Scientific Survey of Turners Lake, Isle-au-Haut, Maine. New York State Museum, Albany, NY. 22 pp. [*Physella heterostropha* and *Helisoma anceps* collected]

BLANEY, D. 1904. The land-shells of Ironbound Island, Maine. Nautilus, 18(4):45-46. [*Stagnicola caperata* also from this Hancock County island]

BONNEY, L.E. 1935. A collection of shells made at Turner, Maine. Arthur Herbert Norton Papers, Box 406. Special Collections Department, Raymond H. Fogler Library, University of Maine-Orono. One sheet. [*Campeloma decisum*, *Stagnicola caperata*, and *Physella heterostropha* collected]

BOOBAR, L.R. 1997. Effects of Landscape on Macroinvertebrate Assemblages in Beaver-mediated Wetlands, Aroostook County, Maine. Doctor of Philosophy Dissertation. University of Maine-Orono. 454 pp. [seven genera of freshwater snails collected]

BURCH, J.B. 1989. North American Freshwater Snails. Malacological Publications, Hamburg, MI. 365 pp. [eight species from Maine, including *Physella magnalacustris*]

BURCH, J.B., and J.L. TOTTENHAM. 1980. North American Freshwater Snails: Species List, Ranges and Illustrations. Transactions of the POETS Society, (3):81-215. [eight species from Maine, including *Physella magnalacustris*]

CALL, R.E. 1894. On the geographic and hypsometric distribution of North American Viviparidae. American Journal of Science (3rd Series), 48(284):132-141. [*Campeloma decisum* from three Maine counties]

CHAMPION, M.E. 1947. Edward Sylvester Morse with a bibliography and a catalogue of his species. Occasional Papers on Mollusks, 1(11):129-144. [published by Department of Mollusks of Harvard University's Museum of Comparative Zoology] [*Ancylus borealis* and *Ancylus ovalis* from Maine]

CHICKERING, J.W., Jr. 1854. List of Marine, Fresh Water, and Land Shells Found in the Vicinity of Portland, Maine. Double sheet. Privately printed by the author. [reproduced on pp. 243-245 of *Bibliography of North American Conchology Previous to the Year 1860*, by W. G. Binney (Smithsonian Miscellaneous Collections, vol. 5, 1864)] [17 freshwater snails from Cumberland County]

CLAPP, G.H. 1900. Land Mollusca of Kennebunkport, Me. Nautilus, 14(6):63-64. [*Stagnicola caperata* also collected]

CLENCH, W.J., and S.L.H. FULLER. 1965. The genus *Viviparus* (Viviparidae) in North America. Occasional Papers on Mollusks, 2(32):385-412. [*Cipangopaludina chinensis malleata* from Kennebec County, Maine]

DALL, W.H. 1905. Land and fresh water mollusks of Alaska and adjoining regions, pp. 1-171. Harriman Alaska Expedition, vol. 13. [*Valvata sincera nylanderi* from Aroostook County, Maine]

DAVIS, G.M., and M. MAZURKIEWICZ. 1985. Systematics of *Cincinnatia winkleyi* (Gastropoda: Hydrobiidae). Proceedings of the Academy of Natural Sciences of Philadelphia, 137(2):28-47. [*Cincinnatia winkleyi* from two Maine counties]

DAVIS, G.M., M. MAZURKIEWICZ, and M. MANDRACCHIA. 1982. *Spurwinkia*: Morphology, systematics, and ecology of a new genus of North American marshland Hydrobiidae (Mollusca: Gastropoda). Proceedings of the Academy of Natural Sciences of Philadelphia, 134:143-177. [*Cincinnatia winkleyi* from Cumberland County, Maine]

DUNDEE, D.S. 1974. Catalog of introduced molluscs of eastern North America (north of Mexico). Sterkiana, 55:1-37. [*Cipangopaludina chinensis malleata* in Maine]

EMERSON, W.K., M.K. JACOBSON, H.S. FEINBURG, and W.E. OLD, Jr. 1976. The American Museum of Natural History Guide to Shells: Land, Freshwater, and Marine, from Nova Scotia to Florida. Alfred A. Knopf, New York, NY. 482 pp. Plates I-XLVII. [three freshwater snails from Maine]

GOULD, A.A. 1870. Report on the Invertebrata of Massachusetts. 2nd Ed. Wright and Potter, Boston, MA. 524 pp. Plates XVI-XXVII. [three freshwater snails also found in Maine]

HALDEMAN, S.S. 1840-45. A Monograph of the Freshwater Univalve Mollusca of the United States. Parts I-VIII. E. G. Dorsey, Philadelphia, PA. [six species from Maine]

HUNTER, M.L., Jr., J.J. JONES, K.E. GIBBS, J.R. MORING, and M. BRETT. 1985. Interactions Among Waterfowl, Fishes, Invertebrates, and Macrophytes in Four Maine Lakes of Different Acidity. United States Fish and Wildlife Service, Eastern Energy and Land Use Team. Biological Report No. 80(40.20). 80 pp. [*Helisoma anceps* from Salmon Pond, Hancock County]

JACKSON, C.T. 1837. First Report on the Geology of the State of Maine. Smith & Robinson, Augusta, ME. 127 pp. [lists four freshwater snails in Appendix]

JACKSON, H., Jr. 1908. The Mollusca of North Haven, Maine. Nautilus, 21(12):142-144. [five freshwater snails from Knox County]

JOHNSON, C.W. 1908. Shells of the lake region of Maine. Nautilus, 21(9):106. [*Helisoma anceps* from Piscataquis County]

JOHNSON, C.W. 1915. Fauna of New England. 13. List of the Mollusca. Occasional Papers of the Boston Society of Natural History, 7:1-231. [many Maine citations; 36 freshwater snails]

JOHNSON, R.I., and K.J. BOSS. 1972. The fresh-water, brackish, and non-Jamaican land mollusks described by C. B. Adams. Occasional Papers on Mollusks, 3(43):193-236. Plates 36-42. [*Stagnicola catascopium* and *Physella ancillaria* from Maine]

JOKINEN, E.H. 1982. *Cipangopaludina chinensis* (Gastropoda: Viviparidae) in North America, review and update. Nautilus, 96(3):89-95. [this exotic snail in Maine]

LERMOND, N.W. 1908. Shells of Maine: A Catalogue of the Land, Fresh-water and Marine Mollusca of Maine. Privately published by the author, Thomaston, ME. 46 pp. [reproduced verbatim in 1909 on pp. 217-262 of *Seventh Annual Report of the Commissioner of Agriculture of the State of Maine*] [many Maine citations; 32 freshwater snails]

LERMOND, N.W. 1914. Additions to the list of Maine Mollusca. Nautilus, 28(2):18-20. [four freshwater snails listed]

MIGHELS, J.W. 1843a. Catalogue of the marine, fluviatile and terrestrial shells of the state of Maine and adjacent ocean. Boston Journal of Natural History, 4(3):308-345. [many Maine citations; 20 freshwater snails]

MIGHELS, J.W. 1843b. Descriptions of six species of shells regarded as new. Boston Journal of Natural History, 4(3):345-350. Plate XVI. [*Stagnicola mighelsi* from Aroostook County, Maine]

MIGHELS, J.W., and C.B. ADAMS. 1841. Descriptions of twenty-five new species of New England shells. Proceedings of the Boston Society of Natural History, 1:48-50. [*Stagnicola catascopium* and *Physella ancillaria* from Maine]

MIGHELS, J.W., and C.B. ADAMS. 1842. Descriptions of twenty-four species of the shells of New England. Boston Journal of Natural History, 4(1):37-55. Plate IV. [*Stagnicola catascopium* and *Physella ancillaria* from Maine] MORONEY, JOHN F. 1973. A Study of the Macrophytes and Benthos in the Lower Penobscot River. Master of Science Thesis. University of Maine-Orono. 120 pp. [five genera of freshwater snails collected]

MORSE, E.S. 1864. Observations on the terrestrial Pulmonifera of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the state. Journal of the Portland [Maine] Society of Natural History, 1(1):1-63. Plates 1-10. [29 freshwater snails listed]

MORSE, E.S. 1865. New locality of *Limnæa ampla*, Mighels. American Journal of Conchology, 1(3):286. [*Stagnicola mighelsi* from Cumberland County, Maine]

MORSE, E.S. 1870. Our common fresh-water shells. American Naturalist, 3:530-535, 648-651. [*Stagnicola catascopium* from Maine]

MORSE, E.S. 1880. The gradual dispersion of certain mollusks in New England. Bulletin of the Essex Institute, 12:171-176. [mentions four freshwater snails from Maine]

NYLANDER, O.O. 1895. Shells of Aroostook Co., Maine. Nautilus, 8(11):125-126. [12 freshwater snails listed]

NYLANDER, O.O. 1897. Fresh water shells in the northeast of Maine. Nautilus, 11(1):9-12. [16 freshwater snails from Aroostook County]

NYLANDER, O.O. 1899. Agassiz Association Department. Nautilus, 13(5):59-60. [*Gyraulus crista* from Aroostook County, Maine]

NYLANDER, O.O. 1900a. A list of shells from northeastern Maine. Nautilus, 13(9):102-106. [18 freshwater snails from Aroostook County]

NYLANDER, O.O. 1900b. Corrections to list of shells from northeastern Maine. Nautilus, 13(10):118. [makes slight corrections to above article; no new freshwater snails]

NYLANDER, O.O. 1901a. Shells of the marl-deposits of Aroostook County, Maine, as compared with the living forms in the same locality. Nautilus, 14(9):101-104. [10 freshwater snails listed]

NYLANDER, O.O. 1901b. Distribution of *Limnæa emarginata*, Say, and the var. *mighelsi*, Binney, in Fish River, Aroostook Co., Maine. Privately published by the author, Caribou, ME. 4 pp. Plates I-IV. [*Stagnicola emarginata* and *Stagnicola mighelsi* studied]

NYLANDER, O.O. 1902. The original locality of *Limnæa ampla* Mighels. Nautilus, 15(11):127-129. [10 freshwater snails from Aroostook County]

NYLANDER, O.O. 1908. Additional shells found in Aroostook County, Maine. Nautilus, 22(2):19. [four freshwater snails listed]

NYLANDER, O.O. 1909. Fossil and living shells found in Little Mud Lake, Westmanland, Aroostook County, Maine. Nautilus, 22(10):105-106. [eight freshwater snails listed]

NYLANDER, O.O. 1912. Lymnæidae of Aroostook County, Maine. Nautilus, 25(9):107-108. [eight freshwater snails listed]

NYLANDER, O.O. 1914a. Distribution of some fresh water shells of the St. John's River Valley in Maine, New Brunswick and Quebec. Nautilus, 27(12):139-141. [10 freshwater snails from Aroostook County]

NYLANDER, O.O. 1914b. Fresh water shells in Moose River, Somerset County, Maine. Nautilus, 28(8):89. [five freshwater snails listed]

NYLANDER, O.O. 1914c. *Lymnæa emarginata mighelsi* absent in its old localities. Nautilus, 28(8):95-96. [this snail no longer found at its original Aroostook County sites]

NYLANDER, O.O. 1921. The type localities of *Lymnaea emarginata* Say and *L. ampla* Mighels. Nautilus, 34(3):77-80. [*Stagnicola emarginata* and *Stagnicola mighelsi* from Aroostook County]

NYLANDER, O.O. 1922. History of *Lymnaea emarginata*, Say. The Maine Naturalist, 2(2):74-77. [*Stagnicola emarginata* and *Stagnicola mighelsi* from Aroostook County]

NYLANDER, O.O. 1928. Nadeau Lake, Fort Fairfield, Aroostook County, Maine. Nautilus, 41(3):84-85. [nine freshwater snails collected]

NYLANDER, O.O. 1930a. The *Valvata* of Aroostook Co., Maine. Nautilus, 44(1):30-31. [three *Valvata* species listed]

NYLANDER, O.O. 1930b. *Lampsilis radiata* Gmel. in Aroostook County, Maine. Nautilus, 44(2):69-70. [five freshwater snails also listed]

NYLANDER, O.OLSSON. 1936a. Land and Fresh Water Shells of Aroostook County, Maine. Privately published by the author, Caribou, ME. 23 pp. [28 freshwater snails listed]

NYLANDER, O.O. 1936b. The History of the Lymnaeidae of the Northern Part of Maine. Privately printed by the author, Caribou, ME. 7 pp. [*Stagnicola mighelsi* and *Physella ancillaria* from Aroostook County]

NYLANDER, O.O. 1938. The Crustacea and Mollusca of Caribou Stream. Privately published by the author, Caribou, ME. 12 pp. [14 freshwater gastropods listed for this Aroostook County stream]

NYLANDER, O.O. 1941. Marl deposit in Houlton, Aroostook County, Maine. Nautilus, 54(4):143-144. [seven freshwater snails listed]

NYLANDER, O.O. 1943a. Marl deposits in Bonaventure, north of Bay Chaleur, Quebec, Canada, and in Houlton, Maine. Nautilus, 57(2):45-46. [seven freshwater snails listed]

NYLANDER, O.O. 1943b. The Lymnaeidae of Northern Maine and Adjacent Canadian Provinces and Notes on Anson Allen and His Collection. University of Maine Studies. 2nd Series. No. 58. 42 pp., Appendix. Plates I-X. [17 freshwater snails collected mostly by Nylander in 3 northern Maine counties; 19 freshwater gastropods listed in Allen collection]

PILSBRY, H.A. 1895. New American fresh-water mollusks. Nautilus, 8(10):114-116. [*Helisoma anceps aroostookensis* from Aroostook County, Maine]

PILSBRY, H.A. 1905. Land and fresh-water mollusks of Alaska and adjoining regions. By William H. Dall. Nautilus, 19(8):93-95. [*Valvata sincera nylanderi* from Aroostook County, Maine, mentioned in this book review]

PILSBRY, H.A. 1912. A new species of *Amnicola*. Nautilus, 26(1):1. Plate I. [*Cincinnatia winkleyi* from York County, Maine]

SAY, T. 1821. Descriptions of univalve shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia, 2(1):149-179. [*Stagnicola emarginata* from "lakes of Maine"]

STIMPSON, W. 1851. Shells of New England: A Revision of the Synonymy of the Testaceous Mollusks of New England, with Notes on Their Structure, and Their Geographical and Bathymetrical Distribution. Phillips, Sampson & Co., Boston, MA. 56 pp. Plates I-II. [three freshwater snails from Maine]

TRUE, N.T. 1869. Influence of location on the growth of shells. Proceedings of the Portland [Maine] Society of Natural History, 1(2):126-127. [*Physella ancillaria* from Kennebec County, Maine]

TRYON, G.W., Jr. 1865a. Catalogue of the species of *Physa* inhabiting the United State. American Journal of Conchology, 1(2):165-173. [*Physella ancillaria* from Maine]

TRYON, G.W., Jr. 1865b. Catalogue of the species of *Limnæa* inhabiting the United States. American Journal of Conchology, 1(3):247-258. [five freshwater snails from Maine]

WALKER, B. 1897. *Planorbis nautileus* L. in America. Nautilus, 10(10):117. [four freshwater snails from Aroostook County, Maine]

WALKER, B. 1904. Notes on eastern American ancyli. III. Nautilus, 18(6):75-83. Plates V-VI. [*Ancylus borealis* and *Ferrissia parallela* from Aroostook County, Maine]

WALKER, B. 1906. Notes on *Valvata*. Nautilus, 20(3):25-32. Plate I. [*Valvata sincera* from Aroostook County, Maine]

WALKER, B. 1909. Notes on *Planorbis* II: *P. bicarinatus*. Nautilus, 23(1):1-10, 23(2):21-32. Plates I-III. [*Helisoma anceps* from six Maine counties]

WALKER, B. 1918. A Synopsis of the Classification of the Fresh-water Mollusca of North America, North of Mexico, and a Catalogue of the More Recently Described Species, with Notes (Parts I-II). Miscellaneous Publications No. 6, Museum of Zoology, University of Michigan, Ann Arbor, MI. 212 pp. [four freshwater snails with type localities in Maine]

WENTWORTH, E.P. 1896. Along the Damariscotta. Nautilus, 9(12):140-143. [three freshwater snails from Lincoln County]

WHITE, G.C. 1972. Establishing a Quantitative Ecological Base in the Penobscot Estuary Using Benthic Macroinvertebrates. Master of Science Thesis. University of Maine-Orono. 102 pp. [freshwater snails of four families identified to generic level only]

WINKLEY, H.W. 1896. The Goose Fair Brook. Nautilus, 10(2):15-16. [unidentified *Amnicola* from York County]

WINKLEY, H.W. 1909. Variation. Nautilus, 23(1):15-16. [large-sized *Planorbella trivolvis* from northern Maine]

WINKLEY, H.W. 1914. Mollusca of Maine. Nautilus, 28(4):48. [*Cincinnattia winkleyi* from York County]

NOTE: The author has compiled a list of freshwater snail synonyms to facilitate the use of the bibliography of this paper. He also has gathered selected references on the natural history of a number of the aquatic gastropods reported from Maine that would be advantageous to anyone commencing such studies. Both are available free upon request.

ADDITIONAL READING ON PIONEER MALACOLOGISTS

ANONYMOUS. 1862. A sketch of the history of conchology in the United States. American Journal of Science and Arts (2nd Series), 33(98):161-180. [capsulizes the careers of America's early malacologists, many of whom were still alive and contributing at the time of this publication; author was probably George W. Tryon, Jr.]

BOARDMAN, S.L. 1884. The late Mr. Anson Allen. The Home Farm, 4(16):2. [this elusive former serial was published by Boardman & Hall, Augusta, ME; the sketch in the Feb. 28th issue was reproduced in Nylander (1943b)]

BRUNNER, L. 1998. William Healey Dall 1845-1927. American Conchologist, 26(4):13.

FRANZEN, D.S. 1956. Types of mollusks described by F. C. Baker. Part I, University of Illinois. Nautilus, 70(1):21-27.

FRANZEN, D.S. 1957. Types of mollusks described by F. C. Baker. Part II, University of Wisconsin. Nautilus, 71(1):30-35.

FRANZEN, D.S. 1958. Types of mollusks described by F. C. Baker. Part III, Chicago Academy of Sciences. Nautilus, 72(1):30-34.

GOODRICH, C. 1936. Bryant Walker, 1856-1936. Nautilus, 50(2):59-64.

GOODRICH, C. 1939. The scientific writings of Bryant Walker. An annotated bibliography. Occasional Papers of the University of Michigan Museum of Zoology, (402):1-28.

JOHNSON, C.W. 1918. Henry W. Winkley. Nautilus, 31(4):136-137.

JORDAN, W.B., Jr. (Ed.) 1997. The Civil War Journals of John Mead Gould: 1861-1866. Butternut and Blue, Baltimore, MD. 564 pp. [This lifelong friend of Edward S. Morse served gallantly in the Civil War, attaining the rank of major. This book chronicles Gould's Civil War service and also contains photos of Gould and his family.]

LESLEY, J.P. 1881. Memoir of Samuel Stedman Haldeman, 1812-1880. National Academy of Sciences Biographical Memoirs, 2:139-172.

MARTIN, S.M. 1995. Maine's remarkable Edward Sylvester Morse: quintessential naturalist. Maine Naturalist, 3(2):81-102.

PILSBRY, H.A. 1926. James H. Ferriss: November 18, 1849-March 17, 1926. Nautilus, 40(1):1-6.

PILSBRY, H.A. 1927. William Healey Dall. Nautilus, 41(1):1-6.

ROSEWATER, J. 1975. Tribute to William Healey Dall. Bulletin of the American Malacological Union, pp. 4-6.

TRYON, G.W., Jr. 1861. List of American Writers on Recent Conchology. Balliere Brothers, New York, NY. 68 pp. [provides a listing of papers on malacology by the early American workers in the field]

VAN CLEAVE, H.J. 1943. Frank Collins Baker (December 14, 1867 to May 7, 1942). Nautilus, 56(3):97-99.

VAN CLEAVE, H.J. 1945. A memorial to Frank Collins Baker (1867 to 1942), pp. pp. xvii-xxiv. *In* The Molluscan Family Planorbidae, by F. C. Baker. University of Illinois Press, Urbana, IL. [a bibliography of Baker's publications appears on pp. xxv-xxxvi in this same book]

WEBB, W.F. 1942. United States Mollusca: a Descriptive Manual of Many of the Marine, Land and Fresh Water Shells of North America, North of Mexico. Privately published by the author, Rochester, NY. 220 pp. [sketches of early American workers in malacology appear on pp. 191-197]