THE MYSTERIES OF MYSTERY SNAILS

Facts and Myths

Gerry Mackie

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DEDICATION

To my nurturing family: My wife, Liz, my daughter Carolyn and her husband Robert Percival, their children Katlyn and Matthew, and dogs Jack and Murphy; my son Einar and his wife Kara, their sons Ewan and Griffin, and dogs Moose and Brutus. Thank you for your love and patience while writing this book.

I am so impressed by how well our four border terriers have trained me; Zeus (August 24, 1984-September 15, 1999), Xena (May 26, 1992-April 1, 2007), Thor (August 4, 2000-September 14, 2015), and Willo (September 6, 2010-).

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A comprehensive book relies heavily on images to illustrate several concepts, mainly in the chapters on biology and ecology. I relied primarily on images in iNaturalist, most of which are copyrighted and not for commercial use. Still, some are available to share and adapt under Creative Commons license, BY (see Appendix C for link), allowing re-users to distribute, remix, adapt, and build upon the material in any medium or format, so long as possible attribution provides to the creator. The figures with images Appendix C give the names, photograph numbers, and URL links to each image. The backgrounds were removed in most photos, focusing only on the snail or parts (e.g. the operculum). All images illustrate vital concepts and diagnostic characteristics of the Chinese and Japanese mystery snails. I thank the following people for sharing their photos; the names are in alphabetical order according to that listed on their site(s): Alexis Williams, Andrew Sebastian, David McCorquodale, Elissa Totin, Elliot Greiner, Erik Erbes, Judy Gallagher, Hyun-tae Kim, Marcus Rosten, Mathew, Oceanicadventures, Quinten Wiegersma, Robert T. Jackson, Rod, Sandy Wolkenberg, Steven Bodzin, Tia Offner, and Threelark.

LIST OF ABBREVIATIONS

AGL - African Great Lakes
Al – Aluminum
Alberta IASWG - Alberta Invasive Alien Species Working Group
AWS - American Fish and Wildlife Service
Ca - Calcium
Cd - Cadmium
Cl - Chlorine
CMR - Capture, Mark, Recapture
CMS - Chinese Mystery Snail
COSEWIC - Committee on the Status of Endangered Wildlife in Canada
Cr - Chromium
Cu - Copper
DO - dissolved oxygen
EC - Electrical conductivity
EDDMaps - Early Detection and Distribution Mapping System
Fe - Iron
GISS - Generic Impact Scoring System
GLM - Gerald Lloyd Mackie
Hg - Mercury
ICZN - International Code of Zoological Nomenclature
INS - Invasive Non-native Species
JMS - Japanese Mystery Snail
LDD – Long-Distance Dispersal
LGM - Last Glacial Maximum
Mg - Magnesium NaCl - Sodium Chloride
Mn - Manganese
N - Nitrogen
NCWRC - North Carolina Wildlife Resources Commission
NGSWG - National Status Working Group (Canada)
Ni - Nickel
NNS - Non-Native Species
NSW - New South Wales (Australia)
OFHA - Ontario Federation of Anglers and Hunters
P - Phosphorous
Pb - Lead

PCA – Principal Component Analysis
PIT - Passive Integrated Transponder
QM- Quagga mussel
RH - Relative humidity
RINSE - Reducing the Impacts of Non-native Species in Europe
SARA - Species at Risk Act (Canada)
SEM - Scanning Electron Microscopy
TDS - Total dissolved solids
TSS - Total suspended solids
USGS - United States Geological Survey
USGS-NAS - U.S. Geological Survey - Nonindigenous Aquatic Species
USWFS - United States Fish and Wildlife Service
WMSDB - Worldwide Mollusc Species DataBase
ZM - Zebra mussel
Zn - Z

PREFACE

Invasive species, especially molluscs, have been a staple for much of my research interests and time spent in the laboratory and field and publishing books and peer-reviewed articles. The publications include 7 books, 11 chapters in books, and more than 160 peer-reviewed articles, with 70 on the most invasive and nuisance freshwater species in North America, the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis rostriformis*). In addition, Mackie and Claudi (2010) describe several other invasive molluscs. Those regarded as nuisance species impact water quality, native species, ecosystem processes, and even the quality of human life; ironically, and most regrettably, humans are primarily responsible for the introductions of invasive species in North America. However, some species are regarded as somewhat benign. Indeed, some molluscs have questionable origins. That is, there are some evidence of fossil records (Pleistocene) of some "introduced" species (e.g., the Faucet Snail, *Bithynia tentaculata*) in some North American paleontological surveys, suggesting it has been here for thousands of years.

There are two motivations for this book. The first was several requests for confirmation of identification of the Chinese Mystery Snail (CMS) along with queries about the snail. The requests came from provincial ministries (e.g., Alberta, Ontario, and Quebec), colleagues, and cottage associations. The queries included the following:

(i) "Based on images sent, is this a Chinese Mystery Snail?"
(ii) "Apparently, there are two species of mystery snails in Canada, the Chinese Mystery Snail and the Japanese Mystery Snail. How do we tell the difference?"
(iii) "Is there enough scientific evidence to justify completing a risk assessment for CMS for a lake that is identified to have them?"
(iv) "Our lake has a history of toxic algae blooms (Cyanobacteria containing microcystin) in the last several years. Could CMS help or hinder the occurrence of these blooms?"
(v) "Does CMS have the potential to attack bass embryos, as has been documented with the related species *Viviparus georgianus*?"
(vi) "Will CMS proliferate in a lake with calcium levels typical of Canadian shield lakes?"

(vii) "Does CMS have the potential to die off in the mud where ice forms to the lake bottom in the winter, or does that even happen; what about winter anoxic areas?"
(viii) "Are there other concerns that you may be aware of when CMS seems to be proliferating in lakes?"
(ix) "Is there a potential for the snail to act as a vector for diseases new to the ecosystem and introduce organisms and parasites or enhance existing pathways?
(x) "Why are they called 'mystery' snails"?

The second motivation relates to one of the above questions: CMS as a nuisance species. I wrote a chapter (21) in the book "Nonindigenous Freshwater Organisms, edited by Claudi and Leach (2000), that suggests neither the CMS nor the Japanese Mystery Snail (JMS) appear to have any impact potential. However, some reports since then have disagreed with this assessment and dispute that they do have impacts. These disagreements prompted me to search for convincing evidence to ascribe the level of impact that these two mystery snails have in North America.

There are myriad peer-reviewed publications on CMS, JMS, and their related species (this book reviews more than 1,500 in my library, about 930 of which are cited herein) to address the above concerns and others. As an aside, I have a fishpond in my backyard that has several generations of CMS. The pond was built in 2005, and submersed vegetation (species of *Elodea*, *Potamogeton*, *Myriophyllum*) were transplanted from a local stream into the pond. The CMS could have been introduced at that time within some of the submersed vegetation. However, the snails were not noticed until 2015, when a dozen or so were found in the spring while scooping leaves and debris off the bottom. The more likely vector for their establishment is waterfowl, namely mallards (*Anas platyrhynchos*), that frequent the pond, especially in the spring (see Chapter VII. Dispersion). In 2008, a pair of mallards produced 13 ducklings in a nest at the pond's edge. Only 12 were counted (Figure 1) before the mother moved the ducklings to another pond across the road. But she forgot one that our dog found and gently picked up in his mouth and gave unharmed to my wife. We named him Marvin, and she fostered it for three to four weeks, then moved him (see Figure 1) to an Ontario Ministry of Natural Resource's licensed facility to finish raising him until he flew off.

There was a range in size classes of CMS, suggesting that they had been there for four to five years. Perhaps they were introduced by waterfowl, which frequently visit the pond. The pond is aerated every winter with two large air stones supplied with air from a pump through two plastic hoses. In the winter of 2018, a red squirrel chewed through the hose trying to get into the shed housing the pump sometime in January and cut off the air supply to the pond and the pond went anoxic. All goldfish (~50) except three died. Most of the mystery snails also died, except four that I found in the spring. Some of the dead snails are used as images in this book and some water chemistry of the pond.

My science and research background encouraged me to twist, or "tort," in snail jargon (see Chapter V), the questions into null hypotheses and place myself as a devil's advocate. There is a preponderance of evidence in the literature inculpating CMS and JMS as nuisance species. Chapters VI to X, in particular, defend the two mystery snails. Null hypotheses are scientific statements that generally require statistical analyses of support before their acceptance or rejection. However, most of the statistical analyses are those performed by the authors of the literature cited. Thus, I prefer to call the following statements merely hypotheses, proposing these mystery snails are not misery snails, but rather gentle giants, not the tyrannical titans of invasive freshwater gastropods!

1. The two species are not a nuisance for the following reasons:
    a) They do not compete with and displace native species.
    b) They do not eat eggs of fish, especially sport fish.
    c) They do not cause or abet blue algae blooms.
    d) They are not tolerant of anoxia or contribute to it.
    e) They do not carry infectious diseases and/or parasites unique to them.
    f) They cannot tolerate a wide range of water chemistry (e.g., acidic to alkaline waters; near-complete anoxia).
    g) They are intolerable of degraded habitat conditions.
    h) They do not disperse themselves but are introduced by people, either intentionally or unintentionally.
    i) They are not edible.
    j) They are not so invasive that they need a risk assessment for each jurisdiction (province, state, etc.).
2. Why are they called mystery snails?

Figure 1. Family of mallards, with 12 ducklings following the mother, with the father in the lower left, and the 13th duckling, Marvin, in the lower right. The ducklings were swimming on the winter blanket of our pool in the spring. Photos taken May 15, 2008, by GLM.

CHAPTER I

INTRODUCTION

The Mollusca is an exceptionally diverse phylum with between 80,000–100,000 described species (marine, freshwater, and terrestrial) with potentially 100,000 more species to be defined (Strong, Gargominy, Ponder, and Bouchet 2008; Pyron and Brown 2015). Bouchet and Rocroi (2005) estimate 409 families of Recent gastropods; they recognize 26 taxa that are wholly or mostly restricted to freshwater. The largest molluscan classes are Gastropoda (stomach foot, from Ancient Greek: *gastḗr* = stomach and *poús* = foot) with about 4,000 freshwater species and Bivalvia (from Latin *bis* = two, and *valvae* = leaves of a door; also known as Pelecypoda, or axe-foot) with about 1,200 species (Pyron and Brown 2015). Freshwater gastropods occur on all continents except Antarctica and in nearly all aquatic habitats, including rivers, lakes, streams, swamps, underground aquifers and springs, temporary ponds, drainage ditches, and other permanent waters (Strong, Gargominy, Ponder, and Bouchet 2008).

This book is a comprehensive review of the taxonomy, morphology, anatomy, behavior, ecology, distribution, impacts, and control of "viviparid" (defined below) snails, with a focus on the Chinese Mystery Snail (often referred to herein as CMS, Figure 1-1) and the Japanese Mystery Snail

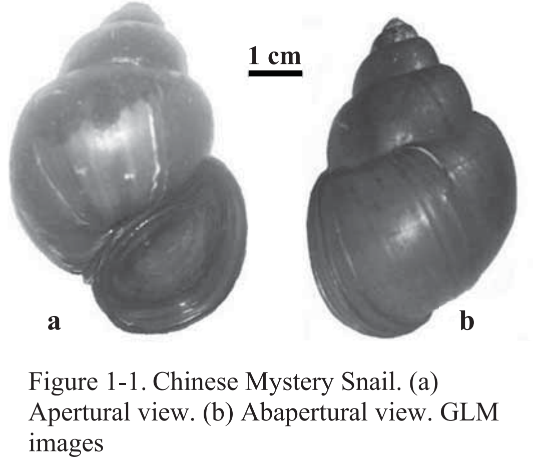

Figure 1-1. Chinese Mystery Snail. (a) Apertural view. (b) Abapertural view. GLM images

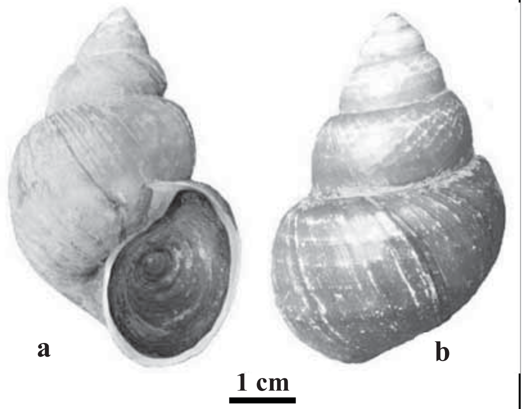

Figure 1-2. Japanese Mystery Snail. (a) Apertural view. (b) Abapertural view. Images are courtesy of Brian Watson.

(often referred to herein as JMS, Figure 1-2). More than 1,500 publications including books, monographs, peer-reviewed articles, reports, and websites were reviewed, with about 930 referenced herein. The most time-consuming topic is the taxonomy of the myriad issues of viviparid snails (e.g., names, shell morphology, ecology, impacts, control options). The taxonomic studies are from many parts of the world, and, fortunately, the distributions of CMS and JMS fall out pretty much in the same reviews. I have relied on studies of other closely related viviparids here in North America, Europe, and Asia for articles on morphology, anatomy, behavior, ecology, etc. The closely related species referred to herein are often lumped together as "viviparids," the family of which is commonly known as "mystery snails," my preferred family name. Other common family names are river snails, mud snails, and apple snails, the river snails being a select name in European literature.

The Chinese Mystery Snail is more common in North America than the Japanese Mystery Snail and has captured most of the interest of provincial resource departments, cottagers, fishpond and aquarium enthusiasts as well as students of freshwater molluscs, especially gastropods (snails). CMS and JMS are members of the family Viviparidae, which contains several native species, many of which share the same attributes as the mystery snails. These attributes include a trap door (an operculum covering the shell opening (aperture), all both filter feed and deposit feed, the right tentacle in males serves as a penial organ, and all females brood their young. In many instances, there is more information for closely related native viviparid species than for CMS or JMS, and inferences are made for some biological aspects of each species. The family Viviparidae has many species in several genera. This book focuses on species of *Viviparus* and *Cipangopaludina*, the latter of which includes the Chinese and Japanese mystery snails; this categorically applies to the expression “no viviparids” (i.e., no species of *Viviparus* or *Cipangopaludina* are present). Alternatively, the phrase “viviparids are present” categorically implies any or all species of Viviparidae are present. For example, there are 22 genera in the family. Van Bocxlaer and Strong (2020) and Galli (2017) attribute 80 species to *Viviparus* and 27 species to each of *Cipangopaludina* and *Bellamya* in these three genera alone.

There is substantial scientific terminology throughout the book that perhaps many laypersons, aquarists, and cottagers cannot decrypt, so some effort is made on defining much of it, especially for taxonomy. Chapter 3 (Classification, Taxonomy, and Etymology of Mystery Snails) is replete with scientific terms and would likely be more interesting to graduate students, malacologists, academia, and authorities in charge of natural resources, conservation, aquatic invasive species experts, and so on than the layperson. The remaining chapters untangle most of the scientific terms, and once identified, common names are used. The last chapter (X. Mysteries Addressed, Conclusions, and Recommendations) provides answers to the questions proffered in the Preface, sums up my pleasant findings and the more significant disappointments, and makes several recommendations that mainly relate to addressing impacts. The questions are a preamble to making risk assessments, a necessity for most invasive species. Risk assessments are comprehensive, requiring confidence in the knowledge of several concepts, including these:

- Species descriptions (Chapter V. Biology)
- Probability of introduction (Chapter VII)
- Probability of establishment (Chapter VI. Ecology)
- Pathways and vectors (Chapter VII. Dispersion)
- Negative and positive impacts (Chapter VIII, Impacts)
- The need for control and control options (Chapter IX, Control options)

The assessments are based on peer-reviewed literature dating back to Linnaeus (1735) up to the present for obtaining information on the classification, taxonomy, etymology, global distribution (i.e., Europe, Asia, Africa, Australia, West Indies, South America, Central America, North America), and variations in biological and ecological attributes fundamental to evaluate dispersion potential and risk assessments. Of more than 1,650 records, many (or perhaps most) are in cottage lakes for which many cottage owners are genuinely concerned about potential impacts. These impacts include parasites that use snails as intermediate hosts, the final hosts being humans and wildlife; potable water supplies; and algal accumulations. The book contributes to current and potential research and sources of information for risk assessments. Some impacts are challenged herein, primarily because they are based on parenthetical remarks perpetuated in fact sheets.

The book is the derivative of information from several publications and several websites. The oldest publication is the tome by Linnaeus (1735), who introduced gastropods as a group of “Testacea” in the class “Vermes.” More than 930 publications referenced herein deal with some aspect of mystery snails or species closely related to them from as many as 79 countries (42 European and 37 Asian). While the viviparids appear in several countries, only a few languages represent the literature, the more prolific contributions to this book being in French and German, others being in Chinese, Croatian, Czech, Japanese, Portuguese, Russian, and Spanish. I have relied chiefly on Google Translate to translate the different languages into English, and when some parts of the translation made little sense, I relied on friends for clarifications.

The next chapter (II) describes two schools of taxonomy: The New School, or “Nouvelle École,” and the Old School, or the “L’ Ancienne École.” While searching the literature, an attempt was made to determine whether the “L’ Ancienne École” and “Nouvelle École” influenced the number of studies of viviparids. Before proceeding with the distributions, morphologies, anatomies, behaviors, ecologies, and so on of the Chinese and Japanese mystery snails, it was necessary to filter through all the taxonomic disparity of both the old and new schools. The search dictated much time and effort to find all species of viviparids and the synonymies of the Chinese and Japanese mystery snails. Table 1-1, from Strong, Gargominy, Ponder, and Bouchet (2008), gives some idea of the extent of searches needed to appropriately describe the attributes of both mystery snails around the globe.

The considerable taxonomic confusion necessitated querying several common and scientific names during literature searches. CMS was first described in 1840 by Gray and JMS in 1864 by von Martens. Indeed, substantial disagreement and debate on CMS taxonomy prompted Lu, Du, Li, and Yang (2014) to examine the morphology of several species of viviparids in China, where the existing taxonomy for Viviparidae includes approximately 61 recognized species in nine genera. Much of the morphology of CMS relies on descriptions by Lu, Du, Li, and Yang (2014).

Table 1-1. The total number of validly described species of freshwater gastropods arranged by zoogeographical regions. The number of introduced species is in parentheses.

Taxon	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Viviparidae	20–25	27	1	19	40–60	19(1)	0(2)	0	125–150
Total	1,408–1,711	585	440–533	366	509–606	490–514	154–169	0	3,795–3,973

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

The articles on taxonomy of the two mystery snails for this book date back to 1840 (e.g., Gray 1840), the original description of the Chinese Mystery Snail, and Thompson (1840), which is a catalogue of the land and freshwater Mollusca of Ireland. Prashad (1928) is a 99-page treatise on the recent and fossil viviparids, their distribution, evolution, and paleogeography. Blainville (1825) introduces the history of malacology, the importance of the study and knowledge of molluscs, and the early systematics of Vivipare and Paludine mystery snails as well as the structure and function of terrestrial, freshwater, and marine molluscs.

Not surprisingly, while searching for facts and answers to the mysteries of mystery snails, some myths are unveiled. As with many myths, they are perpetuated over time, mainly because no one has challenged them and instead they have been accepted as facts. Most of the myths about the Chinese and Japanese mystery snails relate to their dispersal agents and impacts on the environment, human health, and industries.

I look forward to rebuttals to my challenges, summarized in Chapter X.

CHAPTER II

CLASSIFICATION, TAXONOMY, AND ETYMOLOGY OF MYSTERY

A. Introduction

There is no question that the greatest challenge herein was in synthesizing the systematics of mystery snails. As a result, considerable time is spent in this chapter attempting to select a valid classification system for the mystery snails. There are myriad systematics, partly because many taxonomists opted for the “new school” (also called “splitters”) instead of the “old school” (often called “lumpers”). Audibrert and Breure (2017), review Jules N. René Bourguignat (1829–1892), who founded the Nouvelle École (or “école transformiste,” Bourguignat, 1882), was the progenitor of criticisms of the disparity between the old and new schools. Bourguignat was a prolific author and a well-known malacological oeuvre but a controversial person who was disliked by many of the old school conformists, including Crosse, Drouët, and Fischer in France and Clessin, Kobelt, and Pfeiffe, in Germany (Audibrert and Vivien 2007; Audibrert and Breure 2017; Bank, Falkner, Falkner, and Neubert 2019; Breure and Audibrert 2019). Vinarski (2018) described the “Bourguignatians” as “notoriously known as horrendous species splitters, whose scientific production consisted mostly in the description of tens and hundreds of new species of snails and bivalves (42).”

The disparity in principles between “L’ Ancienne École” and “Nouvelle École” and the unusual nomenclatural procedures are elucidated in the first volume of Bourguignat’s “Société Malacologique de France” (SMF; Anonymous 1884). There are 18 articles in the statutes of the Société (Anonymous, 1884). In the preamble to the statutes are two key paragraphs that characterize the questionable nomenclatural procedures (translated from French). Page 6 states, “Based on nature, without preconceived ideas, after having made a clean sweep of all definitions, our colleague [presumably Bourguignat] has proposed to raise to the specific rank of any form distinguished from its neighbors at least by three characters, and reject, to that of variety, any other separated by a lower number of differential signs.” In other words, only three key characters were needed to diagnose a species, ignoring varieties and ecomorphs. Dance’s (1970) interpretation is “Any form with less than three constant characters was a variety; any form with three or more was a species and merited a name” (70). The second appears on page 71: “Of all the taxonomic methods, our favorite is based on the subordination of characters, because it is the only natural, the only truly French. It is that of the Jussieu, the Lamarck, the Cuvier, the Alcide d’Orbigny, all the great scholars, the glory and the honor of our country.” Is this a political statement, that the French taxonomists should be favored, and therefore honored, for their contributions?

The Société’s main scope of the study was “Molluscs of the globe, terrestrial, fluvial and marine, living or fossils, the latter only since the beginning of the Tertiary period” (Article 3). The Société consisted of 12 founding members (Article 4), three of the sycophants who contributed to the viviparid literature in the first volume: Jules René Bourguignat; Arnould Locard; Georges Servain. The 14th Article lists the Société as the umbrella for three journals; *Bulletins de la Société Malacologique* (seven volumes between 1884–1890); *Revue Biographique et Bibliographique*; *Annales de Malacologie* (two volumes, 1884–1886, both edited by G. Servain), all evidently, in reaction to the *Journal de Conchyliologie*, co-edited by Hippolyte Crosse and Paul N.H. Fischer (Audibrert and Breure (2017). Locard (1884), referred to malacologists as either “L’ Ancienne École” and “Nouvelle École,” declaring that the old school claims to stick to the so-called Linnean and Draparnault types. The new school, on the contrary, created a considerable number of new species, although some species were perplexing to him (Bourguignat 1853). Many of the species reported in the journals are eponyms or words based on or derived from a person’s name. For example, Bourguignat (1884) lists species he described and species that his friends described: *Vivipara. imperialis*, Bourguignat, 1884; *V. contecta*, Bourguignat; *V. brachya*, Letourneux; *V. lacustris*, Beck, 1847; *V. communis*, Moquin-Tandon, 1855; *V. paludosa*, Bourguignat, 1880; *V. occidentalis*, Bourguignat., 1870; *V. bouriguinati*, Servain, 1884; *V. subfasciata*, Bourguignat, 1870; *V. fasciata*, Dupuy, 1851; and *V. penthica*, Servain, 1884.

The new taxonomy imposed by Bourguignat fomented wide criticism, ire, and hatred by taxonomists of L’ Ancienne École. As Servain (1891), one of 12 founders of SMF, stated, “Among the Malacologists, there are few scholars whose scientific ideas have aroused as violent enmities as those with which our colleague is honored, enmities inherent in his role as innovator” (10). Locard’s (1884) account of the mutual excoriations between the two schools is quite evident when he stated, "regrettable and deplorable question of non-reasoned bias, have split into two, singularly baptized under the term of the old and new school (61)." Dollfus (1901) described the study conditions of existence and publication of major works, many of whom were founders, in each of the three journals of the Malacological Society of France Annals of Malacology. Much of the recent criticism is described by Bouchet (2002), Backhuys and Breure (2016), and Audibert and Breure (2017). They are recommended for those interested in the chronology of the criticisms.

Audibrert and Breure's (2017) study are particularly revealing; they explored the nature of the relations between the contributors of the *Bulletins de la Société Malacologique de France* and *Annales de Malacologie* with other malacologists in France. They used both these publications and other malacological literature (e.g., contemporary European malacology journals, such as *Journal de Conchyliologie* (edited by Crosse and Fischer), Zeitschrift für Malakozoologie (edited by Menke, Pfeiffer followed by Clessin), and the Jahrbücher der Deutschen Malakozoologischen Gesellschaft (edited by Kobelt) (Audibert and Breure 2017). They examined positive, neutral, or negative connotations to other people, most of them not being members of this Société. They found some founding members of SMF had positive relationships with the membership. Four of the founding members (Bourguignat, Fagot, Locard, and Servain) received the most egregious relationships. The establishment of the Nouvelle École led to reinforcement between the members and favored French malacologists who were considered role models. The editors of the mainstream journals (Crosse and Fischer in France; Clessin, Kobelt, and Pfeiffer in Germany) were all among those attacked. When Audibrert and Breure (2017) examined the nationalities, they found a relatively high number of Germans were also attacked.

B. Higher Classifications

In my attempt to determine the provenance of mystery snails, it was necessary to search for articles that reveal some aspect (distribution, biology, ecology, etc.) of closely related species, especially those in the same family. The approach used for historical searches was to start with the most recent publication and work backwards, using literature cited in the publications. The discussion that follows is *not* a critique of classifications, merely a summary of the classification schemes for that period. There were no formal rules for establishing taxonomic names during the early classification schemes until the International Code of Zoological

Nomenclature (ICZN) in 1964. For example, Article 29 states that family names must end in -idae (e.g., Viviparidae), subfamily names in -inae (e.g., Viviparinae), superfamily names in -oidea (e.g., Ampullarioidea), and tribes in -ini- (e.g., Ampullarini). Fortunately, scientific names (genus and species) are the same in any language. The most prolific writers of prosobranch classifications were French and German, and the most rewarding searches came through these two languages.

My search began with articles from 2019 (not including websites accessed in 2020) and ended with (or actually started with), surprisingly, Linnaeus' 1735 publication "Systema Naturae." Linnaeus (1735) included snails in "Vermes," a class occupying the sixth slot of his animal systematics. It was divided into five orders, two of which included Mollusca that were not what we think of today; in Mollusca, he included slugs, sea slugs, polychaetes, jellyfish, starfish, and sea urchins, and in Testacea he included chitons, barnacles, clams, cockles, nautiluses, snails, and polychaete worms. Unfortunately, Linnaeus' "Testacea" included only marine species, as in his Volume 1, Part 6 (Linnaeus 1788).

In Lamarck's (1801) tome," Système des Animaux Sans Vertèbres," he revised Linnaeus' system and created seven different classes, the first being "Mollusques" (60). While the family of mystery snails is not described, the ancient group "Cy'clostome" is described (87), "LXIII GENRE"). Lamarck's later book (1853) does list the genus of mystery snails, "Paludine," as discussed below.

In the following text, the earlier classification systems are examined and compared to the classification systems reported in the 21st century. These different classification schemes, highlighted in ***bold italics*** or tables, certainly helped me find literature on all aspects of mystery snails, from taxonomy, distribution, anatomy, physiology, ecology, invasiveness, and so on for the mystery snails.

Early classifications of molluscs relied heavily on "conchology," the study of molluscan shells. The evolution of molluscan classification is expounded by Johnson (1850), who examined several classification systems, notably those of Linnaeus' (1735, "Systema Naturae"), Darwin's (1872) *Origin of Species*, Cuvier (1800), and Lamarck (1801). Scudo (1990) analyzes the prophetic theories of Darwin and his approach to phylogenetic systematics, and Barsanti (2000) discusses Lamarck's theory of classifications, his holistic approach to the biosphere, and coining the term "biology."

Cuvier (1800, Table 5) was the first to use Mollusca in its present meaning. The Gastropoda were initially referred to as "Testaceous Gasteropods," by Cuvier (1800), with turbinate shells. Lamarck's system was similar, but he described them as unilocular ("containing a single chamber”) univalves (Johnson 1850). The customary classification recognizes two groups (subclasses), Prosobranchia and Pulmonata in the class, Gastropoda (“stomach foot”) (16). However, the phylogeny and classification of the Pulmonata are controversial, with new clades, Heterobranchia and Eupulmonata (Haszprunar and Huber 1990, 196; Bouchet and Rocroi 2005, 281), but they are all referred to herein as pulmonates. The freshwater prosobranchs have three diagnostic features: (a) gills (branchia), which extract dissolved oxygen (DO) from the water and are located ahead (pros, Greek for toward) of the heart; (b) an operculum, a hard lid or trap door made of protein and/or calcium) on the dorsal surface of the foot and seals the aperture of the shell when the animal retracts; and (c) separate sexes. Additionally, some species are ovoviviparous (often cited as viviparous), whereas others lay eggs. In contrast, the pulmonates (a) have lungs (*pulmo*, Latin for lung) instead of gills, giving them the amenity of being able to breath air and to extract DO from the water through their vascular mantle; (b) they lack an operculum; and (c) they are hermaphrodites. All pulmonates are oviparous (“*oviparus,”* Latin for egg [*ovum*], meaning egg laying); none produce living young.

Much of the literature refers to “viviparids” as “viviparous” (e.g., Woodward 1851; Horsley 1915; Hamilton-Bruce 2002; Jakubik 2009), but Van der Schalie (1936) argues they are “ovoviviparous” because ovoviviparity “is to be applied to any group which hatches its young from the egg before expelling it. This term should obviously be applied in many instances where viviparous is used (16).” He further maintains that viviparity “is almost universally used in cases where ovoviviparous is implied, it should obviously not be used where it applies to groups of Mollusca. Its use should be restricted to cases (such as mammals) where there is a placental or immediate connection between parent and offspring.” The etymology of ovoviviparous is derived from combining Latin, *ovum* (egg) with *vivus* (alive, living), and *pario* (give birth, bring forth). The case for ovoviviparity is given in Section VII.B.a. Reproduction.

The higher classification systems using morphological (mainly shell) characters had evolved considerably since Linnaeus’ (1735), “Systema Naturelle,” when he termed the Mollusca “Testacea.” Linnaeus’ (1767) first volume, “Systema Naturæ per regna Tria Naturæ’ (“System of Nature through the Three Kingdoms of Nature”), describes classes, orders, genera, and species of marine molluscs (1106–1269), but not of freshwater mystery snail’s relatives. Lamarck revised Linnaeus’s system in 1801.

Lamarck (1801) divided the series of animals into seven distinct classes: 1. Molluscs; 2. Crustaceans; 3. Arachnids; 4. Insects; 5. Worms; 6. Jellyfish; and 7. Cnidarians. For molluscs that include mystery snails and their relatives, Lamarck assigned them to his second of four divisions of molluscs with heads, “Mollusques Céphalés,” under “Conchiliféres,” which have a complete spired shell with a single chamber. These were further divided into two subdivisions: 1. Spired shell with scalloped or channeled apertures (e.g., Cones, Volutes, Olive shells) and 2. Spired shell without a channel at its base (e.g., *Ampullaria*, or Apple snails) and would include but did not list mystery snails. Later, Lamarck (1853) classified Gastropoda as a division of molluscs called “Trachélipodes.” Included under this division were the “Péristomiens,” translated from French as “Lidded fluvial trachelipods, breathing only water, operculated shell, conoid or subdiscoidal, with the edges of the opening united.” (Tracheliopods are an artificial group of gastropods containing a spiral shell and the foot attached to the base of the neck). Lamarck (1853) did include mystery snails under “The Paludine,” including 21 living species of *Paludina* and 13 fossil species. ***Summary of Lamarck’s (1853) higher classification: Class - Trachélipodes; Order - Péristomiens; Family(?) - Paludine.***

However, Linnaeus was not the first to try to organize a complete system of conchology. Blainville’s (1825) higher classification scheme was based on the presence or absence of a shell; if a shell is present, they are either conical or limpet-like. They also have sense organs (e.g., tentacles); a radula (ribbon of teeth in the mouth) is usually present; gills are present but of different types; the position of the anus is different; they can be dioecious, or monoecious. Blainville (1825) relied on contributions from several naturalists from 15 different countries, notably France, Germany, and Italy, with the largest literature bases on prosobranchs. ***Summary of Blainville’s (1825) higher classification: Type - Malacozoa; Class - Paracephalophora; Order - Asiphonobranchiata; Family - Cricostomata***

Reeve (1841) recounted the contributions of Daniel Major in 1675 and several other naturalists who contributed to the advancement of conchology classification schemes. Reeve’s (1841) classification was distinctly based on the principles established by Linnaeus’ simple arrangement described in his “Systema Naturelle.” His views emulated, as closely as possible, the general views and intentions of Lamarck. Reeve (1841) referred to his system as “Conchologia Systematica.” His classification scheme seems to influence later classification schemes, such as Cuvier (1849), discussed next. ***Summary of Reeve’s (1941) higher classification: Phylum - Mollusca (Conchifera); Class - Gasteropoda; Order - Pectinibranchiata; Family - Peristomata.***

Cuvier’s (1849) higher classification of Mollusca consisted of three classes, one of which was “Gasteropoda.” Within the Gasteropoda, the mystery snails were classified under the order “Pectinibranchiata,” which includes *Paludina*, an early genus name for mystery snails and their relatives. Within the pectinibranchs is the genus *Cyclostoma*, a terrestrial group that once included *Paludina* (as a subgenus), but Cuvier extracted it from *Cyclostoma*. In Cuvier's classification, *Paludina* is a member of the family "Trochusidae." ***Summary of Cuvier's (1849) higher classification: Phylum - Mollusca; Class - Gasteropoda; Order - Pectinibranchia; Family - Trochusidae.***

Moquin-Tandon (1855a, b) incorporated several anatomical characteristics into his classification of viviparids. Table 2-1 summarizes Moquin-Tandon's (1855a, b) classification system.

Table 2-1. Classification of gastropods by Moquin-Tandon (1855a, b).

Taxon	**Name**
Class	Gastéropodes
Tribe	Opercules
Order	Branchiféres
Family	Péristomiens

Several other classification schemes were published in the 19th and early 20th centuries, and as time passed, systematists focused on a broader array of systems and incorporated them into the classification of prosobranchs. For example, Bouvier (1887) published a detailed account of the nervous systems. Bouvier (1888) also published an analysis of the anatomy of stenoglossal prosobranchs. Perrier (1889) described the anatomy and histology of the kidney of prosobranch gastropods. Amaudrut (1898) described the anterior part of the digestive tract and the torsion in several gastropod species. Hannibal (1912) did an ontogenetic classification of molluscs, including the Japanese Mystery Snail. The details of all these studies are described later under 6. a. ii. Anatomy.

Much work has been done on phylogenetics of prosobranch molluscs in the 20th century. Cox (1960), Ponder (1973), Bieler (1992), Haszprunar (1988), Perrier (1889), Walker (1919), and Ponder and Lindberg (1997) have examined the origin, evolution, classification systems, and the phylogenetic relationships of prosobranchs. The classification was based on morphological characters, including shell; operculum; muscles; mantle cavity; and gills. The circulatory, excretory, reproductive, alimentary, and nervous systems and sense organs were also included in their analyses.

Cox (1960) incorporated both neontology and palaeontology in his systematic survey of Gastropoda. Neontology is the study of extant taxa, such as species, genera, and families, with taxa still alive instead of their being extinct. Neontologists used “taxobases” (singular, taxobasis) to distinguish between higher gastropod taxa. As a basis for the primary taxis, Cox (1960) gives examples of the presence and nature of the shell, respiratory organs, mode of reproduction, nervous system, orientation and structure of the heart, nephridia, and operculum. The radula, the presence or absence of a proboscis, an inhalant siphon, foot, mode of life, and feeding habits have all been used as taxobases at somewhat lower levels. Cox (1960) argued that “higher gastropod taxa recognized by neontologists are mostly true natural groups, distinct branches of the tree of descent (247).” In the scope of neontology and paleontology, Cox (1960) distributed Prosobranch gastropods between two orders, “Mesogastropoda” and “Stenoglossa,” the latter of which was renamed, “Neogastropoda” by Wenz (1938–1944, cited by Cox 1960). The two orders were included in a single order, Pectinibranchia, but Cox (1960) suggested replacing it with Caenogastropoda (*Caeno* from Ancient Greek, *kainós*, = new), which had their origin in the Archaeogastropoda (from the Latin form of Greek *arkhaios* = ancient, primitive). Cox and Knight (1960) included the Archaeogastropoda (formerly Aspidobranchia) and the later taxa in the Caenogastropoda (formerly Pectinibranchia). The Caenogastropoda is a currently supported clade and includes the Architaenioglossa groups (snails having gills and often an operculum), as originally proposed by Cox (1960) and adopted by Taylor and Sohl (1962), Ponder and Warén (1988), and Ponder and Lindberg (1997). ***Summary of Cox’s (1960) higher classification: Class - Prosobranchia; Order – Pectinibranchia (Caenogastropoda).***

Taylor and Sohl (1962) reviewed publications on the classification of living and fossil Archaeogastropoda and other Paleozoic gastropods between 1938 and 1960. In their classification, they divided Gastropoda (consisting of 7,324 genera and subgenera) into two subclasses, Streptoneura (with 4,218 genera and subgenera) and Euthyneura (with 3,106 genera and subgenera). The subclass Streptoneura precedes Prosobranchia and includes marine, freshwater, and land operculate gastropods that, due to torsion, have the loop of visceral nerves twisted into a figure eight. This configuration resulted in the intestines, heart, nephridia, gills, and nerve cords migrating from the animal’s left side to its right side. (See section 6. Biology, a. Morphology and anatomy, ii. Internal Morphology for details.) Taylor and Sohl’s (1962) classification of Gastropoda is summarized in Table 2-2.

Table 2-2. Classification of gastropods by Taylor and Sohl (1962).

Taxon	Name
Class	Gastropoda
Subclass	Streptoneura
Order	Mesogastropoda
Superfamily	Viviparacea
Family	Viviparidae

Ponder and Warén (1988) added to Prosobranchia two other orders: Neotaenioglossa (with three suborders) and Neogastropoda. They also listed a second subclass of gastropods, Heterobranchia (with one order. They proposed the classification for the family Viviparidae summarized in Table 2-3.

Table 2-3. Classification of Gastropoda by Ponder and Warén (1988).

Taxon	Name
Class	Gastropoda Cuvier, 1797
Subclass	Prosobranchia Milne-Edwards, 1848
Superorder	Caenogastropoda Cox, 1960*
Order	Architaenioglossa Haller, 1892
Superfamily	Ampullarioidea Gray, 1824

*Ponder and Warén (1988) listed Cox (1959), but it should be Cox (1960).

Over the last several years, many classification schemes have been established using different methods, as the foregoing attests to. The different methods and philosophies have been extensively reviewed by many, including Wiley (1979), Mayr (1981), Haszprunar (1986, 1988), Salvtni-Plawen (1990), Lydeard and Lindberg (2003), McArthur and Haraseych (2003).

Many significant contributions to gastropod phylogeny occurred in the 1980s (Ponder and Warén 1988). Additionally, significant is the Austrian Haszprunar's (1988) phylogeny, which was based on several gastropod features: radula, nervous system, osphradium, ctenidia (gills) types, kidney, and sperm morphology. However, he favored the nervous system in his classification system because all Archaeogastropoda have a streptoneurous and hypoathroid (Greek *hypo*, meaning "under," *athroid*, meaning "gathered together") condition in which the pleural and pedal ganglia lie close to each other or are dystenoid (the two ganglia lie in the anterior region of the body) nervous system. He compared four classifications of Recent streptoneuaran gastropods: (a) a clado-evolutionary system based on the nervous system (his preferred version); (b) a clado-evolutionary system based on the gill-types and the alimentary tract; (c) sequential, according to the rules of Wiley (1979); and (d) cladistic, according to the rules of Hennig (1966), summarized in Table 2-4.

Bieler (1992) attributes the frequency of higher-level phylogenetic revisions and classifications in recent literature "as not so much a reflection of major breakthroughs in phylogenetic research as it is an indication of a new exciting phase of data gathering and discussion after a long period of relative stasis (330)." He concluded that "despite the many new discoveries and advances in methodology, the group is far from having a sound taxonomic framework," and any attempt to present the classification of Gastropoda at this point would be premature. Nevertheless, other classification schemes continued to be developed.

Bouchet and Rocroi (2005) were among the first to complete gastropod taxonomy that primarily employed the concept of clades (Greek = "*one clan*"), or a "natural grouping" of organisms based on a cluster derived statistically. Most of the previous taxonomic schemes (e.g., Darwin, Linnaeus, Lamarck) for gastropods and other taxa relied on morphological features to classify animals and used taxonomic ranks such as order, superorder, and suborder. Without going into a lot more detail above the family level, Bouchet and Rocroi (2005) placed Viviparidae under the order "Vivipariformes." Sitnikova and Starobogatov (1982) listed them in the Superorder, "Vivipariformi," containing suborders "Viviparoidei" and "Valvatoidei." The Viviparoidei, contained the superfamilies, "Archimedielloidea," "Pomatioidea," "Neocyclotoidea," and "Viviparoidea." Poppe and Tagaro (2006) list the "New classification of Gastropoda according to Bouchet and Rocroi (2005)" shown in Table 2-5.

Perhaps the most detailed phylogenetic analysis was by Ponder and Lindberg (1997). Their research used 117 characters among 40 taxa, the most common being the prosobranchs—five outgroup taxa representing four conchiferan groups and one polyplacophoran group. Of the 117 characters reviewed and included in the analyses were 9 shell features; 2 opercular; 2 muscular; 4 ctenidial; 12 renopericardial; 24 reproductive features, including 17 based on sperm and spermatogenesis; 27 of the digestive system, 32 of the nervous system and sense organs; and 3 were developmental of the foot and hypobranchial gland.

Bank (2006) prepared a catalogue of all the species-group and genus-group names applied to the freshwater molluscs of Greece. He included information on distribution, type localities, source of type material, and an extensive bibliography. His classification of viviparids given in Table 2-6 is similar to the version shown in Fauna Europaea by De Jong, Verbeek, Michelsen, Bjørn, et al. (2014), but the subfamily name used is Viviparinae.

Table 2-4. Classification of the Recent streptoneuran Gastropoda by Haszprunar (1988).

(a) Clado-evolutionary, primarily based on the nervous system
Class: Gastropoda
Subclass: Streptoneura
Order: Archaeogastropoda Thiele, 1925
Suborder: Architaenioglossa Haller, 1892
Superfamily Ampullarioidea Guilding, 1828 = Viviparoidea Gray, 1847

(b) Clado-evolutionary, primarily based on the gill-types and the alimentary tract
Class Gastropoda Cuvier, 1797
Subclass: Prosobranchia
Order: Aspidobranchia
Suborder: Architaenioglossa Haller, 1892

(c) Sequential, according to the rules of Wiley (1979)
Class Gastropoda Cuvier, 1797
Superorder: N.N. (Flexoglossata) (N.N. = newly created taxon)
Order: N.N. Taenioglossa
Suborder: Viviparina

(d) Cladistic, according to the rules of Hennig (1966)
Class Gastropoda Cuvier, 1797
Superorder: N.N. Flexoglossata
Order: Vetigastropda
Suborder: Taenioglossa
Section: Ampullarioidea

Table 2-5. Classification of Gastropoda by Bouchet and Rocroi (2005).

Taxon	Name
Class	Gastropoda Cuvier, 1797
Clade	Cycloneritimorpha Frýda, 1998
Superfamily	Abyssochryoidea Tomlin, 1927
Zygopleuroid Group	Abyssochrysidae Tomlin, 1927
Informal group	Architaenioglossa Haller, 1892

Table 2-6. Classification of viviparids in Greece by Bank (2006).

Taxon	Name
Class	Gastropoda Cuvier, 1795
Subclass	Orthogastropoda Ponder and Lindberg, 1995
Superorder	Caenogastropoda Cox, 1960
Order	Architaenioglossa Haller, 1890
Superfamily	Viviparoidea J.E. Gray, 1847

The previous are just a few of the published higher classifications that proposes alternatives from the 19th century to the 21st century, at which point some consensus is apparent. A thorough review of the higher classifications is given in Ponder and Lindberg (1997); Haszprunar (1985c, 1988, 1993); Ponder and Warén (1988); Harasewych, Adamkewicz, Plassmeyer, and Gillevet (1998); and Colgan, Ponder, Beacham, and Macaranas (2007). There are still many questions to be answered, and the higher classification presented below may change with more phylogenetic studies. The family and subfamily names that follow are built on the higher classification from class to the superfamily Viviparoidea shown in Table 2-7.

Table 2-7. A summary of the higher classification of mystery snails based on the analyses of numerous phylogenetic studies described above.

Taxon	Name
Class	Gastropoda Cuvier, 1795
Subclass	Prosobranchia Milne-Edwards, 1848
Superorder	Caenogastropoda Cox, 1960
Order	Architaenioglossa Haller, 1890
Superfamily	Viviparoidea J.E. Gray, 1847

The study of shells (conchology) was pre-eminent and resulted in a plethora of somewhat rudimentary classifications. The above classifications are rather laborious descriptions of shell morphology, radula structure, nervous system components, osphradial structure, and all systems (e.g., digestive reproductive, nervous systems, etc.) of several taxa, resulting in many higher classification schemes. Falniowski (1989) did a critical analysis of these characters and pointed out limitations of the usefulness of practically all the characters to recognize the genuine phyletic relationships among the higher prosobranch taxa, which may explain the excess of higher classification schemes.

For family and lower taxonomies, Falniowski (1989) proposed some new characters based on scanning electron microscopy (SEM) of protoconch (embryonic shell) and teleconch (adult shell) outer surface sculpture, teleoconch inner surface sculpture, and structures visible in shell cross-sections. Studies on the outer and inner surfaces of both the protoconch and teleoconch were rather poorly differentiated and more variable within than between families. At the same time, the organization pattern of shell cross-sections seemed characteristic for a given family and thus a good character. Wagner (2001) postulated that species- or genus-level relationships typically use more shell characters and states than studies evaluating supra-generic relationships, as is to be expected if shells evolve rapidly. His studies substantiate the traditional wisdom that teleoconch character distributions reflect abundant homoplasy (a shared character between two or more animals that did not arise from a common ancestor). Still, his results suggest that these distributions reflect phylogeny as well. Unfortunately, for the Viviparidae, the taxonomic value of principal characters is still not widely agreed upon, especially in the extraordinary similarity in shell features among species within *Viviparus* (Anistratenko, Ryabceva, and Degtyarenko 2013).

The superfamily Viviparoidea is rich in modern and fossil species, currently estimated from about 150 species combined into approximately 30 genera to more than 500 species relating to 22–26 taxa of the genus-group (Anistratenko, Degtyarenko, Anistratenko, and Prozorova 2014). If one includes the paleontological data, Anistratenko and Gozhik (1995) and Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) estimated that the diversity of Viviparoidea has about doubled at the present time by at least 26 extinct genera and subgenera of Viviparidae.

C. Family and Subfamily Names

Bouchet and Racoi (1992) estimated 4,900 family-group names and 12,700 genus-group names for molluscs since 1960. Their evaluation compared data for 1758–1965 and 1966–1989; the former yielded 23,000 genus-group names, and the latter produced 5,400 genus-group names, for a total of 28,400 genus-group names in Mollusca. The Gastropoda accounted for 44.7% of genus-group names since 1758. Of these, 56.2% were the Prosobranchia, 36.1% pulmonates, and 7.7% Opisthobranchia. Dubois (2008) attributes the increase in the number of taxa recognized by taxonomists to (a) the discovery of new taxa or data, (b) conceptual taxonomic inflation due to different methodological approaches using the same data, and (c) nomenclatural inflation due to unwarranted descriptions of new taxa that are treated later as synonyms.

The review of family and subfamily names are based on checklists and taxonomic authority lists, but classifications for many lists did not agree. As Bouchet (2006) points out, taxonomic checklists are only as good as the quality of the science behind them. Strong, Gargominy, Ponder, and Bouchet (2008) describe global patterns of freshwater gastropod species diversity and the difficulty in evaluating them.

The first family name for viviparids was Cricostomata, assigned by Blainville (1825) for *Pauludina vivipara*. He characterized the family as, “Shell variable in its general form, but whose opening, always almost circular, is completely closed by a calcareous or horn cover, with few turns of the coil, and with a sublateral apex (436).” But Article 29 of ICZN (1964) mandates that family names of animals must end in -idea (e.g., Viviparidae) and subfamily names in -inae (e.g., Viviparinae). For a long while, there were two family names for CMS and JMS: Viviparidae Gray, 1847 (from the Latin word *vivus*, meaning alive, and *parere*, meaning to bring forth) and Paludinidae Gray, 1840 (from the Latin word *palūs*, meaning marsh or pool).

According to the International Commission of Zoological Nomenclature, only one of the two-family names can be valid; the other must be rejected.

Ellis (1957) proposed adding the family-group name Viviparidae over Paludinidae to the official list under Section 9(7) and rejecting and invalidating Paludinidae under Section 9(8). Forcart (1957) proposed the determination of interpretation of and addition to the official list of the family-group name Viviparidae. ICZN (1959) approved the validation of Viviparidae under "Section 6" and rejection of Paludinidae under "Section 7" of Opinion 573. Bouchet and Rocroi (2001) summarized the correction of the index for Paludinidae as follows: "INDEX: (Opinion 573. 1959) Gray, 1840, Synopsis of the contents of the British Museum Ed. 42: 117. CORRECTION: Fitzinger, 1833, Beiräge zur Landeskunde Oesterreich's unter der Enns, 3: 109 (as 'Gruppe' Paludinoidea). First used as the vernacular 'Les Paludinides' by Risso, 1826 Histoire Naturelle … de l'Europe Meridionale, 4: 100, but there is no current usage to attribute the name to Risso. PALUDINIDAE is based on the name *Paludina* Ferussac, 1812 (a junior objective synonym of *Viviparus* Montfort, 1810) (174)."

In addition to the ICZN 573 declaration, there is consensus among more recent taxonomists that the mystery snails belong to the family Viviparidae. Hannibal (1912) had only one family, Viviparidae, under the superfamily, Viviparoideae, but he divided the family into two genera, *Viviparus*, Montfort and *Idiopoma* (Pilsbry). He further divided the genus *Viviparus* into two subgenera, *Viviparus* s. str. and *Callina*. Under *Idiopoma* he placed *Cipangopaludina*, as a subgenus, listing CMS as *Idiopoma* (*Cipangopaludina*) *malleatus* and JMS as *Idiopoma japonica* all of which is discussed further below under D. Genus Names and Species Names.

Golikov and Starobogatov (1975) followed the taxonomy of malacologists in the former Soviet Union and combined Viviparidae of continental water bodies into the superfamily Viviparoidea Gray, 1847, and three families, (a) Viviparidae Gray, 1847; (b) Pilidae Preston, 1915; and (c) Pliopholygidae Taylor, 1966. Bouchet and Rocroi (2017) revised their classification of nomenclator and typification of gastropod families. Ponder and Warén (1988) classified the family Viviparidae Gray, 1847 under the superfamily Viviparoidea Gray, 1847, and included three subfamilies: (a) Viviparinae Gray, 1847 [= Paludinidae Fitzinger, 1833; = Campelomatinae Thiele, 1929]; (b) Bellamyinae Rohrbach, 1937; and (c) Lioplacinae Gill, 1863.

Of the three families in the superfamily Viviparoidea, Bellamyidae is the most widespread and diverse. These living viviparids are represented in Africa, East Asia, and Australia (Starobogatov 1985; Anistratenko, Degtyarenko, Anistratenko, and Prozorova 2014; Van Bocxlaer and Strong 2016). Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) suggest that Bellamyidae was initially established as an endemic for the Amur River and perhaps spread in more southern basins (e.g., Yangtze and

Mekong). Compared with Bellamyidae, representatives of Viviparidae (Europe and North America) and especially Lioplacidae (eastern North America) have much less broad geographical ranges (Anistratenko, Degtyarenko, Anistratenko, and Prozorova 2014).

The most diverse subfamily of viviparids is Bellamyinae with 13 genera (*Angulyagra, Bellamya, Cipangopaludina, Eyriesia, Filopaludina*, *Idiopoma, Larina, Margarya, Neothauma, Notopala, Taia, Trochotaia,* and *Viviparus*; Van Bocxlaer and Strong 2016). The subfamily Lioplacinae (= Campelomatinae Thiele, 1929) contains two genera: *Campeloma* Rafinesque, 1819, and *Lioplax* Troschel, 1856. Viviparinae has two genera, *Viviparus* de Montfort, 1810 and *Tulotoma* Haldeman, 1840 (Vail 1977a). Bellamyinae has abundant diversity but restricted systematics and treatment in anatomical studies in comparison to Viviparinae and Lioplacinae (e.g., Leydig 1850; Baudelot 1863a, b; Bouvier 1888; Perrier 1889; Bernard 1890; Auerbach 1896; Crabb 1929; Mattox 1938; Vail 1977a, b, 1978; Clench and Fuller 1955; Clench and Turner 1955; Haszprunar 1985b; Falniowski 1990).

Simone (2004) examined the morphology and phylogeny of *Viviparus contectus* and *V. acerosus*. He concluded that Viviparidae is paraphyletic (i.e., a group's last common ancestor and all descendants of that ancestor, excluding a few monophyletic subgroups). He therefore included them in the monotypic superfamily Viviparoidea. The viviparid features included adaptations to filter feeding, closed ureter and open-pore communication between kidney and ureter, male pallial ducts running by integument and opening in the right cephalic tentacle, and a brood pouch in the pallial oviduct. Smith (2000) considered the Australian viviparids that he studied to belong to the subfamily Bellamyinae, which is characterized mainly by the testis positioned in the pallial cavity, by the side of the rectum.

Vail (1977b) compared the reproductive anatomies of three viviparid species (*Campeloma geniculum*, *Lioplax pilsbryi*, and *Viviparus georgianus*). He proposed that it is possible to delineate viviparid subfamilies and genera based on the organization of the reproductive system. He separated the Viviparinae (containing *Viviparus* and *Lioplax*) from the Lioplacinae (containing *Campeloma* and *Lioplax*) based on the seminal vesicle and prostate gland, the length of the vas deferens in males and the position of the albumen gland, and the seminal receptacle and pallial oviduct in females. The size of the seminal vesicle and prostate gland help distinguish genera. Vail (1977b) suggests the essential organization of the reproductive system is uniform at the generic level in the Lioplacinae and Viviparinae. Unfortunately, he did not examine any *Bellamya* species and was unable to compare Bellamyinae and Viviparinae anatomies. The subfamily Bellamyinae comprises species in the Ethiopian and Oriental regions. However, he believes that the male and female reproductive anatomies in all the Bellamyine genera are uniform. His subfamilial classification of viviparids with genera is given in Table 2-8.

Table 2-8. Vail's (1977b) subfamilial classification of Viviparidae.

Viviparinae	**Lioplacinae**	**Bellamyinae Rohrbach, 1937**
Tulotoma	*Campeloma*	*Bellamya*
Viviparus	*Lioplax*	*Cipangopaludina*
		Filopaludina
		Idiopoma
		Margarya
		Siamopuludina
		Taia

Smith (2000) examined both CMS and JMS and suggested that anatomical studies are necessary to assess the validity and application of the generic and subfamilial characters. In addition, there is a need to examine molecular genetics in association with anatomical features (e.g., reproductive, renal, nervous, embryonic, and adult shell morphology, as in Simone 2000), of the additional viviparid taxa, including CMS and JMS, before assigning family and subfamily names. Until such time, I elect to remain with the current taxonomy of Viviparidae with the subfamily Bellamyinae, as accepted by Smith (2002; Sengupta, Kristensen, Madsen, and Jørgensen (2009); Lu, Du, Li, and Yang (2014); and Van Bocxlaer and Strong (2016), as shown in Table 2-9.

Table 2-9. Classification of Gastropoda to subfamily level accepted herein, the subfamily of CMS and JMS being Bellamyinae as underlined.

Taxon	**Name**
Class	Gastropoda Cuvier, 1797
Subclass	Prosobranchia Milne-Edwards, 1848
Superorder	Caenogastropoda Cox, 1960*
***Informal group**	Architaenioglossa Haller, 1892
Superfamily	Viviparoidea J.E. Gray, 1847
Family	Viviparidae Gray, 1847
Subfamily	Viviparinae Gray, 1847
Subfamily	Bellamyinae Rohrbach, 1937
Subfamily	Lioplacinae Gill, 1863

Simone (2004) concluded in his morphological and phylogenetic analyses that Architaenioglossa is not monophyletic but paraphyletic, and thus it should not be used as a formal taxon. Bouchet and Rocroi (2005) refer to it as an informal group (see Table 2-7); Galli (2017) refers to it as an order and Caenogastropoda as a subclass.

D. Genus and Species Names

Viviparidae is represented in North America by two introduced species and several native species described later. The first was *Viviparus japonicus* by Wood (1892) in San Francisco, but later identified as *Viviparus chinensis* (expanded upon below), and the second by Pilsbry (1894) as *Viviparus japonicus* at Victoria, British Columbia, who acknowledged the initial finding by Rev. G. W. Taylor. In addition, several native species of viviparids belonging to four genera—*Viviparus*, *Tulotoma*, *Campeloma*, and *Lioplax*—are expanded upon later.

In the genus history, there are five names to address: *Paludina*, *Vivipara*, *Viviparus*, *Cipangopaludina*, and *Bellamya*. Fischer (1887) considered the genus *Paludina* Férussac, 1812, the oldest genus name of the group. But *Paludina* was placed on the Official Index of Rejected and Invalid Generic Names in Zoology by ICZN (1959) Opinion 573 as outlined earlier (B. Family and Subfamily Names) in favor of *Viviparus*. Similarly, *Vivipara* s. str., which is well described by Annandale (1821), Leydig (1850), Stearns (1901, 1908), Taylor (1883), and especially Kobelt-Schwanhetuft (1909), who labored through the synonymies of 267 species, was rejected in the same opinion.

The debate about the identification (genus and species) and authority of the introduced mystery snails began when Wood (1892a, b) described CMS as *Paludina japonica*, but Hannibal (1911) examined the specimens and identified them as *Viviparus malleatus*. In redescribing the species in 1912, Hannibal had recalled Pilsbry's (1902) proposal to assign similar species of *Viviparus* from Southeastern Asia to the subgenus *Idiopoma*, the Type species being his newly described *Vivipara henzadensis* n. sp. Hannibal (1912) extended *Idiopoma* to embrace the entire genus and proposed *Cipangopaludina* as a subgenus of *Idiopoma* with the type being *Paludina malleata*, Reeve, 1863. However, the following year Pilsbry (1902) grouped the species with *Viviparus,* and this grouping was used for years by many others. Later, Prashad (1928) included *Idiopoma* and other genera in *Viviparus* and considered *P. lecythis* in the same subgenus as the Japanese *Paludina malleata* Reeve. Yen (1943) raised *Cipangopaludina* to the genus level. Based on anatomical data, Smith (2000) proposed to accommodate

Cipangopaludina as a subgenus of *Bellamya*, the type species being *Bellamya bellamya* Jousseaume, 1886, by singular designation, and is considered a synonym of *Vivipara duponti* De Rochebrune, 1881 by Germain (1920) and Van Bocxlaer and Strong (2016). Some of the impetus for Smith's (2000) studies were from previous studies by Pace (1973), Taylor (1981), and Rao (1989), who considered *Cipangopaludina* a genus of Bellamyinae, as reported by Jokinen (1991). Smith (2000) placed both *Cipangopaludina chinensis* and C. *japonica* in the subfamily Bellamyinae. His conclusions were based on differences in the male and female anatomy, the morphology of the intra-uterine juvenile shell, and the sculpture (spiral carinae and periostracal hairs) of the adult shells. He found the radula had no specific or distinctive characters for interspecific differentiation. These analyses agree with studies by Van Cleave and Richey (1936), who studied five North American species of Viviparidae (*Viviparus contectoides, V. intertextus, V. subpurpureus, V. georgianus,* and *V. intertextus illinoisensis*) and concluded that individual variation was so great intraspecifically and interspecifically that species identification could not rest on radular features alone. In working with marine prosobranchs, Hickman (1980) identified seven factors that contribute to the form and pattern of the radula: (a) phylogenetic, (b) mechanical, (c) ecological, (d) programmatic, (e) maturational, (f) degenerative, and (g) constructional. These analyses suggested some aspects of form and pattern conveyed important information about non-evolutionary processes and phenomena, best examined outside of the evolutionary framework. Yet Anistratenko, Ryabceva, and Degtyarenko (2013, 149), after reviewing four species of *Viviparus* using SEM, found "a certain value of rachidian tooth dimensional parameters as an efficient tool for taxonomy and discrimination of closely related species in the family."

The Asian, African, and Australian genera all belong to the subfamily Bellamyinae. Some species of *Bellamya* have also been introduced into Europe (Soes, Menno, Majoor, and Keulen 2011; Collas, Breedveld, Matthews, van der Velde, *et al.* 2017; Van den Neucker, Schildermans, and Scheers 2017; Van Bocxlaer and Strong 2020). *Bellamya* in Africa constitutes only 18 species with several subspecies or ecophenotypic morphs (Sengupta, Kristensen, Madsen, and Jørgensen 2009). Representatives of *Bellamya* Jousseaume 1886 mainly live in Africa and the Indostan Peninsula (except the Lower Ganges), while in Southeast Asia, the generic diversity of Viviparoidea is much higher. This distribution suggests East Asia as the region where the genetic diversity of the superfamily was initially formed (Starobogatov 1985). Sengupta, Kristensen, Madsen, and

Jørgensen (2009) indicated that *Bellamya* was introduced to Africa during a Miocene dispersal event from Asia.

To sum up, of the five genera, only two emerge as valid: *Cipangopaludina* and *Bellamya*. Only Smith (2000) has provided rationales for *Bellamya* in North America. He made convincing arguments and has been cited by many since this publication, including Prezant, Chapman, and McDougall (2006); Bury, Sietman, and Kams (2007); Waltz (2008); Olden, Larson, and Mims (2009); Chaine, Allen, Fricke, Haak, *et al.* (2012); Chapman, Prezant, and Shell (2012); Olden, Mims, and Horner-Devine (2013); Unstad, Uden, Allen, Chaine, *et al.* (2013); Wong, Allen, Hart, Noelle, *et al.* (2013); Haak, Stephen, Kill, Smeenk, *et al.* (2014); Haak (2015); Twardochleb and Olden (2016); and Burnett, Wong, and Haak (2018), to mention only one or two per year. While there are numerous North American citations for *Bellamya*, most do not cite Smith (2000), but more recent studies indicate *Cipangopaludina* is the valid genus name. Lu, Du, Li, and Yang (2014) examined 18 species of Chinese *Cipangopaludina*. They performed morphometric analyses using principal component analyses on several adult features: operculum features, external morphology (e.g., head, foot, tentacles), radula, alimentary canal, genital system, and circulatory and excretory systems. They synonymized two species and added two subspecies, which reduced the 18 species to 11 and two subspecies. *Cipangpaludina japonica* was not included in their investigations, but they synonymized *Bellamya* (*Cipangopaludina*) *chinensis* (Gray) (Smith 2000) with *C. chinensis*. Hirano, Saito, and Chiba (2015) examined their phylogeny based on the mitochondrial cytochrome oxidase subunit I and 16S rRNA genes for East Asian viviparids, and found three clades of which Clade 2 was represented by *Cipangopaludina chinensis laeta* and *C. c. chinensis*. Clade 3 by *Cipangopaludina japonica*, fossils of which have been recorded from Pleistocene deposits in the areas around Lake Biwa. Interestingly, Hirano, Takahiro, Saito, Takuni *et al.* (2015) state, "*C. japonica* and *C. c. chinensis/laeta* were introduced to the USA by Japanese immigrants as a potential food resource" (438). See below for species and common names attributed to CMS in the North American literature. Finally, Gu, Husemann, Wu, Dong, *et al.* (2019) examined the phylogeography of *Bellamya* snails from China and East Africa. Their phylogenetic analysis revealed a monophyletic group in China and one in East Africa. The Chinese group showed little genetic differentiation but a deep divergence among East African populations, suggesting that strong divergence does not necessarily depend on the intrinsic characteristics of a species but instead on the landscape dynamics of a region.

Important in these analyses is the identification of factors that contribute to the form and pattern of the shell, both embryonic and adult; phylogenetic analyses of species of *Viviparus*, *Cipangopaludina*, and *Bellamya*; mechanical properties of the shell; ecological relationships of forms; and maturational changes, similar to Hickman's (1980) approach for the radula.

Galli (2017) and the Worldwide Mollusc Species Data Base (WMSDB) list several extant species of *Cipangopaludina*, *Bellamya*, *Viviparus*, and *Paludina* (= *Viviparus*). The most diverse genus of extant species globally is *Viviparus,* with 80 species; *Cipangopaludina* and *Bellamya* each have 27 extant species (Tables 2.10 and 2.11).

Having examined the lower classifications within the family Viviparidae, the consensus, according to Van Bocxlaer and Strong (2020), is as follows:

- Three extant subfamilies: Viviparinae, Bellamyinae, and Lioplacinae
- Within Viviparinae, three extant genera are considered valid (listed alphabetically):
    - *Rivularia* Heude, 1890
    - *Tulotoma* Haldeman, 1840
    - *Viviparus* Montfort, 1810 (type genus)
- Within Bellamyinae, 17 extant genera are considered valid (listed alphabetically):
    - *Angulyagra* Rao, 1931
    - *Anularya* Zhang & Chen, 2015
    - *Anulotaia* Brandt, 1968
    - *Bellamya* Jousseaume, 1886 (type genus)
    - *Cipangopaludina* Hannibal, 1912
    - *Eyriesia* Fischer, 1885
    - *Filopaludina* Habe, 1964 (with its subgenera *Filopaludina* s.s. and *Siamopaludina* Brandt, 1968)
    - *Idiopoma* Pilsbry, 1901
    - *Larina* Adams, 1855
    - *Margarya* Nevill, 1877 (with its subgenera *Margarya* s.s. and *Tchangmargarya* He, 2013)
    - *Mekongia* Crosse & Fischer, 1876
    - *Neothauma* Smith, 1880
    - *Notopala* Cotton, 1935
    - *Sinotaia* Haas, 1939
    - *Taia* Annandale, 1918
    - *Torotaia* Haas, 1939
    - *Trochotaia* Brandt, 1974

- Within Lioplacinae, two extant genera are considered valid (listed alphabetically):
    - *Campeloma* Rafinesque, 1819,
    - *Lioplax* Troschel, 1857 (type genus)

In conclusion and support of Hirano, Saito, and Chiba (2015), the incompatibility between phylogeny and taxonomy may be due to "incomplete lineage sorting, introgressive hybridization and phenotypic plasticity (435)." More research is recommended before superseding *Cipangopaludina* with *Bellamya*. The ensuing chapters deem *Cipangopaludina* as the genus for both CMS and JMS.

E. Chapter II Summary

The classification schemes of family and subfamily names from Linnaeus' (1735) "Systema Naturelle" to Bank (2006), during which some stability was achieved, was reviewed. The taxonomy of both scientific and common names for genus and species from before the Official Index of Rejected and Invalid Generic Names in Zoology by ICZN (1959), Opinion 573 to Galli (2017) were also reviewed, with the final accepted classification and taxonomy of the Chinese and Japanese mystery snails being as follows:

Taxon	**Name**
Class	Gastropoda Cuvier, 1797
Subclass	Prosobranchia Milne-Edwards, 1848
Clade	Caenogastropoda Cox, 1960*
Informal group	Architaenioglossa Haller, 1892
Superfamily	Viviparoidea J.E. Gray, 1847
Family	Viviparidae Gray, 1847
Genus	*Cipangopaludina* (Hannibal, 1912)
Species	*chinensis* (CMS) (Gray, 1834)
Species	*japonica* (JMS) (von Marten, 1860)

Table 2-10. Galli's (2017) Worldwide mollusc species database (WMSDB). Checklist of extant species of Bellamyinae and Viviparidae. *Paludina* species are *Viviparus* species (see ICZN 1959). Species are listed alphabetically.

Bellamyinae: *Cipangopaludina* H.B. Hannibal, 1912 (27 species, subspecies)	**Bellamyinae: *Bellamyia* F.P. Jousseaume, 1886 (27 species)**	**Extant: Viviparidae: *Paludina* A.E.J. Férussac, 1812 (21 species)**
ampullacea (J.G.F. de Charpentier, 1863) *aubryana* (P.M. Heude, 1890) *cathayensis* (P.M. Heude, 1890) *chinensis* (J.E. Gray, 1834) *chinensis compactus* (G. Nevill, 1869) *chinensis formosensis* (W. Kobelt, 1876) *chinensis laeta* (E.C. Von Martens, 1860) *dianchiensis* S.P. Zhang, 1990 *fluminalis* (P.M. Heude, 1890) *haasi* B. Prashad, 1928 *hainanensis* (O.F. von Möllendorff, 1909) *hehuensis* Lu, Fang & Du, 2016 *japonica* (E.C. Von Martens, 1860) *japonica iwakawa* (H.A. Pilsbry, 1902) *japonica sclateri* (G.R. von Frauenfeld, 1865)	*bellamya* F.P. Jousseaume, 1886 *bengalensis* (J.B.P.A. Lamarck, 1822) *bengalensis annandalei* (W. Kobelt, 1909) *constricta* E.C. von Martens, 1889 *contracta* F. Haas, 1934 *costulata* E.C. von Martens, 1892 *crassispiralis* T.N. Annandale, 1921 *duponti* (A. de Rochebrune, 1882) *ecclesi* T.E. Crowley & T. Pain, 1964 *heliciformis* (O.F. Müller, 1774) *hilmandensis* (W. Kobelt, 1909) *jeffreysi* (G.R. von Frauenfeld, 1865) *jucunda* E.A. Smith, 1892 *lapidea* (P.M. Heude)	*ampulliformis* J.F.T. Eydoux & L.F.A. Souleyet, 1852 *araucana* R.A. Philippi, 1887 *atra* G.J. De Cristofori & G. Jan, 1832 *castanea* A. Valenciennes, 1827 *danieli* L.J. Morlet, 1889 *draparnaudi* P. Nyst 1836 *duchieri* H. Fischer, 1898 *fisheriana* J.F. Mabille & G. Le Mesle, 1866 *frauenfeldi* G.P. Deshayes, 1875 *kmeriana* (L.J. Morlet, 1890) *lamarckii* G.P. Deshayes, 1875 *laosiensis* L.J. Morlet, 1892 *lutosa* L.F.A. Souleyet, 1852

kurilensis Y.I. Starobogatov in I.M. Moskvicheva, 1979
latissima (P. Dautzenberg & H. Fischer, 1905)
lecythis (W.H. Benson, 1836)
lecythoides (W.H. Benson, 1836)
malleata (L.A. Reeve, 1863)
menglaensis Zhang, H.X. Liu & Wang, 1981
patris (W. Kobelt, 1909)
sujfunensis I.M. Moskvicheva, 1979
ussuriensis (P.M. Heude)
ventricosa (P.M. Heude, 1890)
yunnanensis Zhang, H.X. Liu & Wang, 1981
zejaensis I.M. Moskvicheva, 1979

leopoldvillensis S. Putzeys, 1898
liberiana M.M. Schepman, 1888
micron T.N. Annandale, 1921
mindanensis (P. Bartsch, 1909)
monardi F. Haas, 1934
pagodiformis (E.A. Smith, 1883)
phihinotropis (E.C. Von Martens, 1892)
philippinensis (P. Bartsch, 1909)
phthinotropis E.C. von Martens, 1892
robertsoni (G.R. von Frauenfeld, 1865)
rubicunda (E.C. Von Martens, 1879)
tanganyicense (E.A. Smith, 1880)
trochlearis E.C. von Martens, 1892

madagascariensis J.C.H. Crosse & P.H. Fischer, 1872
oxytropoides P.M. Heude, 1889
porrecta (J.W. Mighels, 1845
savignyi M.S. Merian, 1847
simonis A.R.J.B. Bavay, 1898
thomsoni L.J. Morlet, 1885
tiranti L.J. Morlet, 1885
tricostata R.P. Lesson, 1831

Table 2-11. Galli's (2017) WMSDB. Checklist of extant species of Viviparidae. *Viviparus* species include *Paludina* species (see ICZN 1959). Species are listed alphabetically. Total *Viviparus* species (including *Paludina*) = 80.

Viviparidae: *Viviparus* P.D. Montfort, 1810. Total extant *Viviparus* species = 80.

acerosus J.R. Bourguignat, 1862
altior H.A. Pilsbry, 1892
ater G.J. De Cristofori & G. Jan, 1832
ater gallensteini W. Kobelt, 1892
ater hellenicus (S. Clessin, 1879)
ater maritzanus (F. Haas, 1913)
aurelianus A.E.M. Cossmann, 1899
bridouxiana J.R. Bourguignat, 1888
brincatiana J.R. Bourguignat, 1888
buluanensis P. Bartsch, 1907
cebuensis (P. Bartsch, 1909)
ceylonica W.L.H. Dohrn, yr?
codomorphus J.H. Hartman, 2015
contectoides W.G. Binney, 1865
contectus P.A. Millet, 1813
costatus (J.R.C. Quoy & J.P. Gaimard, 1832)
crawshayi E.A. Smith, 1893
cumingianus J.E. Walter, 1919
fasciatus (H.P.C. Møller)
foai J. Germain, 1905
georgianus (H.C. Lea, 1834)
goodrichi S. Archer, 1933
henzadensis H.A. Pilsbry, 1901
impolitus H.A. Pilsbry, 1916

Viviparidae: *Viviparus* P.D. Montfort, 1810. Total extant *Viviparus* species listed = 80 (Continued).

lignitarum M. von Neumayr in M. von Neumayr
limi H.A. Pilsbry, 1918
lirata R. Tate, 1887
mainitensis P. Bartsch, 1907
malleatus L.A. Reeve, 1830
mamillatus H.C. Küster, 1852
mearnsi (P. Bartsch, 1907)
microchaetophora T.N. Annandale, 1921
moldavicus W.A. Wenz in Krejci-Graf & W.A. Wenz, 1932
mweruensis E.A. Smith, 1893
nolani G.W. Tryon, 1870
oxytropis W.H. Benson, 1836
phasianella (Boettger, 1887
pipiki T.A. Neubauer & M. Harzhauser in T.A. Neubauer *et al.* 2015
pseudoachatinoides (Pavlov, 1925
pseudocarinatus (B. Walker, 1919)
purgatorius J.H. Hartman, 2015
recurrens Peneck, yr?
sphaeridius (J.R. Bourguignat, 1880)
subpurpureus T. Say, 1829
texana G.W. Tryon, 1862
tricinctus Y.Y. Liu, W.Z. Zhang & Y X. Wang, 1994
viviparus (C. Linnaeus, 1758)
viviparus costae (A. Mousson, 1863)

janinensis (A. Mousson, 1859)
impolitus H.A. Pilsbry, 1916
intertextus T. Say, 1829
janinensis (A. Mousson, 1859)
javanicus von dem Busch in R.A. Philippi, 1844
ladogensis E.V. Chernogorenko & Y.I. Starobogatov, 1987
walkeri H.A. Pilsbry & C.W. Johnson, 1912
waltonii G.W. Tryon, 1866
wilhelmi (T.C. Yen, 1939
zebra (W. Kobelt, 1877
zonatus (S.C.T. Hanley, 1860)

CHAPTER III

SYNONYMY

A. Introduction

The synonyms of scientific names are listed, then the common names. The genus and species names were extracted from the literature by querying the keywords *malleatus*(*a*) for CMS and *japonica*(*us*) for JMS. The genus names are listed chronologically. The list of species synonyms grew as the literature reviews grew; the additional synonyms were also queried and listed alphabetically. Common name queries were less arduous and are listed alphabetically. However, there are no guidelines for assigning common names to species, and the problems arising from this inconsistency are discussed in this chapter.

B. Scientific Names

Assigning a scientific name to a species must follow the rules stipulated by the ICZN, published annually with new and updated taxonomy, genus and species names being relevant here. Both genus and species names have a history in ICZN, as reviewed herein.

1. Genus Names

Kennard and Woodward (1926) list the following names as synonyms of *Viviparus*, Montfort, Type *Viviparus fluviorum*, Montfort = *Helix vivipara*, Linnaeus:

Helix, 1758, Linnaeus (type genus for *viviparus*)
Cyclostoma, Lamarck, 1799
Henterum, Huebner, 1810
Paludina, Férussac, 1812
Viviparella, Rafinesque 1815
Paludinum, Jurine 1817
Vivipara, Fleming, 1818

Recall Opinion 573 of the ICZN placed *Helix vivipara* Linnaeus, 1758, on the Official List of Specific Names in Zoology as the type species of *Viviparus* Montfort, 1810, in Opinion 573, and it was rejected; the following genera were placed as invalid (ICZN 1959):

i. *Paludina* Lamarck, 1812
ii. *Paludina* Ferrussac, 1812
iii. *Vivipara* J. Sowerby, 1813
iv. *Viviparella* Rafinesque, 1815
v. *Viviparous* Collinge, 1891
vi. *Vivipara* Kobelt, 1906

2. Species Names

Considerable research has been completed since the arrival of *Cipangopaludina* species in San Francisco in 1892 (Wood 1892a, b) and in Victoria, British Columbia, in 1894 (Pilsbry 1894). Based on the considerable number of studies on shell morphology, genetics, behavior, and ecology of the two mystery snails since their arrival, the two species are called herein *Cipangopaludina chinensis* and *Cipangopaludina japonica*. The following describes the synonymy of scientific names for each species.

a. *Cipangopaludina chinensis*

Based on the cited literature searches for information on CMS, several scientific names for both genera and species were found, including the following (listed alphabetically):

- *Bellamya chinensis* (e.g., Prezant, Robert, Chapman, and McDougall. 2006; Bury, Sietman, and Kams 2007; Chaine, Allen, Fricke, Haak, *et al.* 2012; Burnett, Pope, Wong, Haak, *et al.* 2018)
- *Bellamya chinensis malleatus* (e.g., Lu, Du, Li, and Yang 2014)
- *Cipangopaludina chinensis* (e.g., Collas, Breedveld, Matthews, van der Velde, *et al.* 2017; Lu, Du, Li, and Yang 2014; Smith and Dillon 2004)
- *Cipangopaludina chinensis malleatus* (e.g., Burch 1982; Lu, Du, Li, and Yang 2014)
- *Cipangopaludina chinensis malleata* (e.g., Kurihara, Suzuki, and Moriyama 1987; Mills, Leach, Carlton, and Secor 1993; Chung and Jung, 1999; Cordeiro 2002)
- *Paludina chinensis* (e.g., Lu, Du, Li and Yang 2014; Kipp, Benson, Larson, Fusaro, and Morningstar 2019)

- *Paludina japonica* (e.g., Wood 1892a, b) but was later confirmed to be *Viviparus malleatus* (Hannibal (1911)
- *Paludina lecythoides* (Benson) (e.g., Fischer 1891)
- *Paludina malleata* (e.g., Lu, Du, Li and Yang 2014); *Viviparus malleatus* (e.g., Clench 1940; Huehner and Etges, 1971, 1977; Stanczykowska, Magnin, and Dumouchel 1971; Schmid 1975)
- *Viviparus chinensis malleatus* (e.g., Lu, Du, Li, and Yang 2014)

To recapitulate, according to the ICZN (1999), Article 23.1, statement of the principle of priority, the valid name is the oldest, and it has priority over other published names for a species; hence, *Cipangopaludina chinensis* (Gray, 1834) is the correct species name. The genus, *Cipangopaludina*, was described by Hannibal (1912). “Cipango” is derived from a poetic word for Japan, used by Marco Polo, who called an island east of Asia “Zipangu” (Japan), the land of gold (Collins Dictionaries 2018). Gray (1834) originally described CMS as *Viviparus chinensis,* and Reeve (1863) later described it as *Viviparus malleatus*. Prashad (1928) assigned *Cipangopaludina* as a subgenus of *Viviparus,* but Hannibal (1912) raised it to full generic status. If subspecies are recognized, then *Cipangopaludina chinensis malleata* (Reeve, 1863) is the subspecies in Canada (Therriault and Kott 2004). The currently accepted scientific name of CMS in North America is *Cipangopaludina chinensis malleata* (Reeve, 1863) (Turgeon, Quinn, Bogan, Coan, *et al.* 1998). Lu, Du, Li, and Yang (2014) list the synonymy of the species, and the references in their article are listed here alphabetically:

- *Bellamya (Cipangopaludina) chinensis* (Gray, 1834); e.g., Smith (2000)
- *Cipangopaludina chinensis* (Gray, 1834); e.g., Prashad (1928)
- *Cipangopaludina chinensis* (Heude); e.g., Prashad (1928)
- *Cipangopaludina chinensis diminuta* (Heude); e.g., Griffith and Pidgeon (1834); Yen (1943)
- *Cipangopaludina chinensis leucostoma* (Heude); e.g., Yen (1943)
- *Paludina chinensis* Gray (1834); e.g., Griffith & Pidgeon (1834); Ponder *et.al.* (2016)
- *Vivipara chinensis* (Gray); e.g., Kobelt (1909)
- *Viviparus chinensis* (Gray); e.g., Yen (1943)
- *Viviparus chinensis chinensis* (Gray); e.g., Yen (1939)

Additional search queries included the following, listed alphabetically, synonyms of CMS appear in bold:

- *Bellamya chinensis* (Reeve, 1863); e.g., Kipp, Benson, Larson, Fusaro, *et al.* (2016).
- *Bellamya chinensis malleatus* (Reeve, 1863); e.g., Kipp, Benson, Larson, Fusaro, *et al.* (2016).
- *Cipangopaludina chinensis compactus* (Nevill, 1869); e.g., Galli (2017).
- ***C. c. chinensis* (Reeve, 1863); e.g. Kipp, Benson, Larson, Fusaro, and Morningstar (2016)**
- ***C. c. laeta* (von Martens, 1860); e.g., Hirano, Saito, and Chiba (2015); Galli (2017)**
- ***C. c. formosensis* (Kobelt, 1876); e.g., Galli (2017)**
- ***C. c. malleata* Reeve, 1863; e.g., Chung and Jung (1999)**
- ***Cipangopaludina latissimi* (Dautzenberg et Fischer, 1905)**
- ***Cipangopaludina limnophila* (Mabille); e.g., Griffith and Pidgeon (1834)**
- ***Cipangopaludina longispira* (Heude); e.g., Prashad (1928)**
- ***Paludina japonicus* (Von Martens, 1861); e.g., Köhler, Sri-aroon, and Simonis (2012a)**
- ***Paludina lecythoides* Benson, 1842; e.g., Fischer (1891); Yen (1943)**
- ***Paludina malleata* (Reeve, 1863); e.g., Prashad (1928)**
- ***Vivipara chinensis* (Gray, 1834); e.g., Köhler, Sri-aroon, and Simonis (2012a)**
- ***Viviparus chinensis malleatus* (Reeve, 1863); e.g., United States Geological Survey (USGS 2005)**
- ***Viviparus lecythoides* Benson, 1842; e.g., Hannibal (1911), Prashad (1928)**
- ***Viviparus malleatus* (Reeve, 1863); e.g., Fofonoff, Ruis, Steves, and Carlton (2018)**
- ***Viviparus stelmaphora* (Bourguignat); e.g., Stearns (1901), Prashad (1928)**

b. *Cipangopaludina japonica*

Hannibal (1911), on a trip to Coalinga Oil Fields in western Fresno County, California, found a species he called *Vivipara japonica*. It differed from *V. malleatus* reported by Wood (1892a, b), "by its more acute spire, flatter whorls and fine spiral striae instead of the four lines of revolving punctures (32)". Hannibal (1912) proposed *Cipangopaludina* as a subgenus of *Idiopoma* Pilsbry, 1901 for the Japanese species *Paludina malleata*

Reeve (Prashad 1928; Van Bocxlaer and Strong 2016). Van Bocxlaer and Strong (2016) and Prashad (1928) consider *Paludina japonica* von Martens, 1861, to belong to *Lecythoconcha* based on the generic description and geographic coverage. Rao (1925) describes three species of *Lecythoconcha*: *L. lecythis* from rice fields in China and Japan, *L. chinensis* f. *catayensis* from China, and *L. sclateri* from Japan. Prashad (1928) and Brandt (1974) synonymized *Lecythoconcha* with *Cipangopaludina*. The most remarkable diversity of *Cipangopaludina* is in Indo China (Siam, Laos, Cambodge, Cochinchine, Annam, Tonkin), with 39 species recorded by Fischer (1891). Of the North American CMS, only *P. lecythoides*, a variety of *C. chinensis* (Prashad 1928), is on Fischer's (1891) list.

Park, Jeong, Jung, and Chung (1997) attempted to distinguish *C. chinensis malleata* and *C. japonica*, both widely distributed in Korea. Still, the latter species is only in a restricted area in the southern part of Korea. They found the spires of *C. c. malleata* were globose with impressed sutures. Those of *C. japonica* have straight with shallow sutures and an obtuse angle in the body whorl. The shell shapes of embryos in the female brood pouch were distinctly different from each other. The apices of the shells of *C. japonica* were much more conic than those of *C. c. malleata*. The anatomical differences between these two species were observed only in exterior body color and sizes of organs. *C. japonica* had five or six cusps on each side of the central cusp of the rachidian tooth, while *C. c. malleata* had five cusps. However, he reported the radular formula for each species as 1,10,11,1,11,10,1, with the marginal teeth lacking a central cusp.

Hirano, Saito, and Chiba (2015) commented that some of the observed incongruences between taxonomy and phylogeny might be due to rapid changes in shell morphology, such as that produced by phenotypic plasticity. According to several previous studies, phenotypic plasticity is a common phenomenon in freshwater molluscs (Ortmann, 1920; Hornbach, Kurth, and Hove 2010; Bronmark, Lakowitz, and Hollander 2011; Dillon, Jacquemin, and Pyron 2013).

The first report of JMS in North America was by Pilsbry (1894), who noted Taylor's description of the appearance of *Paludina japonica* Mart. in the Chinese Market at Victoria, British Columbia. Hannibal (1912), in his "Synopsis of the Recent and Tertiary Freshwater Mollusca of the Californian Province," follows Pilsbry (1901) in classifying *Vivipara* as a subgeneric group and proposed *Idiopoma* von Martens as a new subgenus, with *Vivipara henzadensis* from South Africa and Burma as the type species. But Hannibal (1912) raised *Idiopoma* to the genus level and classified *Paludina japonica* as *Idiopoma japonicus*. According to Jokinen (1982), *Paludina malleata* is regularly considered a synonym of *P.*

chinensis based on a species illustrated by Gray without description. However, Van Bocxlaer and Strong (2016), citing Reeve (1863), argue the native range of *chinensis* to be Eastern China, whereas the type locality of *malleata* is Japan. *Cipangopaludina japonica* was synonymized with *C. chinensis* by Dundee (1974), Clarke (1978), and Jokinen (1982) because shell variations were too minimal to separate the species. Van Bocxlaer and Strong (2016) suggested that both taxa may belong to deeply divergent clades, and molecular analysis of topotypic specimens of *chinensis* and *malleata* are required before synonymizing the two species. However, others have considered the morphological differences sufficiently large to retain them as separate species (Clench and Fuller, 1965; Stańczykowska, Magnin, and Dumouchel 1971; Jokinen, 1982; Smith, 2000; Solomon, Olden, Johnson, Dillon, *et al.* 2010). This was confirmed by molecular analyses (Hirano, Saito, and Chiba 2015). Rigorous molecular studies are also required to elucidate the relationships between *C. malleata* and *C. japonica*. Ideally, these would also include specimens of *C. stelmaphora* (Kobelt 1879) described from Japan, which may be a synonym of *C. japonica* (Van Bocxlaer and Strong 2016).

Synonyms of *Cipangopaludina japonica*, listed alphabetically, are as follows:

- *Bellamya chinensis japonica*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Bellamya japonica*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Cipangopaludina chinensis japonica*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Cipangopaludina chinensis japonicus*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Cipangopaludina japonicus*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Paludina japonica* (or *Helix japonica*); e.g., Clench (1962)
- *Paludina japonica* Reeve 1863; e.g., Kobelt-Schwanhetuft (1909)
- *Paludina japonica* von Martens, 1861; e.g., Kobelt-Schwanhetuft (1909); Van Bocxlaer and Strong 2016)
- *Paludina oxytropis* Kobelt 1879; e.g., Kobelt-Schwanhetuft (1909)
- *Paludina oxytropis* var. *japonica* Iwakawa, 1879; e.g., Pilsbry (1897); Kobelt-Schwanhetuft 1909)
- *Viviparus chinensis japonica*; e.g., Kipp, Benson, Larson, and Fusaro (2020)
- *Viviparus japonica* Reeve, 1863; e.g., Kipp, Benson, Larson, and Fusaro (2020)

- *Viviparus japonicus* 1902; e.g., Kobelt-Schwanhetuft (1909); Kipp, Benson, Larson, and Fusaro (2020)
- *Viviparus japonicus* var. *Iwakawa* Pilsbry, 1892; e.g., Kobelt-Schwanhetuft (1909)

D. Common Names

Arguably, common names of species are used more frequently than scientific names. Unfortunately, unlike scientific names, there are no rules, standards, or criteria for validating common names. The lack of standards creates confusion when querying names in literature searches. For example, querying "mud snail" results in listings of two species, the New Zealand mud snail, *Potamopyrgus antipodarum*, and the mud snail, *Bithynia tentaculatum*, also known as the faucet snail. There are numerous examples, especially for clams and snails, but giving more examples belabors the point.

The family name Viviparidae also has a few common names. Aside from the most common, "viviparids," in North America, "mystery snails" is commonly used (e.g., Clarke 1981); in Europe, "river snails" is widely used (e.g., Cotton 1936). In the days of "Paludinidae," they were called Marsh Shells (Tate 1866).

1. Cipangopaludina chinensis

The two *Cipangopaludina* species also have several common names. CMS has at least eight, listed alphabetically:

- Asian apple snail; e.g., Clarke (1978, 1981).
- Black snail; e.g., Nova Scotia Invasive Species Council, Appendix B
- Chinese applesnail; e.g., Lu, Du, Li, and Yang (2014).
- Chinese Mystery Snail; e.g., Mackie (2000).
- Chinese mysterysnail; e.g., USGS (2005); Jokinen (1992); Turgeon, Quinn, Bogan, Coan, *et al.* (1998); Martin (1999); Karatayev, Mastitsky, Burlakova, and Olenin (2008).
- Mud snail; e.g., Kurihara and Suzuki (1987); Kurniawan, Sato, and Yasuda (2018).
- Oriental mysterysnail; e.g., Mills, Leach, Carlton, and Secor (1993); Eckel (2004).
- Trapdoor snail; e.g. Zack DeAngelis, Appendix B.

2. Cipangopaludina japonica

JMS has several common names as well. They include the following, listed alphabetically:

- Japanese black snail; e.g., Kipp, Benson, Larson, and Fusaro (2020).
- Japanese mysterysnail; e.g., Mackie (2000); Kipp, Benson, Larson, and Fusaro (2020).
- Japanese trapdoor snail; e.g., Kipp, Benson, Larson, and Fusaro (2020).
- Mud snail; e.g., Kurihara and Kadowaki (1988).
- Oriental mysterysnail (e.g., Kipp, Benson, Larson, and Fusaro 2020).

D. Standardizing Common Names

This section describes one attempt to standardize common names under the Species at Risk Act (SARA) in Canada. The Act includes federal, provincial, and territorial ministers who have a wildlife commitment to a national approach to protecting species at risk (Environment Canada 2008). The United States has a similar act called the Endangered Species Act (ESA). Both acts aim to prevent species from becoming extinct because of inappropriate, often selfish, human activity.

In 2002 the SARA appointed the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to identify and assess a species status. COSEWIC was established in 1977 to provide a single, scientifically sound classification of wildlife species at risk of extinction. COSEWIC is an independent committee of wildlife experts and scientists whose purpose is to identify species at risk in Canada (COSEWIC 2019). Further, it designates the conservation status of wild species, including Mollusca. The Mollusca subcommittee consists of 2 co-chairs and up to 10 subcommittee members who are experts on marine, freshwater, and terrestrial Mollusca from coast to coast in Canada. COSEWIC's members are wildlife biology experts from academia, government, nongovernmental organizations, and the private sector responsible for designating wildlife species in danger of disappearing from Canada. They meet twice a year to assess the status of wildlife species at risk of extinction.

Part of the SARA commits to "Monitor, assess, and regularly report on the status of all wild species" (Environment Canada 2008). This commitment is the mandate of the program on the General Status of Species in Canada. The mandate, fulfilled by the National Status Working Group (NGSWG), includes representatives from all provincial and territorial governments in Canada and the federal government. Members of the working group complete assessments of species in their respective province/territory and prepare reports every five years on the general status of wild species in Canada. Wild Species Reports for 2000, 2005, 2010, and 2020 are available from Canadian Endangered Species Conservation Council (CESCC). The council was formed in 1998 by federal, provincial and territorial Wildlife Ministers.

The NGSWG expedites the establishment of common names in both English and French for all species in Canada. One advantage of this approach is to make sure that the most appropriate name is given to each species, allowing consistency when developing the names. Experts provide suggestions of common names in English and French for the species in the taxonomic groups in which they have expertise. Members of the Canadian Wildlife Service then review the suggested common names before they are submitted for acceptance by the Terminology Standardization Division of the Translation Bureau of the Government of Canada.

Common names generally consist of two parts: one indicates the taxonomic group in which the species occurs; one reflects a diagnostic characteristic of the species. The scientific name often provides insight for developing the common name. The experts may consider several aspects of a species:

- The author of the species (e.g., *Euglea henslowana* (formerly *Pisdium henslowanum)*, Pea Clam): *Pisum* is Latin for pea, Henslow was a British naturalist who first reported the species.
- Morphological features (e.g., *Amblema plicata*, Threeridge): *Amblema* is a genus of freshwater mussels with shell sculpture posterior to the beaks and consists of three prominent ridges.
- Economic importance (e.g., *Margaritifera margaritifera*, Freshwater Pearl Mussel): *Margaritifera* represents mussels valuable for their pearls in freshwater and oceans (e.g., *Pinctata margaritifera*).
- Abundance (e.g., *Euglesa casertanum* (formerly *Pisidium casertanum*), Ubiquitous Pea Clam): *Pisum* is Latin for pea, and the species has a worldwide distribution, abundant where it occurs.
- Habitat used by the species (e.g., *Physa johnsoni*, Banff Springs Physa): occurs only in warm or cold springs in Banff.
- A specific behavior (e.g., *Radix peregra*, Wandering Pond Snail): active in quiet and stagnant ponds, wandering the shallows.
- The name of the region where it occurs, (e.g., *Sphaerium nitidum*, called the Arctic-Alpine Fingernail Clam). *Sphaerium* is a genus of clams with a fingernail shape. The name was derived from

Greek *sphairion*, diminutive of *sphaira*, a ball or sphere. *Nitidum* means shiny, as for its glossy shell, a diagnostic feature of the clam most common in Arctic lakes and rivers (Mackie 2007).

- A combination of characters, such as the name of type locality and a diagnostic morphological feature (e.g., *Viviparus georgianus*, Banded Mystery Snail): *Viviparus* refers to the brooding of its young, *georgianus* represents its type locality, Georgia.

In the lists of common names for both CMS and JMS in section V. Synonyms of Common Names, several names conflict or potentially conflict with COSEWIC's and NGSWG's guidelines for common names:

- Every species on COSEWIC's record of assessment results should have a unique common name.
- All common names should be capitalized (e.g., Rocky Mountain Ridges Mussel; Warty Jumping Slug; Rayed Bean). The lower case may be used when it is not part of the common name (e.g., the common name for *Ptychobranchus fasciolaris* is Kidneyshell; if ambiguous, use Kidneyshell mussel).
- Use accepted common name(s) for biological species, subspecies, varieties, and populations (e.g., Puget Oregonian Snail; Banff Spring Snail).
- Invent common names when they do not exist, and document methods/sources for arriving at invented names. (e.g., see list of characteristics of a species above).
- Each taxon has authority for naming the species; for Mollusca, the source is Turgeon, Quinn, Bogan, Coan, *et al.* (1998).

In Turgeon, Quinn, Bogan, Coan, *et al.* (1998, 11), the goal is "to keep the scientific nomenclature of this list up to date while achieving uniformity and avoiding confusion in the common names of the molluscs of the United States and Canada". According to Lindberg (1999), the articles and recommendations of the ICZN and the American Fisheries Society's principles provide algorithmic procedures governing the generation and application of common names. Lindberg (1999, 194) remarked that the use of algorithms is well suited in deriving common names because "they possess three key features: (1) algorithms are substrate neutral; (2) algorithms consist of small, simple steps; and (3) algorithms have guaranteed results" (2). Lindberg (1999) welcomed the standardization of scientific and common names in Turgeon, Quinn, Bogan, Coan (1998) but acknowledged the German Riedl's (1983, 5) counsel, "Wanting to collect constant names is the misleading hope of the dilettante; to become aware of the order itself is the rewarded struggle of the expert".

Herein lies a problem: many, or perhaps most common names in Turgeon, Quinn, Bogan, Coan, *et al.* (1998), are combined (e.g., mystery snail vs. mysterysnail, apple snail vs. applesnail). One must wonder whether these combined or elided words are misspellings, occasionally perhaps due to a broken or unused space bar on the keyboard, or is there an American preference vs. a Canadian choice for separate words. After all, our behavior (I am Canadian) is often different from American behavior. The combined words certainly are not blended or portmanteau words in which parts of multiple words or their sounds combine into a new word (e.g., *smog* is a blend of *smoke* and *fog*). Why all this preamble? Because it is essential to be consistent with the use of either Mystery Snail or mysterysnail. I prefer "Mystery Snail" for two reasons; I was a co-chair for the mollusc subcommittee on COSEWIC for 16 years, and it's hard to break with tradition (see the five bullets above). Secondly, I'm Canadian, eh? So, as you would have surmised by now, it is the Chinese Mystery Snail (CMS) and Japanese Mystery Snail (JMS). When discussing plurals, then the lower case is used, e.g., Chinese and Japanese mystery snails.

Now is an excellent opportunity to segue into the provenance of the common name "Mystery" Snail. I queried the literature for the words "mystery snail" and "mysterysnail," "escargot mystère" (French), "mysteriöse schnecke" (German), and "caracol misterioso" (Spanish). The searches yielded very little. Glaubrecht's (2011) examination of Darwin's Origin of the species, or the "*mystery of mysteries*," concluded that one mystery has become many as further complexities are uncovered in what species are and how they multiply. The complexity of common names likely applies to all gastropod species.

My following approach was searching the internet with the query, "Why the name mystery snail?" One website in Appendix B (Mystery snail?), posed the question, "This might be a dumb question, but why are mystery snails called 'mystery snails?'" The responses were as follows: 1. "It's a mystery." 2. "Because you start with one, then mysteriously have dozens." 3. "Because they mysteriously die on you even though you took perfect care of it." 4. They are "mystery" snails because females give birth to young, fully developed snails that suddenly and "mysteriously" appear.

Unfortunately, the common name, "mystery snail", is also used to describe apple snails (*Pomacea* species), which lay eggs and lack a trap door. All snail species start with one and end up with many—hardly a mystery.

Perhaps the most believable provenance is by the poet José-Maria De Heredia (1843, 28-29). Some preamble would help to explain his poetry. Earlier, Section 3. Classification, Taxonomy, and Etymology of Mystery

Snails, d i. *Cipangopaludina chinensis* included the statement, “Cipango is derived from a poetic name for Japan, used by Marco Polo who called an island (Japan) east of Asia Zipangu” (Appendix B, Mystery snail, Zipangu). De Heredia (1843, 111) incorporated the name Cipango in his poem, “Les Conquérants,” which tells the story of the search for gold (fabulous metal) at Zipangu. The Legend of “Zipangu,” the Land of Gold, can be found in Appendix B (Mystery snail legend). The poem consists of two quatrain stanzas followed by two tercet stanzas; Table 3-1 translates the first two quatrain and tercet stanzas into English. The pertinent part of the poem is the second quatrain stanza shown in quotes (“”) in Table 3-1. Cipango at the “mysterious edges” of the world! Could this be the denouement of “mystery” snails?! One argument arises, Hannibal named the genus, *Cipangopaludina*, in 1912. Yet, there is no use of “mystery snail” until much later, the date of which I could not establish, but it was later in the 20th century.

Table 3-1. The etymology of Cipango, derived from the Italian “Cipango,” named by Marco Polo from the Chinese “Japan, Land of the Rising Sun.”

Les Conquérants	**The Conquerors**
Comme un vol de gerfauts hors du charnier natal,	Like a flight of gyrfalcons out of the birthplace,
Fatigués de porter leurs misères hautaines,	Tired of wearing their haughty miseries,
De Palos de Moguer, routiers et capitaines Partaient, ivres	From Palos de Moguer, truckers and captains
d’un rêve héroïque et brutal.	Left, drunk with a heroic and brutal dream.
Ils allaient conquérir le fabuleux métal	“They were going to conquer the fabulous metal
Que *Cipango* mûrit dans ses mines lointaines,	As Cipango matures in its distant mines,
Et les vents alizés inclinaient leurs antennes	And the trade winds tilted their antennas
Aux bords *mystérieux* du monde Occidental.	At the mysterious edges of the Western world”.
Chaque soir, espérant des lendemains épiques,	Each evening, hoping for an epic tomorrow,
L’azur phosphorescent de la mer des Tropiques	The phosphorescent azure of the Tropic Sea
Enchantait leur sommeil d’un mirage doré;	Enchanted their sleep with a golden mirage.
Ou penchés à l’avant des blanches caravelles,	Or leaning in front of the white caravels,
Ils regardaient monter en un ciel ignoré	They watched it rise in an ignored sky
Du fond de l’Océan des étoiles nouvelles	From the bottom of the Ocean of new stars.

E. Chapter III Summary

The synonymies of genus and species names were extracted from the literature, starting with keywords. As the synonyms became more extensive with continued literature reviews, the synonyms were also queried and listed chronologically for genus and alphabetically for species. Unfortunately, unlike scientific names, there are no rules, standards, criteria, etc., for making common names valid, creating confusion when querying the literature. As a result, attempts to standardize common names and some problems arose. Briefly, the following recommendations for common names are:

- Every species should have a unique common name.
- In Canada, capitalize all common names.
- Use accepted common name(s) for biological species, subspecies, varieties and populations.
- Invent common names when they do not exist—document methods/sources for arriving at invented names.
- Each taxon should have an authority for naming species.

Finally, the question posed in the preface, “Why are they called mystery snails,” has been considered. A proposed provenance to the name is from the etymology of Cipango, derived from a poetic word, “Zipangu,” for Japan, named by Marco Polo. A poet, José-Maria De Heredia, incorporated the name Cipango in his poem, “Les Conquérants,” which tells the story of the search for gold, a “fabulous metal” at Zipangu. The poem includes a stanza, “They were going to conquer the fabulous metal, As Cipango matures in its distant mines, And the trade winds tilted their antennas, At the mysterious edges of the Western world.” Zipangu, a mysterious island (Japan) with snails. Something to contemplate.

CHAPTER IV

GLOBAL DISTRIBUTION OF VIVIPARIDAE

A. Introduction

The focus of this chapter is on the distribution of *Cipangopaludina* species. However, because the name is preceded by both *Viviparus(a)* and *Paludina*, the distributions of all three generic names and species' synonyms of CMS and JMS were queried. Unfortunately, many species reported are not valid viviparid species. Many are of unknown validity, some may be unique (endemic) to a particular country, but they are listed anyway. Table 4-1 lists valid Recent and fossil species and used as a guide. The table is based in part on Fischer (2008).

Prashad (1928) distinguished five groups in the subgenus *Viviparus s.s.*: (i) European, (ii) Asiatic, (iii) Australian, (iv) African, and (v) North American. He distinguished the groups from one another based on different numbers of color-bands on the shells: the European species have three color bands, the Asiatic species have uniform coloration or have many bands, Australian shells have a varying number of bands and are confined to the periphery of the continent, African forms have uniform coloration, and North American species have four bands. Otherwise, Prashad (1928) found that the shells do not show any other distinguishing characteristics. He also found the five groups very similar anatomically. He questioned whether the Australian forms are genetically connected with the Asiatic forms but believed the other three groups originated from separate ancestral forms; the similarity in the form of the shells is only an example of parallel evolution. In other words, the genus, *Viviparus*, has arisen polyphyletically, and Prashad (1928) considers the North American genera, *Viviparus s.s.*, *Cipangopaludina*, *Tulotoma*, *Campeloma*, and *Lioplax* as subgenera of the genus. Nevertheless, Prashad (1928) assigned *Cipangopaludina* (and some of its synonyms) to the following countries: in Asia, India and Burma, China, and Korea (all presumably *C. chinensis malleatus*), as well as Japan, possibly the southern extensions of China into parts of Malay Peninsula, Siam, Cambodia, Cochin-China, and Annam (assuming *C. laosiensis* is related to *C. chinensis*). Prashad (1928) did not report *Cipangopaludina* species from Europe, Africa, or Australia, although *C. chinensis* has been reported in Europe since then (see Soes, Menno, Majoor, and Keulen (2011).

Table 4-1. Valid recent and fossil *Viviparus* species. They are based partly on D'Orbigny (1954) and Fischer (2008).

Recent species	**Fossil species**
Viviparus acerosus (Bourguignat, 1862) – Danube river snail	*Viviparus brevis* Tournouer, 1876
Viviparus achatinoides	*V. b. brevis* Tournouer, 1876
Viviparus ater (de Cristofori & Jan, 1832)	*V. b. carinatus* Tournouer, 1876
Viviparus bengalensis (Lamarck)	*V. b. forbesi* Tournouer, 1876
Viviparus contectus (Millet, 1813) Lister's river snail	*V. b. gorceixi* Tournouer, 1876
Viviparus georgianus	*V. b. trochlearis* Tournouer, 1876
Viviparus hellenicus Westerlund, 1886	*Viviparus crytomaphora* Brusina, 1874
Viviparus incertus	*Viviparus diluvianus* (Kunth, 1865)
Viviparus intertextus	*Viviparus gibbus* (Sandberger, 1880)
Viviparus mamillatus (Küster, 1852)	*Viviparus glacialis* (S. Wood, 1872)
Viviparus monardi (Haas, 1934)	*Viviparus kurdensis* Lörenthey, 1894
Viviparus quadratus Benson, 1842	*Viviparus sadleri* Partsch, 1856
Viviparus quadratus disparis	*Viviparus sublentus* d'orbigny, 1850
Viviparus sphaeridius (Bourguignat, 1880)	*Viviparus suessoniensis* (Deshayes, 1826)
Viviparus viviparus (Linnaeus, 1758) – River snail	*Viviparus symeonidisi* Schütt, 1986
	Viviparus teschi Meijer, 1990

Prashad (1928) divides his discussion of the distribution of viviparids into several countries including, Asia Minor, Arabia, Iraq, Persia, Afghanistan, Tibet, the whole of Central Asia, Mongolia, the greater part of China and, except for the Amur Basin, the whole of Asiatic Russia. The region of Asia and India "may be defined as forming a broad band starting from the Amur Basin in the north, and broadening down south to include the greater part of south-eastern China including Yunnan, French Indo-China, Siam, the Malay Peninsula and Burma, India and Baluchistan to the eastern frontiers of Persia"; Annandale, Prashad, and Kemp (1919) also described viviparids from Inland Waters of Baluchistan and Seistan.

This chapter covers the same regions but divides the global distribution into 9 continents and several countries: (1) Europe, (2) Asia, (3) Africa, (4) Australia, (5) New Zealand, (6) South America, (7) Caribbean Islands (e.g., Puerto Rico, Dominican Republic, Jamaica, Cuba), (8) Central America and Mexico, and (9) North America. Antarctica is a 10th continent but has no habitat for viviparids and is not considered further here. Each continent is further divided into regions, then into countries, or at least the major ones into regions.

The searches included the species' names, *Cipangopaludina chinensis* and *japonicus*, and their scientific and common synonyms, all listed in the previous chapter. In addition, maps show the distribution of Viviparinae (i.e., *Viviparus* species) and Bellamyinae (i.e., *Bellamya* species). However, this survey focuses on the distribution of both the Chinese and Japanese mystery snails highlighted in the maps.

B. Europe

The freshwater gastropods represent about 94% (808 species) of the total number of freshwater mollusc species in Europe, consisting of two groups, the Prosobranchs and the Pulmonates. The list does not include *Paludina* and *Vivipara* species described by Bourguignat (1880) and Locard (1854), many of which have since been synonymized with either *Viviparus viviparus* or *V. contectus* by Kennard and Woodward (1926) and Galli (2017). Some, such as *Paludina tentaculata, P. impura,* and *P. inflata* are synonyms of the faucet snail, *Bithynia tentaculata*. Many are casualties of Bourguignat's "Nouvelle École" (e.g., *Vivipara unicolor*, Bourguignat; *Vivipara subfasciata*, Bourguignat; *Vivipara costae*, Bourguignat; *Vivipara atra*, Bourguignat, etc.). Synonyms of *Cipangopaludina chinensis* are bolded as "**CMS synonym**"; similarly, for *Cipangopaludina japonicus*, "**JMS synonym.**"

Forty-four percent of all European freshwater molluscs' face extinction, by far the most threatened group assessed to date in Europe (Cuttelod, Seddon, and Neubert 2011). In the Viviparidae, the total number of species is five, the number of endemics is three, or 60% of the viviparids; more than 90% of the European molluscs are endemic, not occurring anywhere else globally, and represent Europe's natural heritage (Cuttelod, Seddon, and Neubert 2011).

In the Palearctic part of Eurasia, two viviparid genera are present, *Viviparus* and *Contectiana*. The most common species of the genus *Contectiana* in Europe often referred to as *Viviparus contectus*, but Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) state it should be referred to as *C. listeri*. All viviparids are only absent in the southwestern sector of the Iberian Peninsula and are part of southern Europe's far north. *Viviparus* is present in the region of the Molochnaya River and quite familiar from the mouth to the headwaters of the river at the confluence of the Chin Gul River; they have never been found east of Molochnaya River for all the years of observations from 2000–2010 (Anistratenko, Degtyarenko, Anistratenko, and Prozorova 2014). Chernogorenko (1988) states that *Viviparus viviparus* is the most widespread species, encompassing "all of Europe (except for the far north and far south), and the eastern and southern Black Sea littoral" (7).

Europe is here divided into four regions: Northern, Western, Eastern, and Southern; I searched 41 countries for occurrences of CMS and JMS. Table 4-2 lists the countries examined in each region, illustrated in Figure 4-1.

1. Northern Europe

a. Finland, Norway, Sweden

Both Norway and Sweden have *V. viviparus* (Van Damme, Seddon, and Kebapçı 2014). Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) also show its occurrence in Norway and Sweden, but not Finland. Viviparids are likely absent in Finland. Aho (1978), Aho, Ranta, and Vuorinen (1981), Carlsson (2001), and Carlsson (2006) found freshwater prosobranch assemblages in southern and western water bodies, but viviparids were not among them.

Table 4-2. Countries in four regions of Europe shown in Figure 4-1.

European Regions			
Northern	**Western**	**Eastern**	**Southern**
Finland	Iceland	Poland	Portugal
Norway	Ireland	Czech Republic	Spain
Sweden	United Kingdom	Hungary	Malta
Estonia	France	Slovakia	Italy
Latvia	Switzerland	Serbia	Slovenia
Lithuania	Belgium	Bulgaria	Croatia
Denmark	Netherlands	Romania	Bosnia Herzegovina
	Germany	Moldova	Montenegro
	Austria	Ukraine	Albania
		Belarus	Macedonia
		Georgia	Greece
		Armenia	Crete
		Azerbaijan	
		Russia, Eastern	
		Siberia	

Figure 4-1. Four divisions of Europe.
Countries in each are given in Table 4-2.

b. Estonia, Latvia, Lithuania, Denmark

Of these four countries, only Denmark has CMS at two locations, Ellemosevej, Hadsten, Central Jutland and Over Hornbæk, Midtjylland (Appendix A, Denmark)

The distribution map in Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) shows *Viviparus viviparus* present in all four countries. Van Damme, Seddon, and Kebapçı (2014) state the species is rare in Denmark. Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) report CMS in the, "Uk52:rainian Sea of Azov coastal region; they report a geographical lacuna was revealed in the habitat of Viviparidae, probably related to the hydrochemical characteristics of surface waters in the region" (748). They further state that *Viviparus* covers almost all of Europe's territory, the eastern and southern parts of the Black Sea coast, and Western Transcaucasia. Viviparids are absent in waters of the southwestern sector of the Iberian Peninsula and in a part of the far north and south of Europe. Chernogorenko (1988) reports *Viviparus vistulae* as endemic to the Baltic area only in the Vistula and Niemen basins. Kantor, Vinarski, Schileyko, and Sysoev (2010) record *Viviparus sphaeridius*, in rivers and lakes of the basins of Danube, Dnieper, and Dniester rivers, now through the entire Dnieper basin and the Western Dvina River basin.

In summary, viviparids are present in all four countries, but there are no records of CMS or JMS or the synonyms of their scientific or common names.

2. Western Europe

a. Iceland, Ireland, United Kingdom

Anderson (2005) and Byrne, Moorkens, Anderson, Killeen, *et al.* (2009) record *Viviparus viviparus* in their checklists of non-marine molluscs of Ireland, but Byrne, Moorkens, Anderson, Killeen, *et al.* (2009) have not assessed its status on IUCN's Red List of level of risk in nature. Some of the earliest records of viviparids in Britain are from Brown (1845). He described and illustrated *Paludina vivipara* and other species from Britain, but they are synonyms of *Bithynia* and *Achatina* species. Forbes and Hanley (1853) recorded *Paludina listeri* (= *contectus*) and *Paludina vivipara*, chiefly from the southern half of England. Watson (1955) described *Viviparus viviparus* and *V. contectus* from England. Watson (1957) provided a detailed description for distinguishing *V. viviparus* from *V. contectus*, the former having a narrow shell, the latter a more ventricose (markedly swollen or distended) shell. He also asserted that *V. listeri* is a synonym of *V. contectus*. Dixon and Watson (1858), who reported *Paludina vivipara* from the rivers Ex, Taw, Lea, and Isis (at Blenheim) and a stream near York; Taylor (1900) described several anatomical features of both *V. contecta* and *V. viviparus* from the British Isles. Adams (1902) and Horsley (1911, 1915) also recorded both species from England but not from Wales, Scotland, or Ireland. Glover (1906) records "*P. vivipara* [= *Vivipara contecta*]" from ditches in Birkdale (370). Macan (1950) reported a third viviparid, *Viviparus (Paludina) fasciatus*, spreading into the Severn basin via the Thames and Severn and the Stroudwater canals. Boycott (1932) and Briers (2003) reported the calcium requirements of several freshwater gastropods, including *V. contecta* and *V. viviparus,* from several water bodies in Britain, including canals in Breton and Newport and other detached or isolated canals. Anderson (2005, 2008) listed the two viviparid species from both Great Britain and Ireland. None of the viviparids found in the United Kingdom and Ireland are synonyms of CMS or JMS, indicating that Bellamyinae appears to be absent from both countries.

I could not find any extant Viviparidae in Scotland, but *Viviparus garwoodi* is present in the Lower Carboniferous (Yen 1949). Fossil molluscs occur in the United Kingdom, but Hudlston (1869) challenged conchologists who doubted whether *Paludina* extends as far back as the Jurassic. Yet *Paludina* occurs abundantly in the Upper Purbecks in Wessex Coast in southern England. Wood (1848) uncovered fossils of *Paludina lenta* (*unicolor*), in The Crag, a locally important aquifer, up to about 80 m thick, comprising Norfolk, Suffolk, and Cambridgeshire. He also recorded *Paludina tentaculata* but said it is a synonym of the faucet snail, *Bithynia tentaculata*. Tate (1873) recovered fossils of *Paludina scotia* from the Infra-Oxfordian beds of Loch Staffin, Scotland, in his Palaeontology of Skye and Eaasay (p. 349, Figure 3, Plate XII). In the same year, Beyce (1873) found the same species in the Jurassic rocks of Skye and Eaasay, Scotland.

Iceland appears to be depauperate of freshwater molluscs.

In summary, *V. contectus* is present in Ireland and Britain, but *V. viviparus* has not been reported from Britain. Viviparids are absent in both Iceland and Scotland; CMS and JMS lack in all three countries.

b. France, Switzerland

Perhaps the largest number of studies on viviparids is from France. Bourguignat (1801), Draparnaud (1801, 1805, 1818, 1831), and Deshayes (1864) were among the earliest malacologists to record viviparids from France. Deshayes (1864) listed 15 viviparids (as Péristomiens) for France, including seven that he described*, all under the genus *Paludina*. However, the only valid viviparid is *P. vivipara*; the rest are primarily hydrobiids, according to Moquin-Tandon (1855a, b, c), as shown in Table 4-3. The species are listed alphabetically as follows:

P. abbreviata Draparnaud (1805), from Lyon, in Rhône River alluvium (possibly a **CMS synonym**)
P. achatina, no location given
P. acuta, no location given
P. anatine, no location given
P. bicarinata, from a small river of Couze, near Lalinde
P. brevis, from Lyon, in the alluvium of the Rhône
P. bulimoidea, from Lyon, in the Rhône alluvium
P. diaphana, from Lyon, in the alluviums of the Rhône
P. ferussina, from a spring in St.-Médard, near Bordeaux, at the Château d'Eyran
P. gibba, no location given
P. impura, no location given
P. marginata, from Draguignan
P. sirnilis, from St.-Médard, near Bordeaux, at the château d'Eyran
P. viridis, no location given
P. vivipara, from much of France

Maudyt (1839) described five species of *Paludina* from France, listed alphabetically here:

P. brevis, found in La Vergue, on the banks of the Clouère River, and in the Poitiers River in the Boivre
P. impura, in ponds and shallow areas in rivers around France
P. viridis, an uncommon species, in the current of the Fée aux Fées and Marnay River and among the flood debris discharged by the waters on the banks of the Clouère at La Vergue and Gençay
P. vitrea, from the banks of the Rhône, at Migné and Traversonne in Auxance, in the Clouère around Usson, and Gençay
P. vivipara commonly occurs in all rivers, streams, and ponds in France

Grateloup and Raulin (1855) List six "Paludineens," species/varieties living in France, listed alphabetically:

P. achatina; from the Seine, Rhine, Garonn. and L'Adour rivers
P. anatine from Corsica Island
P. impura from Corsica Island and Hyeres, France
P. ventricosa var. *similis* from Royan
P. v. decipiens from Angers.
P. vivipara from all of France and its variety, *major*, from Orange

Drouet (1867) described only one viviparid, *Paludina vivipara*, from Cote d'Or, France, in rivers, canals, marshes; on aquatic plants and stones in the Burgundy Canal; and in the Dijon, Velars, Saône, Auxonne, Doubs, Verdun, and the Loire rivers. Lallemant and Servain (1869) listed *V. fasciata* from the Marne River, France. Dubrueil (1869) reported *Paludina contecta* from the Canal du Midi and in the Vidourle River near Lunel.

Germain (1903) listed eight species and varieties of *Vivipara*, three of which he described*, from the Angers area under the family Viviparidae, listed below alphabetically*:*

**V. fasciata* var. *minor*, from La Mayenne near Angers and in the Loire River at Ponts-de-Cé, and in the Louet River
**V. locardi*, from culverts and locks in Mayenne
**V. subfasciata* var. *minor*, from a pond at Saint Nicolas
V. bourguignati, from Le Mayenne, near the viaduct of the West Railway, in Angers
V. brachya, from Marais, opposite La Baumette, near Angers
V. contecta var. *seghersi*, an uncommon species in marshes, ditches, and canals near La Baumette, Saint-Nicolas pond, lime towers canal, all near Angers.
V. lacustris, from Etang Saint-Nicolas, near Angers
V. penthica, from Mayenne, at Port-de-l'Ile, near Angers

Table 4-3. *Espèces a exclure* (Species to be excluded) by Moquin-Tandon (1855a, b, c) in the descriptions of *Paludina* species of France. Note: *Bithynia* was spelled as *Bythinia* by Moquin-Tandon (1855). Marine molluscs are indicated by ‰.

Species name (Synonym)	Synonym of
Paludina abbreviata, Mich	= *Bithynia abbreviata*.
P. acuta, Desh	= *Bithynia acuta*. ‰
P. adjaciensis, Req	= *Bithynia adjaciensis*. ‰
P. anatina, Mich	= *Bithynia anatina*. ‰
P. bicarinata, Des Moul	= *Bithynia bicarinata*
P. brevis, Mich	= *Bithynia brevis*.
P. bulimoidea, Mich	= *Bithynia vitrea*, var. bulimoidea
P. conoidea, Reyn	= *Bithynia conoidea.*
P. decipiens, Mill	= *Bithynia leachii*.
P. desnoyersii, Payr	= *Truncatella desnoyersii*, Req. ‰

P. diaphana, Mich = *Bithynia vitrea*.
P. ferussina, Des Moul = *Bithynia ferussina*.
P. gibba, Mich = *Bithynia gibba*.
P. idria, Fer = *Bithynia idria*. ‰
P. impura, Brard = *Bithynia tentaculata*.
P. impura, var. curta, Garn = *Bithynia tentaculata*, var. *B. curta*.
P. jaculator, Stud = *Bithynia tentaculata*.
P. klcknii, Yestend = *Bithynia leachii*.
P. marginata, Mich = *Bithynia margin*ata.
P. michaudii, Duv = *Bithynia leachii*
P. minuta. Req = *Bithynia minuta*. ‰
P. moquimana, Part = *Bithynia pygmea*. ‰
P. muriatica, Lam = *Bithynia anatina*. ‰
P. rubiginosa, Boub = *Bithynia viridis*, var. *B. rubiginosa*
P. saxatilis, Reyn = *Bithynia brevis*, var. *B. saxatilis*
P. similis, Des Moul = *Bithynia leachii*.
P. similis, Mich = *Bithynia similis*.
P. similis, Pot et Mich = *Bithynia similis*, var. *B. rufescens*.
P. simoniana, Charp = *Acme simoniana*.
P. spirata, Req = *Bithynia spirata*. ‰
P. stagnorum, Turt = *Bithynia spirata*. ‰
P. tentaculata, Fiera = *Bithynia tentaculata*
P. thermalis, Pot et Mich = *Bithynia anatina*. ‰
P. tricarinata, Pot et Mich = *Bithynia bicarinata*.
P. truncata, Payr = *Truncatella truncatula*, Risso. ‰
P. ventricosa, Gray = *Bithynia leachii*.
P. viridis, Hartm = *Bithynia viridjs*.
P. viridis, Pot et Mich. = *Bithynia viridis*, Var. *B nigricans*
P. vitrea, Menke = *Bithynia vitrea*.
P. vitrea, Moq = *Acme simoniana*.

Locard (1882) described the habitat and distribution of *Vivipara fasciata* (= *V. viviparus*) in France as uncommon; it was fairly numerous in dispersed colonies in Saône River and at the mouths of the various streams that flow into it, such as Seille River, Reyssouze River, Veyle River, and Chalaronne River; it was of greater abundance in the southern part than in the northern part of France. Locard (1895) listed several species of *Cyclostoma* that Draparnaud deposited at the Imperial Museum of Natural History in France and reduced *Vivipara* species to synonyms of *Cyclostoma*. They include *elegans*, *sulcatum*, *obtusum*, *simile*, *viviparum*, *achatinum*, *impurum, anatinum, viride, brevis, gibbum, patulum, maculatum, obscurum, acutum, vitreum*, and *truncatulum*. All except *viviparum* are synonyms of other prosobranchs, as listed in Table 4-3.

In Switzerland, Charpentier (1837) listed three species of *Paludina*: *P. achatina* in Lake Maggiore, in Locarno; *P. vivipara* throughout Switzerland; and *P. impure*, common in ditches and lakes all over Switzerland. Wittenberg (2005) listed *Viviparus ater*, a “probably harmless” species in Southern Switzerland (236).

In summary, most of the species reported as viviparids in France and Switzerland are synonyms of other prosobranchs (e.g., *Bithynia, Truncatella, Acme*) as shown in Table 4-1. The valid species of viviparids in France include *Viviparus viviparus*, *V. contecta*, and *V. fasciata*; Switzerland has only one viviparid, *V. ater*. Neither CMS nor JMS occur in either country.

c. Belgium, Netherlands

There are two indigenous viviparids in The Netherlands, *Viviparus viviparus* and *V. contectus* (Soes, Glöer, and de Winter 2009). *Viviparus viviparus* occurs from the Holocene, the Bavel Interglacial, and the Tiglian in the Netherlands (Meijer 1989). In 2006 a non-native viviparid, *Viviparus acerosus*, the Danube River Snail, was found in the Dutch city of Dordrecht in 2009 (Beran 2019). Soes, Menno, Majoor, and Keulen (2011) reported finding ***Bellamya chinensis*** (**CMS synonym**) in three locations in the Netherlands: (1) in a village in the western part of the Netherlands in November (Soes, Glöer, and de Winter 2009); (2) in a village in the central part of the Netherlands in June and August 2010; and (3) in Eijsder Beemden in the very south of the Netherlands in the floodplains of the river Meuse in July 2010. ***Bellamya chinensis*** (**CMS synonym**) is a recently introduced species into the Rhine and Meuse rivers of the European Union (Collas, Breedveld, Matthews, van der Velde, *et al.* 2017); and Laak River in Balen, Belgium (Van den Neucker, Schildermans, and Scheers 2017). The Meuse River starts in France and goes through Belgium and the Netherlands. It ends in the North Sea. The Rhine River is the longest in western Europe, with its sources in Switzerland, and it passes through several countries, including the Netherlands, France, Germany, Austria, Italy, and Belgium.

In summary, viviparids are present in Belgium and the Netherlands, and CMS occurs in both countries; JMS is currently absent.

d. Germany, Austria

Pfeifer (1821) recorded *Paludina vivipara* at Hanau and *Paludina impura* as very common in the Cassel area of Germany.

Martens (1870) lists molluscs from several areas in Germany, including these, listed alphabetically:
P. fasciata at Hamburg and Mecklenburg
P. troscheli and *P. t.* form *fasciata* from Lanseen, northern Germany
P. vivipara at Magdeburg
P. vivipara, *P. v. impure* at Hamburg
P. viviparus and *P. v.* f. *fasciata*, at Pommern
P. viviparus at Rugen Island

Pfeifer (1841) recorded *Paludina parreyssii* (unknown synonymy) in Germany bordering Austria. Gloer and Zettler (2005), in their checklist of molluscs in Germany, list four species of *Viviparus*, *V. contectus, V. ater, V. acerosus*, and *V. viviparus*, but no localities were given. Kebapçı, Seddon, and Van Damme (2014) list *V. contectus* from Austria and Germany, but it is endangered in the western part of Germany. Van Damme, Seddon, and Kebapçı (2014) list *V. viviparus* as endangered in Germany, where populations in Neckar River have been lost.

Fischer (2008a) searched a channel that protects Vienna from floods in New Danube, Austria, and found *Viviparus acerosus acerosus*. Fischer (2008b) supported the endangered status of both *V. contectus* and *V. acerosus* in Austria after seeing only a few remaining populations in the Neustädter Canal south of Vienna, Lower Austria. Many of the sites examined in 1969, 1973, and 1990 had disappeared in Fischer's (2008a) study. Both species appear on the updated checklists of living viviparids in Austria (Fischer 2008c, d; 2015).

In summary, viviparids are present in Germany and Austria, but CMS and JMS are currently absent.

3. Eastern Europe

a. Poland, Czech Republic

Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) cite *V. viviparus* from numerous localities in Poland. However, Van Damme, Seddon, and Kebapçı (2014) state the species is rare in Poland (as well as Sweden, Norway, and Denmark), likely attributable to the destruction of habitats and water pollution. Chernogorenko (1988) reports *Viviparus vistulae* from the Vistula River basin in Poland. Adding to the potential of mistaken identities, Falniowski, Kozik, and Szarowska (1993) found a hybrid fertile female specimen, *Viviparus contectus* x *V. viviparus*, in the Niepolomice Forest, South Poland. During their morphological/electrophoretic study of the European Viviparidae, the specimen showed intermediate characters in its shell, anatomy, and embryonic shell. Later, Falniowski, Kozik, Szarowska, Fialkpwski, *et al.* (1996) confirmed the occurrence of interspecific hybrids in *V. viviparus* and postulated its probable origin from a highly restricted founder population. They suggested that the species likely originated in an unusual habitat of melt water at a glacier foreland that could have promoted genotypic differentiation and sympatric speciation.

Before 2005, *V. viviparus* “was limited to the largest Czech rivers (Elbe, and Vltava), but with increasing nutrient load, it moved its occurrence to smaller rivers, while in the Elbe and Vltava it almost disappeared after a period of mass occurrence” (Beran 2005, 81). It presently occurs in the Elbe downstream of Brandýs Nad Labem to the state border; the species is the dominant mollusc in many places in the Elbe. *Viviparus contectus* is a European-West Siberian species, but it is rarer in habitat with overgrown cropped vegetation in ponds and other water and slowly flowing floodwaters. Horsák, Juřičková, Beran, CeJka, *et al.* (2010) found *Viviparus contectus* in Bohemia and Moravia, *V. acerosus* in Moravia, and *V. viviparus* only in Bohemia. In the Czech Republic, *V. acerosus* is listed as endangered, found in only 2 of 15 localities, and *V. contectus* as vulnerable, found in 12 of 15 localities on the Czech Red Data List (Hejda, Farkač, and Karel 2017, 70-74). The occurrence of *V. acerosus* in the Elbe itself is not frequent and was found in only one locality by Beran (2005). Beran (2013a) collected *Viviparus acerosus* from the Korana River by a bridge near Koranska Strana, and in the Dyje (Thaya) River and its tributaries (Beran 2013b) and found *V. viviparus* from the Ohře River near the northwest border of the Czech Republic (Beran (2015a, b). The first record of *Viviparus acerosus* from the Czech Republic outside its native range was reported by Beran (2019).

Viviparus acerosus, which resembles *V. ater*, has a southern Alpine distribution, but was introduced in the Bodensee Lake in south Germany. *Viviparus ater* occurs in Western Europe in a few localities.

In summary, viviparids are present in both Poland and Czech Republic, but CMS and JMS are currently absent.

b. Hungary, Slovakia

Fehér, Majoros, and Varga (2006) list the freshwater molluscs occurring in Hungary and include *Viviparus contectus* and *Viviparus acerosus acerosus*. Horsák, Juřičková, Beran, Čejka, *et al.* (2010) reported both *V. acerosus* and *V. contectus* from Slovakia. Kebapçı, Seddon, and Van Damme (2014) recorded *Viviparus contectus* from both countries. However, Van Damme, Seddon, and Kebapçı (2014) did not list either country in their records for *V. viviparus* in Europe. Chernogorenko (1988) describes *Viviparus rossmaessleri* (Bourguignat, 1880) from several localities in the "central Danube basin", which presumably includes both countries (10). He further states that the species is widely known in northern Italy, but under *Viviparus pyramidalis* Rossmaessler, 1835, but Kantor, Vinarski, Schileyko, and Sysoev (2010) list both species as synonyms of *Viviparus ater*.

In summary, viviparids are present in Hungary and Slovakia, but CMS and JMS are currently absent.

c. Serbia, Bulgaria, Romania

While Beran (2018) and Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) did not find *V. viviparus* in Serbia, Martinovic-Vitanovic, Rakovic, Popovic, and Kalafatic (2013) found three species in the Danube River, *V. viviparus, V. contectus*, and *V. acerosus.* Furthermore, they state that the only endemic species of gastropod found in the Danube was *Viviparus acerosus.* Curiously, after finding no *V. acerosus* in (Beran 2018), Beran (2019) collected the species from three locations in Serbi—the Tisa River at Ada, Velika Morava River at Bagrdan, and the Danube River—to evaluate its potential as a bioindicator species of metal pollution in freshwater ecosystems.

In their checklist of freshwater gastropods of Bulgaria, Georgiev and Hubenov (2013) list three species of viviparids: *Viviparus acerosus*, an introduced species to Central and South European areas, found in the Danubian Plain, Pre-Balkan or foothills north of Stara Planina Mountains, Eastern Stara Planina Mountains, Thracian Lowland, Podbalkan Basins, and Western Rhodope Mountains; *Viviparus contectus*, occurring in the Danubian Plain; *Viviparus viviparus* in the Danubian Plain and Sofia Basin. Trichkova, Tyufekchieva, Kenderov, Lyubomir, *et al.* (2013) found a high frequency of occurrence of *Viviparus* spp. in reservoirs of the Danube River basin of Bulgaria, along with several other invasive species. They concluded that invasive alien species should be used in the development of macroinvertebrate metrics and assessment tools for lakes and river basins and reservoir management strategies. Georgiev (2014) describes *V. viviparus, V. contectus*, and *V. acerosus* from Bulgarian waters. Kolev, Georgiev, and Dedov (2015) collected two species of viviparids in Northern Bulgaria: *Viviparus acerosus* from Russe at the Liulyaka base and *Viviparus viviparus* from Rusenski Lom River in the village and from Russe at the Liulyaka base. Georgiev (2012) collected freshwater gastropods in Upper Thracian Lowland of Southern Bulgaria and found *Viviparus acerosus* from the canal near the village of Belozem; he did not find *Viviparus viviparus* or *Viviparus maritzanus*, but they had been reported from the area by others.

Sîrbu, Sîrbu, and Benedek (2010) recorded two viviparids living in Romania: *Viviparus contectus* in the Bega River near Timișoara and *Viviparus acerosus* in the Mureș River at Pecica. *Viviparus acerosus*, described by Bourguignat (1862), lives in marshes and ponds near Timisoara and the “Danube’s sector from Banat, from Baziaș to Orșova, in the whole riverbed and on all substratum types, being often the dominant species within the benthic communities” (25). However, viviparids are absent from the upper Tisa River basin (Sîrbu, Sîrbu, and Benedek 2011). Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) and Anistratenko, Furyk, Anistratenko, and Degtyarenko (2019) collected *V. viviparus* from all three countries, with numerous locations in each of Romania. Bourguignat (1870–1884, 1880) listed 15 species, five of which he named (shown with*) Bourguignat (1869) of *Viviparus* from the “lower Danube” (Romania?), among which were *acerosa**, *ater, contectus**, *costae, fasciata**, *mamillata**, *pyamidalis**, and species synonymous with *V. viviparus.* Neubauer, Harzhauser, Georgopoulou, Mandic, *et al.* (2014) proposed *Viviparus deleeuwi* as a primary homonym of *Viviparus muscelensis* from Romania. They also proposed *Viviparus lubenescuae* as a primary homonym of *Viviparus conicus* from Romania.

In summary, viviparids are present in Serbia, Bulgaria, and Romania, but CMS and JMS are currently absent.

d. Moldova, Ukraine, Belarus

Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) and Anistratenko, Furyk, Anistratenko, and Degtyarenko (2019) collected *V. viviparus* from numerous locations in Ukraine. In addition to *V. viviparus, V. sphaeridius* was recorded for the first time from beyond the Carpathian Mountains in southwestern Ukraine. Balashov, Son, Coadã, and Welter-Schultes (2013) list *V. viviparus* and *V. contectus* in their updated list of molluscs for Moldova but do not give details. *Viviparus viviparus* also appears to be present in Belarus (Anistratenko, Degtyarenko, Anistratenko, and Prozorova 2014); as of 2008, CMS and JMS have not been reported in Belarus (Semenchenko, Rizevsky, Mastitsky, Vezhnovets, *et al.* 2009). Neubauer, Harzhauser, Georgopoulou, Mandic, *et al.* (2014) proposed species status for *Viviparus wesselinghi*, formerly a variety of *Viviparus neumayri* var. *incerta* from Ukraine.

In summary, viviparids are present in Moldova, Ukraine, and Belarus, but CMS and JMS appear to be currently absent.

e. Georgia, Armenia, Azerbaijan

Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) show *V. viviparus* present in Georgia and Azerbaijan, as do Van Damme, Seddon, and Kebapçı (2014). *Viviparus contectus* appears to be absent from these three countries (Kebapçı, Seddon, and Van Damme 2014). Chernogorenko (1988) reports finding several samples of *Viviparus costae* from western Georgia. Kantor, Vinarski, Schileyko, and Sysoev (2010) report *Viviparus costae* from rivers in Transcaucasia (northwest Georgia, eastern Azerbaijan, and Armenia, mainly situated on a high mountainous plateau south of Georgia and west of Azerbaijan).

In summary, viviparids are present in Georgia, Armenia, and Azerbaijan, but CMS and JMS are currently absent.

f. Russia, Eastern Siberia

According to Chernogorenko (1988), the genus *Viviparus* consists of eight species that fall into three groups in European Russia. The first group contains the type-species of the genus *V. viviparus* as well as V. *vistulae*. *V. ater*, and *V. costae*. The second includes *V. rossmaessleri* (or *V. hunqaricus*). The third consists of three species from western Greece (*V. hellenicus. V. blanci, and V. qraecus* sp. n.). Chernogorenko (1988) believes *V. acerosus* to be a junior synonym of *V. ater*. However, some European malacologists (e.g., Falkner, Gerhard, Bank, and von Proschwitz 2001) regard both *V. acerosus* and *V. ater* as distinct species. Within the first group are: *V. costae*, from rivers in Georgia, Azerbaijan, and Armenia; *V. sphaeridius,* in rivers and lakes of the basins of Danube, Dnieper, and Dniester rivers; *V. vistulae*, from rivers and lakes of the basin of the Baltic Sea; and *V. viviparus*, from rivers and lakes of Europe except for extreme north and south, western Transcaucasia, introduced into the Novosibirsk Reservoir.

Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) show several localities in European Russia in which *V. viviparus* occurs: south of the White Sea near Arkhangelsk; Lake Ladoga and south of the Gulf of Finland near St. Petersburg; several locations on the lower Volga and Ural rivers; the Don River below and above the Tsimlyansk Reservoir; the Rika Pechora River in Komi Republic.

The distribution of the Chinese Mystery Snail in Russia was updated by iNaturalist (2020), which added three locations—Ivanovo Oblast, Vladimir Oblast, and Moskovskaya Oblast—as well as two sites in Asiatic Russia, as discussed in Section 2. Asia a) (1). Russia.

In summary, including CMS, viviparids are present in European Russia, but JMS is currently absent. In addition, Eastern Siberia lacks *Viviparus* and *Cipangopaludina* species. See the overview of overall distribution in Europe in figures for *V. viviparus*, *V. contectus*, *V. acerosus*, and *C. chinensis*.

4. Southern Europe

a. Portugal, Spain, Malta

Graells (1846) catalogued six species of *Paludina* (listed alphabetically below) for Spain, but five are synonyms of other prosobranchs (see Table 4-3). Only *P.* (*Viviparus*) *vivipara* (*viviparus*) is a valid viviparid species in the list.

- *P. vivipa*ra from Alta Catalonia and Aragón, Spain
- *P. achatina* (= *Bithynia achatina*), from Alta Catalonia, Aragón
- *P. impura* (= *Bithynia tentaculata*) from eastern and northern provinces
- *P. i.* var. *matritensis*, from eastern and northern Provinces
- *P. muriatica* (= *Bithynia achatina*), from Catalonia and Valencia, Spain
- *P similis* (= *Bithynia similis*), from Catalonia and Valencia
- *P. acuta* (= *Bithynia acuta*), from eastern provinces

The exact synonyms are perpetuated by Servain (1880) in his catalogue of prosobranchs in Portugal and Spain.

Soler, Moreno, Araujo, and Ramos (2006) studied freshwater molluscs around Madrid and found 33 species, of which 25 were gastropods and eight were bivalves. None of the gastropods were viviparids.

Morelet (1845) listed six species of *Paludina* for Portugal, but all or most appear to be synonyms of other prosobranchs, based on the synonymy of Moquin-Tandon (1855a, b, c): *P. achatina* (= a synonym of *Bithynia* a*chatina* sp.)*; P. impura (= Bithynia tentaculata); P. similis* (= *Bithynia* *similis*)*; P. acuta* (= *Hydrobia brondeli* or *Bithynia acuta*?)*; P. anatina* (= *Bithynia achatina*)*;* and *P. gibba* (= *Bithynia gibba*); he listed three species for Spain: *P. impura; P. similis;* and *P. acuta*. Most species are unlikely viviparids because of the habitats in which they occur. Morelet (1845) describes them as *P. acuta* in the Algarve, in the brackish stream near Villar-Keale off the west coast of the Balearic Sea; *P. achatina* in an isolated swamp on the northern limit of the Alentejo, Portugal; *P. impura* in "all the waters of Portugal"; *P. similis* "extremely multiplied" in all waters of southern Portugal, particularly in Tegus Valley; *P. achatina* around Setubal, Portugal off the coast of the Atlantic Ocean; *P. gibba* in abundance in Fontaine-des Lunnes, near Coimbra (90-91).

Castro (1873) found several zebra mussels on the banks of the River Douro at Porto, Portugal, following a severe flood, with "an enormous quantity of *Vivipara fasciata*" (245–246). Castro (1873) mused that the mussels might have arrived there in the ballasts from English naval ships and that the same may also be possible for the snail. This dispersal route is probably unlikely given the limited dispersal prowess of viviparids (see Chapter V. Dispersal Mechanisms). Holyoak, Holyoak, and Mendes (2019, 155) referred to some old records for *V. viviparus* for Setúbal, Pôrto (Porto), and São Martinho do Porto but were stated by others "to be of uncertain significance, perhaps based on temporary introductions".

The presence of viviparids in Spain is questioned because none were found in studies by Larraz (1986) for Navarra, northeastern Spain; by Perez-Quintero, Taberner, and Dionisio (2004) for Huelva Province, southwestern Spain; by Soler, Moreno, Araujo, and Ramos (2006) for Madrid; or by Perez-Quintero (2011) for Guadana River basin in southern Spain.

Van Damme, Seddon, and Kebapçı (2014) list Portugal as a country with *V. viviparus*. However, Holyoak, Holyoak, and Mendes (2019) list six families of freshwater gastropods, including several species of Hydrobiidae, but no viviparids in Portugal. Viviparids appear to be absent in Malta as well.

In summary, viviparids appear to be currently present in Portugal but absent in Spain and Malta, as are CMS and JMS.

b. Italy, Slovenia, Croatia

Alonza (1971) recorded *V. viviparus* in northern and central Italy in lakes, ponds, and marshes; *Viviparus pyramidalis* in lakes, ponds, and swamps in north Italy with a comment (translated from Italian): "*Viviparus pyramidalis* De Cristofori and Jan and *V. ater* De Cristofori and Jan mate by breeding hybrids." He remarked that the two species are the only living viviparids in Italy. Petraccioli, Crovato, Niero, De Riso, *et al.* (2015) did not report any viviparids in southern Italy in their preliminary checklist of freshwater molluscs from the Alburni Mountains, Campania.

Beran (2013a, b) found *V. acerosus* in surveys from 2009 to 2012 in the Korana River, downstream of Plitvice Lake, Croatia. In surveys from 2009 to 2013, Beran (2016) collected *V. contectus* from 6 of 14 sites (including Visovac Lake, Krka and Čikola rivers, and in Rab Island, Croatia (2015a, b), but not in resurveys in 2015 to 2017 (Beran 2018). Both Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) and Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) concur that *V. viviparus* occurs in Croatia but not in Slovenia.

In summary, viviparids are currently present in Italy and Croatia but not in Slovenia, nor are CMS and JMS present in the three countries.

c. Bosnia, Herzegovina, Montenegro

Surveys for non-marine molluscs in Bosnia and Herzegovina appear to be lacking. Still, with viviparids in surrounding Croatia and Serbia, it is probable that some occur there but have not yet been reported. Pešić and Gloer (2013) report *Viviparus mamillatus* Küster, 1852, a species endemic to Adriatic drainage of Montenegro (and Albania and mainland Greece); the species was collected from Skadar Lake and its "sublacustrine springs, adjacent pools, and mouths of the surrounding tributaries (including its downstream part)" (79).

In summary, Montenegro has an endemic viviparid, *V. mamillatus*, but viviparids have not been reported from Bosnia and Herzegovina.

d. Albania, Macedonia, Greece, Crete

Chernogorenko (1988) reports the distribution of *Viviparus hellenicus* from northwestern Greece and on the Ionian Islands. He also reports *Viviparus blanci* and *Viviparus qraecus* from Greece. Bank (2006) lists three species of viviparids for Greece, all in the mainland, including Andikíthira, Evia, the Ionian Islands, Samothráki, the Northern Sporades, and Thassos. *Viviparus ater hellenicus* is a Greece endemic; *V. contectus* is in mainland Kerkira; and *V. mamillatus* in mainland Greece. Pešić and Gloer (2013) report *V. mamillatus*, a species endemic to Adriatic drainage of mainland Greece and Montenegro and Albania. Of 33 countries listed with *V. viviparus* by Van Damme, Seddon, and Kebapçı (2014), Albania is among them. Information on freshwater gastropods in Macedonia and Crete are lacking or were not found.

In summary, viviparids are present in Albania and Greece but absent in Macedonia and Crete. CMS and JMS are not currently present in any of the four countries.

5. Summary of Distribution of Viviparidae in Europe

Of the numerous species reported as viviparids, only a few are valid, with many invalid species belonging as synonyms to other prosobranchs, particularly Bithyniidae (e.g., *Bithynia*) and Hydrobiids (e.g., *Hydrobia*). Numerous species or synonyms could not be validated, or they did not appear on several lists presented in the text. They may have been consumed as synonyms of other species or have since been recognized as valid species. Three species, *V. viviparus*, *V. contectus*, and *V. acerosus*, are among the most common viviparids in continental Europe. Figures 4-2 to 4-4 illustrate the distributions of the three species based on the information in the text. Figure 4-2 questions the presence of viviparids in Portugal reported by some authors. See text for explanations. Figure 4-4 shows the distribution of *V. acerosus*, the stars being locations cited in the text, while the grey area shows the European distribution of the species. Figure 4-5 shows the distribution of the Chinese Mystery Snail in continental Europe up to 2019 as reported in iNaturalist (2020), which added three locations in European Russia—Ivanovo Oblast, Vladimir Oblast, and Moskovskaya Oblast—as well as two sites in Asiatic Russia, as discussed in Section 2. Asia a) (1). Russia. Figure 4-5 shows a locality of CMS in France, based on one of its synonyms, *Paludina abbreviata*. It was reported in the alluvium of Rhône River in Lyon, France, but no other details were given. The other CMS locations in Europe are the Netherlands, two in Denmark, and one in Belgium.

Figure 4-2. Distribution of *Viviparus viviparus* in continental Europe.

Figure 4-3. Distribution of *Viviparus contectus* in continental Europe.

Figure 4-4. Distribution of *Viviparus acerosus* in continental Europe. Stars are locations cited in the text.

Figure 4-5. Distribution of *Cipangopaludina chinensis* (stars) in continental Europe. See text for explanation of France location (*?).

C. Asia

In the following discussion, Asia is divided into 37 countries, many having either CMS or JMS or both, and six regions (Figure 4-6), within which are the countries listed in Table 4-4: (a) Northern Asia, (b) Western Asia, (c) Central Asia, (d) Eastern Asia, (e) Southern Asia, and (f) Southeastern Asia. As for Europe, when a synonym of *Cipangopaludina chinensis* occurs, it is bolded as "**CMS synonym**"; similarly, for *Cipangopaludina japonicus*, "**JMS synonym**."

Table 4-4. Countries in five regions of Asia shown in Figure 4-6.

	Asian Regions				
Northern	**Western**	**Central**	**Eastern**	**Southern**	**Southeastern Asia**
Russia	Syria	Turkey	Mongolia	Afghanistan	Burma
Western Siberia	Iraq	Cyprus	China	Pakistan	Vietnam
	Iran	Kazakhstan	North Korea	India	Laos
	Israel	Uzbekistan	South Korea	Bangladesh	Thailand
	Jordan	Turkmenistan	Japan		Cambodia
	Saudi Arabia		Taiwan		Philippines Guam
	Omen				Malaysia
	Yemen				Indonesia
					Sumatra
					Java

Figure 4-6. Six regions of Asia, each with the countries listed in Table 4-2.

1. Northern Asia

a. Russia, Western Siberia

a. Prashad (1928) states, "In the whole area of Asiatic Russia there are no viviparids except in the extreme southeast in the basin of the Amur River and its tributaries, and these are apparently an extension of the Chinese forms which have become established in this area" (171). However, the following discussion is an update and reveals that viviparids are present throughout Asiatic Russia, but CMS occurs there as well.

Kantor, Vinarski, Schileyko, and Sysoev (2010) list four species of *Cipangopaludina* and five species of *Viviparus* for Russia and adjacent territories. The four species of *Cipangopaludina* are (1) ***C. kurilensis*** with two synonyms, ***Viviparus malleatus*** and ***Paludina malleatus*** (**CMS synonyms***)*, located in southern Kurile Islands, and southern and central Sakhalin Island in lakes and slow-running rivers of Asiatic Russia (the synonymy of *C. kurilensis* suggests the species is *Cipangopaludina chinensis,* but I could not find descriptions of this Russian species); (2) *C. sujfunensis* occurs in lakes in basins of the rivers of southern Primorje, except the Amur basin; (3) *C. ussuriensis* occurs in lakes in the Amur basin, excluding upper and central parts of Zeya and Bureya basins, in lakes; and (4) C. *zejaensis* occurs in lakes of the upper and central parts of Zeya and Bureya basins, middle Amur, and Ussuri basins.

There are five species of *Viviparus* in Asian Russia (Kantor, Vinarski, Schileyko, and Sysoev 2010):

- *V. ater*, from rivers and lakes of the basins of Danube, Dnieper, Dniester rivers, and Western Dvina River in the vicinities of Tolliatti and Pyatigorsk. They remarked on a controversy that the "true *V. ater* is distributed in the South Alps only, and all the findings of this species from the ex-USSR territory belong, in reality, to another species of this genus, possibly to *V. acerosus* (Bourgugnat, 1862)" (13).
- *V. costae*, from rivers in western Transcaucasia, north of Minor Asia.
- *V. sphaeridius*, from rivers and lakes of the basins of Danube, Dnieper and Dniester rivers, now through the entire Dnieper and the basin of the Western Dvina River.
- *V. vistulae*, from rivers and lakes of the Baltic Sea basin (Neman, Visla, Kurshsk Bay).
- *V. viviparus*, from rivers and lakes of Europe except for extreme north and south, western Transcaucasia, and introduced to the Novosibirsk Reservoir.

Anistratenko, Degtyarenko, Anistratenko, and Prozorova (2014) extended the eastern distribution of *V. viviparus* into Asia, adding locations in the Ob River at Narym, the Irtysh River below the city of Tobol'sk, and the Novosibirsk reservoir. iNaturalist (2020) records two new locations for CMS in Asiatic Russia, Novosibirsk City and Novosibirsk Oblast. Kantor (2010) reported the species from southern Kurile Islands and southern and central Sakhalin Island in lakes and slow-running rivers of Asiatic Russia for ***Cipangopaludina kurilensis*, a synonym of CMS**. These are the first occurrences reported for Asiatic Russia.

Western Siberia has diverse freshwater gastropods, but they are mainly pulmonates (86 out of 134 species). Only one viviparid, *Connectiana listeri* (Forbes et Hanley, 1849), occurs in Western Siberia (Vinarski, Andreeva, Andreev, Lazutkina, *et al*. 2007).

In summary, viviparids are present, but CMS has recently (at least by 2004) invaded southern Kurile Islands and southern and central Sakhalin

Island in lakes and slow-running rivers of Asiatic Russia. Two new locations are added for Russia, Novosibirsk City and Novosibirsk Oblast.

2. Western Asia

Western Asia is predominantly desert, the primary freshwater body being the Euphrates and its tributaries with multiple dams, such as Al Assad Lake. The aridity of Western Asia confines viviparids to just a few countries.

a. Syria

Only fossil viviparids have been recorded from Syria. Germain (1921) reported several *Paludina* species, but all are synonyms of *Bithynia*. Prashad (1928) believes the species to be *Viviparus apamae* Blanckenhorn. Recent viviparids appear to be absent in Syria.

b. Iraq and Iran

Annandale, Prashad, and Kemp (1919) describe *Bellamya hilmandensis* (Kobelt, 1909) from Seistan and Baluchestan Province, Iran. They state that the complete synonymy of the forms included by Kobelt is given under the name *Vivipara dissimilis*. Therefore, they provisionally consider it a distinct species. The species was described from the Afghan desert. Single, fairly fresh empty shells were collected at the edge of pools near Nasratabad and Jellalabad and the Hamun near Lab-i-Baring. Chu, Massoud, and Arfaa (1968) record *Viviparus bengalensis* (= *Bellamya bengalensis* = *Filopaludina bengalensis*) in their list for freshwater snails from Khuzestan Province and Mazandaran Province, Iran. Massoud and Hedayeti-Far (1979) reported *F. bengalensis* living to the north of Ahwaz and Mansoorian (2001) in Khuzestan Province, Southwest Iran. In their checklist of freshwater gastropods of Iran, Glöer and Pešić (2012) cited the previous reports in their updated checklist of *B. bengalensis* in Khuzestan Province, Massoud, and Hedayeti-Far and Mansoorian, Mazandaran Province as well as *B. hilmandensis* in Seistan and Baluchestan Province. Van Damme (2014) lists *Viviparus viviparus* from Iran but gives no location. Abbaspour, Yaripour, Gloeer, Zamanpoore, *et al.* (2019) found only planorbids and sphaeriids in the Kor River System, Fars Province, Iran in their 2015–2016 surveys.

Prashad (1928) states that viviparids are absent in Iraq. No records have been reported from Iraq since then. Among 10 freshwater species of molluscs, Plaziat and Younts (2005) found *B. bengalenis* in the Lower Mesopotamian plain of Iraq in muds of ponds, marshes, and channels draining the marshes.

In summary, viviparids are currently present in Iran, the most common species being *B. bengalensis*. Viviparids appear to be absent in Iraq. It is unlikely that CMS or JMS occurs in either country.

c. Israel, Jordan, Saudi Arabia, Omen, Yemen

The only water body in Israel and Jordan is the Dead Sea on the border they share. Viviparids are strictly freshwater, and with the rest of the Isreala and Jordan areas mainly being desert, they are doubtful to ever survive in these two countries. However, Roll, Dayan, Simberloff, and Mienis (2009) reported introducing two viviparids for food, *Filopaludina martensi martensi* and *Filopaludina martensi cambodjensis*, both native to Thailand. Similarly, Saudi Arabia. Oman, and Yemen are desert countries surrounded by the Arabian Sea, and viviparids are highly unlikely to survive in these countries.

3. Central Asia

Within the Eastern Mediterranean, the greatest diversity of freshwater gastropods is 123 species, 48 of which occur in springs, wells, caves, and aquifers. Of the 85 species endemic to the area, the Hydrobiidae are the most diverse group; none are viviparids. Viviparidae is represented by two species found in lakes and marshes of Turkey and Southern Mesopotamia (Smith, Barrios, Darwall, and Numa 2014).

a. Turkey, Cyprus

Şahin and Yildirim (2007) found *Viviparus acerosus costae* at four of six stations in Lake Sapanka, Turkey. Yildirim (1999) recorded two species of viviparids in Turkey: *Viviparus contectus* (Millet 1813) in the Eastern Anatolia Region and *Viviparus viviparus costae* (Mousson 1863) in the Marmara basin. Yildirim, Zeki, Seval, and Kebapç (2006), in their supplement to the list in Yildirim (1999), added *Viviparus mamillatus* (Küster 1852) from Lake Abant. However, Yildirim, Zeki, Seval, and Kebapç (2006) believe the records of *V. mamillatus* from Turkey "are dubious due to the split with their main distribution centres in western

Balkan Peninsula and central Europe" (203). Of 25 countries listed for occurrence of *V. contectus* by Kebapçı, Seddon, and Van Damme (2014), Turkey (Turkey-in-Asia) is among them. And Albania and Turkey are among 33 countries listed for *V. viviparus* by Van Damme, Seddon, and Kebapçı (2014). Chernogorenko (1988) reports the distribution of *Viviparus hellenicus* from northwestern Greece and on the Ionian Islands. He also reports *Viviparus blanci* and *Viviparus qraecus* from Greece. Information on freshwater gastropods in Cyprus is lacking.

In summary, viviparids are present in Turkey, but not Cyprus; CMS and JMS do not currently occur in Turkey or Cyprus.

b. Kazakhstan, Uzbekistan, Turkmenistan

Viviparids are absent in all three countries (Prashad 1928).

4. Eastern Asia

The Chinese Mystery Snail is native to most Eastern and Southeast Asian countries. Still, neither Prashad (1928) nor Kipp, Benson, Larson, and Fusaro (2016) specify which countries: "Southeast Asia to Japan and eastern Russia" (2). However, perhaps the greatest diversity of *Cipangopaludina* occurs in China, based on the morphological analyses of shells of several *Cipangopaludina* species by Lu, Du, Li, and Yang (2014).

a. Mongolia

Viviparids are absent in Mongolia (Prashad 1928).

b. China

Among the earliest records of viviparids in Indochina were 12 species of *Paludina* recorded by Morelet (1846, 1869), here listed alphabetically:

- ***P. ampulliformis*** (= **synonym of *lecythis***, a **CMS synonym**), from Tourane (Da Nang) River, Vietnam
- *P. bengalensis* (= *Filopaludina bengalensis*), from the entire coastline of India and Indochina
- *P. ciliata*, from Siam, waters of Bangkok and Petchahuri, and Thu-dau-mot, Indochina
- *P. cochinchinensis*, from the Stiengs area, on the eastern limit of French Indochina

- *P. eyriesii*, found living in wooded swamps around Battambang, Cambodia
- *P. frauenfeldi*, from Thailand, around Bangkok and Petchaburi
- *P. hainesiana*, from Siam and Cambodia
- *P. javanica*, from Indochina, no specific location given
- *P. lurida*, from Saigon
- *P. praemorsa*, from Bengal, the Philippines, and the waters of Siam
- *P. sumatrensis*, from Sumatra
- *P. trochoides*, from areas around Bangkok and Pelchaburi, Thailand

The list has only two viviparids, *P. ampulliformis* (= CMC) and *P. bengalensis* (= *Filopaludina bengalensis)*. The rest are likely invalid species.

Yen (1942) reported the distributions of 24 species of *Viviparus* in China, and a year later, Yen (1943) examined distributions based on collections of viviparids from China in the British Museum, listing 17 species/subspecies of *Cipangopaludina* (Table 4-5). Yen (1948) updated the list with four more species collected in Chekiang Province, a province not listed in his 1942 and 1943 reports: ***Viviparus chinensis lecythoides*** (Benson), 1842 (**CMS synonym**); *Viviparus quadratus* (Benson), 1842; *Viviparus quadratus lapillorum* (Heude), 1890; and *Viviparus lithophaga* (Heude), 1889.

Yen (1943) examined mollusc material in the British Museum and found several *Viviparus* species that are synonyms of CMS, all listed alphabetically:

- ***V. chinensis*** (Gray) 1834 (**CMS synonym**), from Shih-tao, Shangtung. ***Vlviparus chinensis fluminalis*** (Heude) 1890 (**CMS synonym**), from Yankze Valley and Shanghai
- ***V. chinensis aubryanus*** (Heude) 1890 (**CMS synonym**), from Guizhou Province, Han-lo-si Yunnan Lake, a Rice field, Huang-kiang north border of Yunnan, West China, and some other unknown locations in China
- ***V. c. haasi*** (= ***V. c. longispirus*** (Heude) (**CMS synonyms**), from Chen-tuh, Szechwan, Shang-kuan, near the northeast shore of Lake Tai, Yunnan, Swampy Lake, north of Hoching drainage to the Yangtze River
- ***V. c. lecythoides*** (Benson 1842 (**CMS synonym**), Chow-shan Island, Chekiang, Chusan, Yangtze Kiang, Chusan, and north of China
- ***V. occidentalis*** (Annandale) 1924 (= ***Lecythoconcha malleata*** f. ***occidentalis***) (**CMS synonyms**), Annandale, from Shan-kuan, near the northwest shore of Lake Tai, China.

These and other viviparids are listed in Table 4-5 and compared to the list in Yen (1943). Rao (1989) states ***Cipangopaludina lecythis*** (**CMS synonym**) occurs throughout Yunnan, China. Yen (1948) records four *Viviparus* species, listed alphabetically here:

- ***V. chinensis lecythoides*** (**CMS synonym**) is a widespread form in the lower Yangtze Valley, Yuyao, Tonglu, Fengshiu, Lanchi
- *V. lithophaga* collected from Tonglu, Chekiang Province
- *V. quadratus* collected from Tonglu, Chekiang Province
- *V. q. lapillorum* collected from Chien-tang-kiang and Lanehi

In China, the existing extant taxonomy for Viviparidae includes approximately 61 recognized species in 9 genera (Lu, Du, Li, and Yang 2014; Lu, Mei–Juan, and Du 2016), three of which are *Viviparus* Montfort, 1810; *Bellamya* Jousseaume, 1886, and *Cipangopaludina* Hannibal, 1912. Lu, Du, Li, and Yang (2014) named 18 potential species in China and reduced them to 11 species and two subspecies after a morphological analysis of the Chinese *Cipangopaludina* species. Table 4-6 lists the species and subspecies and their distributions in China, with *C. chinensis* shown in Figure 4-8.

Köhler, Do, and Jinghua (2012a) give the native range and distribution of the Chinese Mystery Snail in China in Table 4-7. Table 4-7 also gleans the locations of CMS cited in the text, all alphabetically listed and plotted in Figure 4-8. The latest viviparid reported in China is *Trochotaia pyramidella*, a new species and genus, from freshwater ponds in the Yousuo village of Er-Yuan County, Yunnan, southwestern China (Du, Yang, and Chen 2015).

In summary, China has a diverse assemblage of viviparids, with CMS present throughout much of the country. JMS may be present because the morphological and genetic analyses done on *Cipangopaludina* species do not include JMS synonyms.

Table 4-5. Records of viviparids for China localities and/or provinces by Yen (1942, 1943). The Chinese Mystery Snail records are shaded and shown in Figure 4-8. The species are listed alphabetically.

Yen (1942) Species/subspecies	**Locality/Province**	**Yen (1943) Species/subspecies**	**Locality/Province**
Viviparus boettgeri (Heude) 1890	Hainan	*Cipangopaludina chinensis* (Gray 1834)	China
V. chinensis (Gray) 1834	Shihtao, Shangtung	Syn. *leucostoma* Heude, 1890	Peihai, Kwangtung
V. chinensis aubryanus (Heude) 1890	Huang-kiang; north border of Yunnan	*diminuta* Heude, 1890	Kwangteh, Anhwei
V. chinensis fluminalis (Heude) 1890	Shanghai	*C. chinensis hainanensis* (Kobelt, 1906)	Hainan Island, Kwangtung
V. chinensis haasi Prashad, 1928	Shang-kuan, Lake Ta-li; Yunnan, Yangtze River	*C. c. stelmataphora* Bourguignat, 1862	Peking, Hopei
V. chinensis lecythoides (Benson)	Cuming; Chusan, Yangtze Kiang	*C. c. lecythis* (Benson, 1836)	Yunnan
V. chui Yen, 1937	Kirin, Kirin Province	*C. delavanyana* (Heude, 1889)	Ta-li-fu, Yunnan
V. costatus (Quoy & Gaimard)	China	*C. haasi* (Prashad 1928), Syn. *longispira*	Chen-tuh, Szechwan
V. margaryoides Annandale, 1924	Lake Ta-li, Shan-kuan, Yunnan.	*C. lapidea* (Heude, 1890)	Chien-tuh, Anhwei
V. occidentalis (Annandale)	Shan-kuan	*C. latissima*	Mongtze, Yunnan
V. polyzonatus Frauenfeld, 1862	Canton	*C. lecythoides* (Benson, 1842)	Chow-shan Island, Chekiang
V. praerosus (Gerstfeldt) 1859	Amur River, Cuming	*C. l. fluminalis* (Heude, 1890)	Yangtze valley
V. quadratus (Benson) 1842	Cuming; Canton; Shangtun; Shanghai	*C. l. aubryana* (Heude, 1890)	Kwei-chow

V. q. aeruginosus (Reeve) 1863	Cuming	*C. l. occidentalis* (Annadale, 1924)	Yunnan
V. q. dispiralis (Heude) 1890	Shan-kuan, Lake Ta-li, Yunnan	*C. ussuriensis* (Gerstfeldt, 1859)	Lower Amur river
V. q. ecarinatus (Kobelt) 1909	Canton, Kwangtung; Shanghai	*C. ventricosa* (Heude, 1890)	Kwei-chow and Yunnan Provinces
V. q. heudei (Dautzenberg & Fischer) 1905	Shanghai; Cuming; Yangtze valley	*C. v. cathayensis* (Heude 1890)	Yangtze valley
V. q. lapillorum (Heude) 1890	Ning-kuo-fu, Anhwei; Shanghai	*C. v. patris* (Kobelt, 1906)	
V. q. limnophilus (Mabille)	Lake Ta-li, Yunnan	Syn. *compacta* Kobelt non Nevill	Hainan Island, Kwangtung
V. smithi sp. nov.	Hunan	*lecythis crassior* Annadale, 1924	Western Yunnan
V. subcostatus (Gray)	China	*lecythoides* Heude, non-Benson	Chow-shan Island, Chekian
V. thersites (Reeve) 1863	Canton river	*C. v. wingatei* (Smith, 1900)	Hunan
V. ussuriensis (Gerstfeldt)	Amur		
V. wingatei (Smith)	Hunan; Yangtze valley		

Table 4-6. Species of *Cipangopaludina* and their distributions examined by Lu, Du, Li, and Yang (2014) in China. Species are listed alphabetically. *Cipangopaludina chinensis* is shaded for locations in Figure X.

Species	**Locality/Province**
ampullacea	Southwest of China, Yunnan, Sichuan Provinces and Macao
ampulliformis (synonym of ***lecythis***)	(**CMS synonym**) Yunnan, China; Burma
aubryana	Sichuan, Hunan, Guangdong, Guizhou and Yunnan Provinces
cathayensis	Jilin, Shanxi, Hebei, Shandong, Anhui, Jiangsu, Zhejiang, Hunan, Sichuan, Guizhou, and Yunnan Provinces
chinensis	(**CMS synonym**) Guangxi, Yunnan, Sichuan, Guangdong, and Jilin Provinces; Chekiang Province (Yen 1948)
dianchiensis	Only known to live in Lake Dianchi, Yunnan
fluminalis	Yangtze River
hassi	Hunan, Jiangxi, Sichuan, Zhejiang and Yunnan Provinces
hainanensis (synonym *C. compacta)*	Only known from Hainan Island
latissima	Only known to be from Mengzi County, Yunnan
lecythis	Yunnan, China (**CMS synonym**)
lecythoides	Zhejiang Province (**CMS synonym**)
menglaensis	Manzhazai Village Pu'er City, Yunnan
patris	Yunnan, Guangdong and Zhejiang Provinces
ussuriensis	Lower Amur River
ventricosa	Yunnan, Sichuan and Guizhou Provinces
wingatei	Yunnan, Sichuan and Guizhou Provinces (**CMS synonym**)
yunnanensis	Maliping village, Pu'er City, Yunnan

Table 4-7. List of native and current ranges of *Cipangopaludina chinensis* in China by Köhler, Do, and Jinghua (2012a) and locations cited in the text. All citations are listed alphabetically, and locations plotted in Figure 4.7.

Kohler, Do, and Jinghua (2012) China Provinces, Regions		**Locations cited in the text**	
Native Range	**Current Range**		
Anhui	Anhui	Anhwei (Anhui)	Peking
Fujian,	Fujian	Chekiang	Shanghai
Guangdong	Guangdong	Chen-tuh	Shanghai. Guizhou
Guangxi	Guangxi	Chow-shan Island	Shang-kuan
Hebei	Hebei	Chusan	Shangtung
Heilongjiang	Heilongjiang	Cuming	Shihtao
Henan	Henan	Fengshiu	Swampy lake
Hubei	Hubei	Guangdong	Szechwan (Sichuan)
Hunan	Hunan	Guangxi	Taiwan
Jiangsu	Jiangsu	Guizhou	Tonglu
Jiangxi	Jiangxi	Hainan Island	Tourane River
Jilin	Jilin	Han-lo-si	Yangtze Kiang
Liaoning	Liaoning	Hoching drainage	Yangtze River
Neimenggu	= Nei Mongol	Hopei	Yankze Valley
Ningxia	Ningxia	Huang-Kiang	Yunnan
Shandong	Shandong	Jilin	Yunnan Lake
Shanxi	Shanxi	Kirin	Yuyao
Sichuan	Sichuan	Kwangteh	Zhejiang
Taiwan	Taiwan	Kwangtung	
Xinjiang	Xinjiang	Lake Tai	
Yunnan	Yunnan	Lanchi	
Zhejiang	Zhejiang	Peihai	

c. North Korea

No viviparids appear to live in North Korea.

d. South Korea

Kimura, Saio, Chiba, and Pak (2019) recorded ***Cipangopaludina malleata*** (Reeve, 1863) (**CMS synonym**) among six freshwater gastropod species in five families in their updated checklist of nonmarine gastropods from Ulleung Island, South Korea.

e. Japan

Annandale (1925) and Iwakawa (1897) listed eight species of *Paludina* for Japan and gave locations for most of them; species are listed alphabetically, and CMS and JMS species and synonyms are in bold print:

- ***P. abbreviata*** Reeve from Japan, no location (**CMS synonym**)
- *P. ingallsiana* Reeve from Biwa Lake
- *Paludina nitens* Reeve from Japan, no location
- ***P. japonica***, v. Martens from Tokyo, Yokohama, Hakone Lake (**JMS synonym**)
- *P. laeta* from Japan, no location
- ***P. oxytropís***, specific locality not given (**JMS synonym**)
- *P. salami* (v. Frauenfeld) from Biwa Lake
- ***P. stelmaphora*** (Bourgnignat) from Tokyo, Yokohama, Biwa Lake, Yawatahama (**CMS synonym**)

Contrary to Ikawawa (1897), Pilsbry (1902) believes *Paludina oxytropis* Benson and *Paludina ingallsiana* Lea do not occur in Japan and lists six *Paludina* species potentially valid in Japan.

- *Paludina histrica* Gould, 1859; ***Paludina japonica*** v. Mart., 1860 (**JMS synonym**).
- *Paludina tata* v. Mart., 1860
- ***Paludina malleata*** Reeve, 1863 (**CMS synonym**)
- ***Paludina abbreviata*** Reeve, 1863 (**CMS synonym**)
- *Paludina nitens* Reeve, 1863
- *Vivipara sclateri* Frauenfeld, 1865

Of these six species, Pilsbry (1902) lists the following as true species of *Viviparus* (listed alphabetically). The others are synonyms or varieties. CMS and JMS species and synonyms are in bold print:

- *Paludina nitens* Reeve. ***Viviparus japonicus*** (v. Martens, 1860) (**JMS synonym**) from Omaki, Yama; synonyms are ***Paludina japonica*** v. Mart; ***Paludina oxytropis* var. *japonica*** Iwakawa; ***Paludina oxytropis* var. *slateri*** Iwakawa (all **JMS synonyms**)
- *Viviparus histricus* (Gould, 1859) from Kagoshima, Sasuma; Synonym *Paludtna histrica* Gould?
- ***Viviparus japonicus* var. *iwakawa*** nov. from Furukawa (Furukawacho), Rikuzen Syn. ***Paludina oxytropis*** Bens., Kobelt (**JMS synonym**s); ***Paludina oxytropis*** Bens., Iwakawa (all **JMS synonyms**)
- ***Viviparus malleatus*** (Reeve, 1863), GMS from the Province Mutsu, at the north end of Nippon, to the middle Riukiu Islands; synonyms are ***Paludina malleata*** Reeve; ***Paludina abbreviata*** Reeve; ***Patudina stelmaphora*** Kobelt; ***Paltudina stelmaphora*** **Iwakawa** (all **CMS synonyms**)
- *Viviparus sclateri* Frauenfeld, 1865 from Lake Biwa, Lake Suwa in Prov. Shinano, and Nagoya in Prov. Owari, its range of distribution is likely in middle Japan and in the southwestern provinces, where it probably also occurs; synonyms are *V. sclateri* Ffld; *Paludina ingallsianus* Reeve; *P. ingallsiana* Reeve, Kobelt; *P. ingallsiana* Reeve, Iwakawa

Pace (1973) and Köhler, Do, and Jinghua (2012a) list CMS as a native species to Japan, Taiwan, and Korea but do not give locations.

Hirano, Saito, and Chiba (2015) reported that Japanese viviparid fauna comprises four species in three genera; *Cipangopaludina japonica* (von Martens, 1860), ***C. chinensis laeta*** (von Martens, 1860) (**CMS synonym**), and *Sinotaia quadrata histrica* (Gould, 1859)] are widely distributed on the Japanese Archipelago, Korean Peninsula, and Taiwan; *Heterogen longispira* (Smith, 1886) is known as an endemic species of Lake Biwa in Japan.

f. Taiwan

Pace (1973) and Köhler, Do, and Jinghua (2012a) list CMS as native to Taiwan. Chiu, Chen, Lee, Sin-Ch, *et al.* (2002), in their morphometric analysis of shell and operculum in CMS, examined four populations: (1) Taro farm wetlands in Chutzuhu (121°31'E, 25°11'N), (2) Laumay (121°32'E, 25°16'N), located in northern Taiwan in a volcanic area, (3) Lantan (120°28'E, 23°23'N), and (4) Wanda (121°07'E, 23°58'N), originally a natural lake but now a reservoir created by dams that were constructed for hydropower generation several decades ago.

In summary, both CMS and JMS currently occur in Japan, South Korea, and Taiwan, with several other viviparids. Figure 4.8 shows the current distribution of the Japanese Mystery Snail in Asia, including Japan, South Korea, and Taiwan.

5. Southern Asia

a. Afghanistan

Viviparidae consist of roughly 125 to 150 extant species worldwide and reach their highest taxonomic diversity (about 40 to 60 species) in Southeast Asia (Strong, Gargominy, Ponder, and Bouchet 2008). Solem (1979) collected 88 specimens of *Bellamya hilmendensis* (Kobelt, 1908) from 10 miles south of Qala-i-Kang, at 518 m. elevation, in Chakhansoor Prov. "Only a single juvenile of less than 5 mm. was collected alive, although several other individuals had the operculum in place. Most examples were juvenile; less than a dozen were considered as adults. The largest was 31.8 mm. high, 24.0 mm. in diameter, with seven whorls.

In summary, viviparids occur in Afghanistan, but CMS and JMS are currently absent.

b. Pakistan

Burdi, Baloch, Begum, Soomro, *et al.* (2008), sampled five stations (Pinyari Canal, Phuleli Canal, K.B. Feeder, Chakumber (Ring Dam) and River Indus) and collected seven genera, including 10 species of gastropods. *Filopauldina bengalensis* was the most dominant gastropod and was abundant throughout all stations; *Bellamya naticoides* was the next most common and abundant at all stations at Kotri Barrage, near Jamshoro, Sindh, Pakistan. Saddozai (2013) reported both *F. bengalensis* and *B. naticoides* from Manchar Lake Sindh, Pakistan. The former had the highest average annual density contribution (16.83%) of 10 gastropod species, with *B. naticoides* next (15.85%). *Filopaludina bengalensis* is common in northeast India, at Indus River and its canals at Kotri Barrage, near Jamshoro, Sindh, and is a common food item.

In summary, viviparids (Bellamyinae) occur in Pakistan, but CMS and JMS are currently absent.

c. India

Annandale (1920 and 1921a, b) described several viviparids from India (e.g., Calcutta, Manipur), which laid the foundation for updates in the 1980s and 2000s. Rao (1989) describes several viviparids under two genera, *Bellamya* and *Cipangopaludina*, in India's handbook of freshwater molluscs: *Bellamya bengalensis* from Chinsurah and Pandua areas of West Bengal, and several forms throughout (e.g., Mandi, Kangra, Punjab, Bombay, Andhra Pradesh); *B. crassispiralis* in Manipur Valley; *B. crassa* in Uttar Pradesh, River Gomati, Jaunpur, West Bengal, Ranaghat, Siliguri, Orissa, Assam, Cachar, Bangladesh, and Hazrapur, Sylhet; *B. dissimilis* in Peninsular and northern India and West Bengal; *B. micron* in Manipur. Rao (1989) states *B. bengalensis* in Chinsurah (and Pandua) areas of West Bengal was considered a pest of *Azola pinnata*, a plant used as a biofertilizer in paddy fields; Rao (1989) lists only one species of *Cipangopaludina*, ***C. lecythis*** (**CMS synonym**) in Manipur Valley. Tripathy and Mukhopadhayay (2015) also give the distributions of all species described by Rao (1989). Germain (1924a, b) reported *Vivipara* (*Bellamya*) *bengalensis* from the Punjab Province in Lahore, India.

Budha, Aravind, and Danie (2010) reviewed the status and distribution of freshwater molluscs in the Eastern Himalaya and listed three genera and eight species of Viviparidae but did not provide the names. Based on other studies reported here, the three genera are likely *Bellamya*, *Filopaludina*, and *Idiopoma*.

Similarly, Aravind, Madhyastha, and Dey (2011) examined the status and distribution of freshwater molluscs of the Western Ghats and reported one genus and three species of Viviparidae but did not name the taxa. Although they did not cite Rao (1989), he had found three species of *Bellamya* (see above), and it may be the same species that Aravind, Madhyastha, and Dey (2011) were referring to.

Pandya and Vachhrajani (2012) examined the species assemblages along a salinity gradient in the Mahi River, India, at Fajalpur (0.05-0.1 ‰), Dabka (0.09-3‰) and Kamboi (9.6-39.3‰) sites. They found *Bellamya bengalensis* and *B. crassa* restricted to the freshwater (Fajalpur) site, which had the highest diversity of molluscs (14 species); the midstream site had the lowest diversity (5 species). They found that higher fluctuations in salinity, total solids, and limited availability of suitable bed form were the controlling factors for lower diversity in the midstream region.

Pakhira and Chakraborty (2016) collected both *B. dissimilis* and *B. bengalensis* in the Subarnarekha River, India. Pati, Sharma, and Sureshan

(2014) recorded both *B. bengalensis* and *B. dissimilis* from Kottayam and Palakkad, and the former also from Thrissur districts in Kerala, India.

Afshan, Mirza, Beg, Ifkhar, *et al*. (2013) studied different water bodies located in Rawalpindi, Islamabad, Fateh Jang, Chakwal, and Attock areas of Pothwar region in India. The site is in a climatic region regarded as subtropical and subhumid. They found *F. bengalensis* predominant in all the studied areas. The adult females were bearing live young inside their marsupium cavities, indicating the recruitment patterns in the natural habitat. Wagh, Patil, and Shejwal (2016) found two Bellamyinae, *B. bengalensis* and *B. dissimilis,* typical in both lentic and lotic (except canals) habitats in the Aurangabad district of India.

Sajan, Tripathy, Biswas, and Varadaraju (2018) made an inventory of land and freshwater molluscs from Andhra Pradesh and Telangana states of India. They recorded two Bellamyinae, *Idiopoma dissimilis* (Müller, 1774) common throughout India, and *Filopaludina. bengalensis* f. *annandalei* (Kobelt, 1909) from Andhra Pradesh, Tamil Nadu, and West Bengal, India. Mukhopadhyay, Tripathy, Biswas, Ghosh, *et al*. (2020) also list two Bellamyinae, *Idiopoma dissimilis* and *F. bengalensis* (Lamarck, 1822), both reported from Haryana and state they are common throughout India.

In summary, many species of viviparids (subfamily Bellamyinae) occur in India, including CMS, as *C. lecythis* in Manipur Valley.

d. Bangladesh

Three viviparids occur in the Buriganga and Turag Rivers, Dhaka (Baki, Hossain, and Bhouiyan 2016), *Filopaludina bengalensis* in rivers and *Bellamya crassa* and *Bellamya dissimilis* in the Turag River only. No CMS or JMS appeared to be living in Bangladesh.

6. Southeastern Asia

Fischer (1891, 1904) catalogued several *Paludina* species from Indochina, in which he included Siam, Laos, Cambodia, and Upper (Tonkin) and Lower (Annam) Vietnam.

a. Burma

Fischer (1891) lists *P. bengalensis (= Filopaludina bugensis)*, from Burma. Preston (1915) describes the mollusc fauna of British India, including Burma. The list includes several viviparids; only those (all *Vivipara*) from Burma are listed below, alphabetically:

- *V.* (*Idiopoma*) *henzadensis*, from Henzada, Burma
- *V.* (*I.*) *h.* Var. *viridis,* from Kabynet, Upper Burma
- ***V. lecithis* var. *ampulliformis* (CMS synonym)**, from Upper Burma
- ***V. lecythis* (CMS synonym)**, from Upper Burma
- *V. siamensis*, Var. Yaylaymaw, from Upper Burma
- *V. theobald*i, from Burma (no location given)

Rao (1989) describes *B. bengalensis* (= *Filopauldina bugensis*) throughout Burma, as well as ***Cipangopaludina lecythis* (CMS synonym)** through Upper Burma to the Southern Shan States. In addition, Rao (1989) reported *Vivipara doliaris* from British Burma but listed no location.

In summary, several species of viviparids occur in Burma, including CMS, but not JMS.

b. Vietnam

Fischer (1891) and Dautzenberg and Fischer (1905a, b) reported 37 species of *Paludina* from Indochina, of which 17 were from Vietnam. Fischer (1904) listed 40 species of *Paludina* from Indochina, of which 21 were from Vietnam, the additional species being shown with an asterisk in the following alphabetical list for Vietnam:

- *P. aeruginosa*, from rivers of Tonkin watershed (= *Bellamya aeruginosa*)
- *P. ampuliformis*, from Touranne, Annam, Luang-Prabang, Long-Trua, Haiphong, Kébao Island, Phuc-Son, Van Bu Muong Bou, and Chu River watershed
- *P. bengalensis* (= *Filopauldina bugensis*), from Srakéo around Saigon in South Vietnam and Chu River in upper Vietnam
- *P. ciliata*, from Thu-Dan-Mot in south Vietnam
- *P. cochinchinensis,* from unknown locations in Stiengs and South Vietnam
- *P. duchieri*, from Song-Ki-Kong River at Déo-Cat, That-Khé, Bae-Kan, and Haut-Tonkin
- *P. frauenfeldi* (= *P. ingallsiana*), from Chu River watershed
- *P. fulva*, from Luang-Prebang and Chu, North Vietnam, and Nam-Hou
- *P. gassiesi*, from Annam, no location given
- *P. hainesiana* (= *Paludina lamarcki*), from an unknown location in Vietnam
- *P. ingallsiana*, from an unknown location in Saigon

- **P. laosiensis,* from Muong-Bou, pond at Cao-Bang, High-Tonkin
- **P. lapilliorum,* Song-Bang-Giang River, High Tonkin
- *P. lurida*, from an unknown location near Saigon
- *P. poIygramma* (= *Vivipara lineolate*) (= *Paludina filosa*), (= *Paludina sumatrensis*) in an unknown locality in Vietnam
- *P. polyzonata* Frauenfeld, Tonkin River watershed
- **P. polyzonota*, from rice paddies in all of Tonkin (Upper Vietnam) and around Hanoi
- *P. quadrata* Benson; var. *aeruginosa* Reeve; Var. *bizonalis*; Var. *heudei*
- *P. rattei*, from unknown locations near Saigon and Chu, north Vietnam
- **P. sabinae*, from Srakéo River
- *P. javanica*, from Srakéo River and South Vietnam
- *P. sphaericula* (= *Paladina hainesiana*, from an unknown location in Vietnam
- **P. vignesi*, from Menam-Ping and Saigon. Tonkin (= *Paludina ampulliformis* Souleyet)

Finally, Rao (1989) describes ***Cipangopaludina lecythis*** (**CMS synonym**) throughout Vietnam.

In conclusion, some valid species of *Viviparus* (e.g., *V. contectus*, *V. viviparus*, *V. quadratus*) currently occur in Vietnam; some belong to Bellamyinae (e.g., *aeruginosa*, *bengalensis*); one, *C. lecythis*, is a synonym of CMS. JMS does not currently occur in Vietnam.

c. Laos

Fischer (1904) catalogues ten species of viviparids from Laos, listed alphabetically below:

- *P. chalannguensis*, from Sé-Sane Valley, Bou-Kiou, and Nam-Hou
- *P. frauenfeldi*, from Namkading, Nam-Si at Ubone, and Luang Prabang rivers
- *P. fulva*, from Luang Prebang River
- *P. laoaiensis*, from Mnong-Kie, Muang Ngoy, and Me-Kong rivers in Laos
- *P. moreleti*, from Xieng-Mai, Nam-Si, at Ubone, and Nam Hinboun rivers
- *P. polyzonata*, from Nam-Si River

- *P. siamensis*, from Xieng-Mai Plateau and Ménam-Ping River
- *P. tiranti*, from Sé-Sane Valley and Nam Khan and Nong Khai rivers
- *P. trochoides*, from Xieng Mai River
- *P. umbilicata*, from Ménam-Ping River at Xieng-Mai

In conclusion, none of the species reported for Laos appears to be valid viviparids based on current synonym lists; some may be unique (endemic?) to Laos. In addition, CMS and JMS are likely absent in Laos.

d. Thailand (formerly Siam)

Fischer (1891) reported 12 species of *Paludina* from Thailand, listed alphabetically below:

- *P. ciliata*, from Bangkok, Pexaburi, Ajuthia, Strang River, and Thu-Dan-Mot
- *P. frauenfeldi,* from Bangkok
- *P. fulva* (= *P. praemorsa*, *P. carinata*), from Siam, no location given
- *P. javanica,* from Srakéo River
- *P. martensi* (= *P. singulata*), from Siam, no location given
- *P. polygramma,* from Siam, no location given
- *P. polyzonata*, from an unknown locality in Thailand
- *P. sabinae,* from Srakéo River
- *P. siamensis,* from an unknown location in Thailand
- *P. sphaericula,* from Siam, no location given
- *P. swainsoniana*, from an unknown location in Thailand
- *P. umbilicate,* from Takrong River

Fischer (1904) listed eight more *Paludina* from Thailand, listed alphabetically below:

- *P. bengalensis* (= *Filopauldina bugensis*), from Srakéo River
- *P. chalannguensis*, from Ayoutia and Patrang rivers, and from Péam-Chelang
- *P. hainesiana*, from an unknown location in Thailand
- *P. ingallsiana*, from Saigon
- *P. javanica*, from Srakéo River
- *P. swainsoniana*, from an unknown location in Thailand
- *P. trochoides*, from Bangkok, Pexaburi, Ayoutia, and Stung-Patrang rivers
- *P. umbilicata*, from the Takrong River

In summary, at least one species of viviparid, *P. bengalensis* (= *Bellamya bengalensis*), is present in Thailand; some species may be unique (endemic?) to Thailand; neither CMS nor JMS currently occur in Thailand.

e. Cambodia

Fischer (1891) reported 24 species of *Paludina* from Cambodia, one being a synonym of CMS; species are listed alphabetically below:

- *P. aeruginosa,* from Kampot
- *P. bengalensis, (= Filopaludina bengalensis)* from Moth-Kasa
- *P. cambodgensis*, from Moth-Kasa, Cambodia
- *P. chalanguensis*, from arroyos of Péam-Chilang, Kompong-Son and on the banks of Tonli-Sap lake
- *P. ciliata,* from Dey-Trochon
- *P. danieli*, from Prec-Thénot
- *P. eyriesi* (= *Paludina fischeriana*), from south of Tonkin Sap Lake; Cheran-Ghomras, near Phnom-Penh, and Oudong
- *P. hainesiana* (= *Paludina lamarcki*), from Mékong to the island of Ca-Lgniou
- *P. jullieni,* from Mékong and Ca-Lgnion Island
- *P. kmeriana* (= *Paludomus conicus*), from Prec-Thénot at Kompong-Toul
- ***P. Iecythoides*** (**CMS synonym**), from Moth-Kasa, Cambodia
- *P. moreleti*, from Halj, in shores and benches of the Mekong Hall above Pnom-Penh, and at Kampot and Kompong-Toul
- *P. obscurata*, from arroyos in Péam-Chilan
- *P. paviei*, from Kampot; *P. thomsonii*, from swamps near the Gulf of Siam in Cambodia
- *P. quadrata*, from Tonli-Sap lake, Kompong-Rath, and the edges of Prec-Péhan
- *P. ratteri* (= *PaIudina frauenfcldi*), from Mekong stalls and arroyos (small, deep channel of an ephemeral stream), Pnom-Penh, and Pum-Po-Bong
- *P. sabinae*, from Srakéo River
- *P. speciosa*, from Prec-Thénot; Kampot; arroyos of Péam-Chilang, and from beaches of Mékong
- *P. sphaericula* (= *Paladina hainesiana*), from Mekong sandbanks up the river from Pnom-Penh
- *P. thompsoni,* from swamps near the coast of the Gulf of Siam
- *P. tiranti*, from Kampot and Sré-Umbell

- *P. trochoides,* from Pnom-Penh
- *P. turbinata,* from Mekong and Ca-Lgnion Island
- *P. vignesi*, from small arroyos in Mekong and near Ca-C'ompung Island

Fischer (1904) listed seven more species or new locations for *Paludina* in Cambodia; the species are listed alphabetically below:

- *P. cochinchinensis*, from the mouth of the Pursat River
- *P. eyriesi*, new locations from Battamburg area, Krang-Chomnés below Pnom-Penh
- *P. fulva*, from Me-Khong valley
- *P. ingalleseana*, from Moth-Kasa
- *P. lagrandierei*, from Mé-Khong and Nam-Hou
- *P. pavieri*, from Kampot
- *P. simonis*, from Me-Khong

DesHayes (1874) lists the following *Paludina* species from Cambodia; none are synonyms of CMS or JMS. The species are listed alphabetically:

- *P. chalanguensis*, from the arroyo of Peam-Ghalang
- *P. frauenfeldi*, from the Mekong River sandbanks and the arroyos
- *P. julliene*, from a small cove of Ca-Lgniou Island
- *P. lamarkii*, from Ca-Lgniou Island
- *P. moreleti,* from the Mekong River sandbanks and upstream of Pnum-Perh
- *P. obscura*, from the Poy-Chelang arroyo
- *P. speciosa*, from the arroyo of Peam-Chelang
- *P. sphaericula*, from the Mekong River sandbanks and upstream of Pnum-Perh
- *P. turbinata,* from a small cove of Ca-Lgniou Island
- *P. vignesi*, from puddles and the shore of Ca-C'ompung Island

In summary, at least two species of viviparid, *P. aeruginosa* and *P. bengalensis* (= *Filopaaludina bengalensis*) are currently present in Cambodia; some species may be unique (endemic?) to Cambodia; CMS presently occurs in Cambodia, but JMS does not.

f. Philippines, Guam

Fischer (1891) reported two species, *Paludina polyzonota*, and *Paludina carinata* from the Philippines with no locations given. Bartsch (1907) lists seven species of *Vivipara* along with 12 new subspecies:

- *V. angularis* Muller
- *V. a. burroughiana* Lea

- *V. a. philippinensis* Nevill
- *V. zamboangensis*
- *V. z. tubayensis*, n. sp.
- *V. z. davaoensis*, n. sp.
- *V. z. surigensis*, n. sp.
- *V. mindanensis*, n. sp.
- *V. m. bagangensis*, n. sp.
- *V. buluanensis*, n. sp.
- *V. carinata* Reeve
- *V. cumingi* (Hanley) Reeve
- *V. mearnsi*, n. sp.
- *V. m. misamisensis*, n. sp.
- *V. pagodula*, n. sp.
- *V. gilliana*, n. sp.
- *V. lanaonis*, n. sp.
- *V. polyzonata* Fruenfeld
- *V. mainitensis*, n. sp.

Bartsch (1910) added four more new species of *Vivipara*:

- *V. cebuensi*
- *V. mindanensis mamanua*
- *V. partelloi*
- *V. clemensi*

Oddly, Bartsch (1910) rescinded his find of *V. polyzonata* in Barsch (1907), stating it likely never occurred in the Philippines. CMS and JMS do not appear to occur in the Philippines so far.

Viviparids are absent in Guam.

g. Malaysia

Fischer (1891) lists *P. poIygramma* (= *Vivipara lineolata*), (= *Paludina filosa*), (= *Paludina sumatrensis*) in the peninsula of Malacca, no location given. *Paludina polygramma* (and its synonyms) appear to be a valid viviparid species, although they may be unique (endemic?) to Malaysia. Ng, Dulipat, Foon, Lopes-Lima, *et al*. (2017) collected *Sinotaia guangdungensis* (Kobelt, 1906) from a pond in Nabawan, Malaysia, which apparently has been introduced to peninsular Malaysia.

CMS and JMS are not currently present in Malaysia.

h. Indonesia, Sumatra

Yen (1942) reported *Viviparus costatus*, from Tondano Lake, North Celebes, no location given. The species is not on any list of valid synonyms of *Viviparus* species. Ng, Dulipat, Foon, Lopes-Lima, *et al*. (2017) collected *Sinotaia guangdungensis* (Kobelt, 1906) from a paddy field stream in Kota Marudu, Indonesia. CMS and JMS do not occur in Indonesia.

Fischer (1891) lists *P. poIygramma* (see Malaysia for synonyms) in Sumatra, with no location given. Thus, valid viviparid species appear to be absent in Sumatra.

i. Java

Fischer (1891) lists *P. javanica* from Java, no location given. The species does not appear to be a valid viviparid, although it may be unique (endemic?) to Java.

CMS and JMS are unlikely to occur in Java.

7. Summary of Distribution of Viviparidae in Asia

Viviparus viviparus extends east of the Ural Mountains in Russia, and introduced to the Novosibirsk Reservoir. The southward distribution of both *V. viviparus* and *V. contectus* into Asia occur in Central Asia (Turkey) and Eastern Asia (e.g., China). Eastern Asia is prominent in *Cipangopaludina* and *Viviparus* species, especially CMS. JMS has a much smaller distribution in Asia, native to and extant in Japan, Thailand, and South Korea. Bellamyinae species dominate Southern Asia, with *Filopaludina bengalensis* occurring in Iran, Pakistan, India, and Southeastern Asia (e.g., Burma, Vietnam, Thailand, and Cambodia) (Figure 4-7). The southeastern islands of the Philippines, Malaysia, Indonesia, Sumatra, and Java are represented mainly by *Viviparus* species, but *Sinotaia guangdungensis* was recently introduced to peninsular Malaysia.

Viviparids appear to be absent in Kazakhstan, Uzbekistan, Turkmenistan, Mongolia, and North Korea.

The distribution of the Chinese Mystery Snail in Asia is shown in Figure 4-8. The occurrences of the Japanese Mystery Snail and the common *Filopaludina bengalensis* in Asia are shown in Figure 4-8.

Figure 4-7. Occurrences of the Japanese Mystery Snail (stars) and *Filopaludina bengalensis* (shaded) in Asia.

Figure 4-8. Native (circles) and extant (stars) occurrences of the Chinese Mystery Snail in Asia.

D. Africa

There are 54 countries in Africa. The continent is represented by a largely desert region in the north and a forested southern part, especially in the tropical Congo basin, which makes up about 30% of the global rainforest, second only to Amazonia (Malhi, Adu-Bredu, Asare, Lewis, *et al.* 2013). Darwall, Smith, Allen, Holland, *et al.* (2011) geographically divided the African freshwater mollusc fauna into the regions north of the Sahara, which consists of Palaearctic fauna, and the areas south of the Sahara where Afrotropical fauna dominates. Northeastern Africa has elements shared with the Palaearctic fauna, Arabian fauna, and African fauna. The southern line for the Palaearctic fauna is through the Ahagger Mountains, northeast toward Libya and west to Mauritania. The African Great Lakes in eastern Africa represent some of the deepest and largest freshwater bodies on earth; the three largest lakes (Tanganyika, Malawi, and

Victoria) contain more than a quarter of the earth's and more than 90% of Africa's surface freshwater (Salzburger, Van Bocxlaer, and Cohen 2014).

There are only two large bodies of water in the desert area: Lake Nasser on the Nile River, which runs through Egypt and Sudan, and Lake Chad, which lies mainly in the southwest corner of Chad and the northeast corner of Nigeria. The Niger River also flows mostly through desert countries, beginning in Nigeria and flowing westward through the southern part of Niger, then Benin, Mali, Burkina Faso, Côte d`Ivoire, Guinea, and empties into the Atlantic Ocean at the Gulf of Guinea. The only other significant river in the desert area is the Senegal River, which flows along the northern border of Senegal and empties into the Atlantic Ocean. The only viviparid in the desert region of Africa is *Bellamya unicolor*, a common species in Lake Chad where two cohorts occur for several months every year (Lévêque 1971).

No valid species of Viviparidae occur in Africa from the southwest coast (de Folin 1846), eastern islands (e.g., Pemba, Mnemba, Unguja, Mafia Islands) (Vesco 1846), or interior areas of Angola and Benguela (e.g., Morelet 1868). Bourguignat (1864) lists *Paludina* only as synonyms of several species of *Bithynia*, *Hydrobia*, and *Amnicola* under the family Paludinidae, (e.g., *Paludina impure* and *P. tentaculata* for *Bithynia tentaculata*; *Paludina acuta* for *Hydrobia brondeli*, and *Paludina similis* for *Amnicola similis*). Again, Bourguignat (1879) listed several species of *Paludina* as synonyms of *Cleopatra*, the type genus in the family Paludomidae within the subfamily Cleopatrinae, but no valid *Paludina* species were listed for Abyssinia (Ethiopia), Zanzibar, or Senegal. Morelet (1868) recorded *Paludina bulimoides* from a large geographical area in Africa, from Lower Egypt to the Sennår dam on the Blue Nile River to Lake Victoria (also known as Lake Nyanza) the Nile Valley. However, *P. bulimoides* is a synonym of *Cleopatra bulimoides* recorded and has been recorded from Cameroon, Central African Republic, Lower Tana River and Lake Baringo in Kenya, and Lake Albert in Uganda, and in northern Africa from the Sudanese Nile Basin and Nile Delta throughout Lake Nasser (Ghamizi, Jørgensen, Kristensen, Lange, *et al.* 2012).

Prashad (1928) distinguished three forms of the African Viviparidae: Group 1, *Vivipari unicolores*, Group 2, *Neothauma,* and Group 3, *Cleopatra*. He agrees with Germain (1920) that *Viviparus unicolor* "is the central species of all the African species of the sub-genus *Viviparus*. It probably represents the ancestral species from which all the recent African species have been derived" (180). Germain (1920) states that *V. unicolor* is very characteristic of tropical Africa, occupying the entire equatorial domain of Africa. Two varieties of the species are significant: *V. u. bellamyi* represents *V. unicolor* in the western regions of Africa, and *V. u. capillata*, has almost completely replaced *V. unicolor* in the Zambesian basin of southern Africa.

Historically, six species of *Viviparus* have been reported from southern Africa. Smith (1892a) recorded *V. abyssinicus*, *V. rubicundus*, *V. capillatus*, *V. victoriae*, *V. juncundus*, and *V. capoides* from Lake Victoria (also known as Nyanza or Oukéréwé). Smith (1892b) subsequently added three more species: *Viviparus phthinotropis* Martens from the southwest part of Lake Njamagolso (though he cautioned that it may be the same species as *V. victoriae*), *Viviparus trochlearis* Martens from Sirwa Island, and *Viviparus costulalus*, Martens from Kassarasi Island.

Bourguignat (1864) did not report any viviparids from Lake Victoria but later recorded *Viviparus henzdensis* Pilsbry from South Africa and Burma without specifying localities (Bourguignat 1885). Germain (1907) recorded *Vivipara unicolor* Olivier (= *Bellamya unicolor*), from Central Africa, but he created several varieties, including *V. u.* var. *elator* Martens, *V. u.* var. *obesa* Germain, *V. u.* var. *jeffreysi* Frauenfaeld, *V. u.* var. *lenfanati* Germain, and *V. u.* var. *bellamyi* Jousseaume. Dautzenberg and Germain (1914) recorded three species of viviparids from the Congo: *Vivipara unicolor* (= *Bellamya unicolor*), *Vivipara crawshayi*, and *Vivipara mweruensis*, but *Bellamya unicolor* appears to be the only valid viviparid there.

Germain (1920) surveyed Lake Victoria, Lake Albert, Lake Edward, and Lake Kivu in the Congo. In Lake Victoria and Lake Edward, he found *Viviparus unicolor* Olivier (= *B. unicolor*); *Vivipara abyssinica* Martens; *Vivipara capillata* Frauenfeld; *Vivipara capoides* Smith; *Vivipara rubicunda* Martens and varieties *subturrita* Martens and *kisumiensis* Preston; *Vivipara mela* Martens; *Vivipara constricta* Martens and varieties *phthinotropis* Martens and *trochlearis* Martens and *pagodella* Martens; *Vivipara costulata* Martens and variety *trilirata* Martens. In Lake Albert, he found only *V. rubicunda*. He found no viviparids in Lake Kivu.

However, recent studies have shown that all the African species belong to *Bellamya* or *Neothauma*. Sengupta, Kristensen, Madsen, and Jørgensen (2009) state that *Bellamya* in Africa constitutes 18 species with several subspecies or eco-phenotypic morphs. Representatives of *Bellamya* Jousseaume 1886 mainly live in Africa and the Indostan Peninsula (except the Lower Ganges), while in Southeast Asia (discussed earlier), the generic diversity of Viviparoidea was much higher. This distribution suggests East Asia as the region where the genetic diversity of the superfamily was initially formed (Starobogatov 1985). Sengupta, Kristensen, Madsen, and Jørgensen (2009) suggest *Bellamya* was introduced to Africa during a Miocene dispersal event from Asia.

Stelbrink, Richter, Köhler, Riedel, *et al.* (2019) found Bellamyinae to be the most diverse and widespread subfamily comprising numerous African species (and Asia and Australia). They found viviparids mainly inhabit lentic waters, such as lakes, rice paddies, wetlands, and ponds (i.e., lentic habitats). Still, they are also common in large rivers and streams (i.e., lotic habitats), such as the Nile and Zambezi in Africa, especially the genus *Bellamya*. Schultheiß, Wilke, Jørgensen, and Albrecht (2011) examined Bellamyinae in the modern Lake Malawi, among the largest and deepest lakes in the world (570 km long, maximum depth 706 m). They examined the phylogenetics of several Bellamyinae and revealed six major clusters. The clusters largely correspond to the major lake systems of and along the African Rift. The Great Rift runs along two separate branches joined to each other only at their southern end in Southern Tanzania and Zambia. The two branches are the Western Rift Valley and the Eastern Rift Valley; Figure 4-9 shows the bifurcation of the rift into two valleys, a Western Rift Valley (also known as the Albertine Rift) and an Eastern Rift Valley. Lake Victoria lies between the two rifts; Lakes Albert, Edward, Kivu, and Tanganyika are in the Albertine Rift Valley. *Bellamya* is monophyletic for lakes Malawi and Tanganyika as well as for the Victoria–Albert system. Specimens from the Zambezi River are paraphyletic, with one group closely related to the likewise paraphyletic Mweru–Bangweulu assemblage. The clusters are composed of *Bellamya costulata*, *B. trachlaris*, and *B. rubicunda* for lake Albert and Lake Victoria; *B. monarda*, cf *capillata*, one cluster in Zambezi River and one in the Mweru–Bangweulu assemblage; *B. robertsoni*, *B. capillata*, *B. jeffreysi*, and *B. ecclesia* in Lake Malawi; *B. pagodiformis*, *B. capillata*, *B. mweruensis*, and *B. crawshayi* in Lake Mweru and Lake Bangweulu; and *Neothauma tanganyicense* in Lake Tanganyika.

Van Bocxlaer, Clewing, Duputié, le Roux, *et al.* (2021), using cluster analyses, found three viviparid gene pools in the Lake Victoria ecoregion: the first in Lake Albert and the White Nile; a second in the Victoria Nile and Lake Kyoga; a third in Lake Victoria and its tributaries, which had the highest genetic diversity. However, all groups had many private alleles and predated the Last Glacial Maximum (the most recent time during the Last Glacial Period that ice sheets were at their greatest extent). Van Bocxlaer, Clewing, Duputié, le Roux, *et al.* (2021) estimated that population collapses in viviparids were an order of magnitude more severe than declines in cichlids. The reestablishment of freshwater ecosystems halted the collapses since the LGM. Recent anthropogenic ecosystem deterioration appears to cause homogenization of previously diversified microhabitats, contributing to (local) extinction and enhancing gene flow among species within the gene pools (Van Bocxlaer, Clewing, Duputié, le Roux, *et al.* 2021).

None of the reported species are synonyms of CMS or JMS. *Bellamya unicolor* appears to be the dominant viviparid species in Africa. Species include *V. crawshayi* and *mweruensis*, according to Galli's (2017) list. The validity of the remaining *Viviparus* species is unknown; perhaps some may be endemic.

1. Summary of Distribution of Viviparidae in Africa

In summary, both *Neothauma* and *Bellamya* species occur in Africa. The most common Bellamyinae is *Bellamya unicolor*, distributed across much of central Africa (Figure 4-9) CMS or JMS are currently absent in Africa. Two *Bellamya* species, *B. crawshayi* and *mweruensis*, occur in the Congo. The validity of many *Viviparus* species is unknown; perhaps some are endemic. Viviparids are absent in the southern countries of Africa (i.e., south of and including Angola, Zambia, Tanzania [excluding Lake Victoria], and Madagascar) as well as northern arid countries (e.g., Algeria, Niger, Mali, Mauritania, Sudan).

Figure 4-9. Distribution of Viviparidae, *Viviparus*, *Neothauma*, and *Bellamy* species, in Africa. Approximate locations of the rift valleys discussed in the text are shown in dashed lines.

E. Australia

Smith (1979) claims that the viviparids are found only in the Murray River, which arises in the Australian Alps and then meanders northward then westward across Australia, reaching the Indian Ocean at Lake Alexandrina. However, there are records from several localities outside of the Murray River. Martens (1865) described three Australian species of Viviparidae: *Paludina australis* Reeve (which he states are probably *P. essingtonensis*), *P. affinis*, and *P. polita*.

Tate (1882) listed six species of *Paludina* from South Australia; listed alphabetically below:

- *P. australis*, from Port Essington, Victoria River, Depot Creek, lagoons by the Gums, near Arnheim's Land, and Yam Creek at Glencoe
- *P diminiata*, from Victoria River
- *P. essingtonensis*, from Port Essington and Victoria River
- *P. kingie,* from King's Pond
- *P. tricincta*, from Victoria River (probable)
- *P. waterhousi*, from Newcastle waters

Smith (1883) listed nine species of *Vivipara* from several localities, listed alphabetically here:

- *V. alisoni,* from Dalmatia River, Queensland
- *V. ampullaroides,* from Victoria and Fitzroy rivers and North Australia
- *V. dimidiate,* from Victoria River, North Australia
- *V. essingtonensis,* from Victoria River, North Australia, and Queensland
- *V. intermedia*, from Murray River
- *V. kingi,* from King's Ponds, Arnheim's Land
- *V. sublineata,* from Darling and Balonne and Bogie rivers as well as Lake Alexandria
- *V. tricincta,* from North Australia
- *V. waterhousi,* from North Australia

Prashad (1928) suggested independent evolution of the Australian form of viviparids, and distinguished three groups: (a) *Vivipari Sublineata* group, including *V. sublineata, V. intermedia*, and *V. alisoni*; (b) *Vivipari Ampullaroides* group with *V. ampullaroides*, V. *waterhousii, V. kingi* and V. *tricinctus*; and (c) *Larina* group, an estuarine series. Cotton (1936) proposed *Notopala* to include the whole series, except the *Lariana* group.

Iredale (1943) added a second genus, *Centrapala*, to include *Paludina zirata*. Prashad (1928) separated the northern series of *Notopala* to the Sublineata group. Kear, Hamilton-Bruce, Smith, and Gowlett-Holmes (2003) documented the oldest viviparid, the fossil *Viviparus albasopularis* Etheridge, 1902 from the Lower Cretaceous in New South Wales. Iredale's (1943) list of *Notopala* emulates that of Smith's (1883) *Paludina* (above) and named *Notopala hanleyi* Frauenfeld as the orthotype of *Notopala*. He also listed the synonymy of each species. To Smith's (1883) list, Iredale (1943) added *N. barretti*, from Innamincka, Cooper's Creek, South Australia. Iredale (1943) also erected a subgenus, *Notopalena*, under which he included *N. essingtonensis*, *N. waterhousii*, *N. barrette*, *N. kingi*, *N. tricincta*, and *N. dimidiata*. One species represented *Centrapala*, *C. lirata*, from Cooper's Creek, Innamincka, Central Australia, and the genus *Larina* by one species, *L. strangei*, from Moreton Bay, Queensland.

Murphy and Shea (2013) recorded a species of *Notopala* from the Great Dividing Range in northern New South Wales (NSW), Australia; however, the record is not referable to any currently described species. Ponder, Hallan, Shea, Clark, *et al.* (2020), in their key to freshwater molluscs of Australia, include *Cipangopaludina chinensis* in their list of Australian molluscs but state, this snail is not established in Australia but is included as a potential invader.

The only valid *Viviparus* species listed is *V. tricinctus*, according to Galli's (2017) list. However, the species has since been included in the genus, *Notopala* (Cotton 1936), which also belongs to the Viviparidae. *Notopala* is native to Australia and includes seven species from the above list:

- *N. ampullaroides* in northern Western Australia, Kimberley Region (Ponder, Hallan, Shea, and Clark 2016a)
- *N. essingtonensis* in the Adelaide River flood plains south of Darwin, Northern Territory (Ponder, Hallan, Shea, and Clark 2016c)
- *N. hanleyi* in the Murray River catchment of Lachlan and Murrumbidgee rivers (NSW Department of Primary Industries 2018)
- *N. sublineata* in Murray Darling drainages in NSW, South Australia, and Victoria (NSW Department of Primary Industries 2007)
- *N. suprafasciata* in western New South Wales and *N. kingi* in NSW (Ponder, Hallan, Shea, and Clark 2016d)
- *N. tricincta* in eastern Northern Territory (Ponder, Hallan, Shea, and Clark 2016e)
- *N. waterhousii* in northern inland Northern Territory, restricted in distribution to a few waterholes in the vicinity of Newcastle Waters and Elliot on the Stuart Highway south of Darwin (Ponder, Hallan, Shea, and Clark 2016f)

Stoddart (1982) examined embryonic development, shell length vs. shell aperture relationships, and habitat of two common species of *Notopala*, *N. essingtonensis,* and *N. waterhousii* from western Australia. Embryos are arranged in a developmental sequence, with small eggs at the rear and miniature adults at the front in both species, the embryonic shells having periostracal hairs. The aperture length of *N. waterhousii* is about half of the shell length in adults and is less than in those of *N. essingtonensis*. The two species occupy very different habitats; *N. essingtonensis* is most common in permanent water bodies, most frequently on rocky substrates, whereas *N. waterhousii* is essentially an inhabitant of temporary swamps, most commonly in muddy substrates, which crack deeply on drying.

The genus occurs in all states and territories except Tasmania, throughout Queensland and New South Wales, northern Western Australia and Northern Territory, and South Australia, except Victoria.

Only one freshwater prosobranch, the New Zealand mud snail, *Potamopyrgus antipodarum,* occurs in Tasmania (Ponder 1997). Ponder (1994) attributes the rarity and endemicity of freshwater molluscs to the existence of only two types of aquatic habitats, springs associated with the Great Artesian Basin and long-term permanent streams in the coastal areas of southeast Australia and Tasmania. Only hydrobiids are characteristic of these habitats.

1. Summary of Distribution of Viviparidae in Australia

Australia has a unique viviparid fauna with the genus, *Notopala*, represented by six species. All are primarily restricted to the eastern part of Australia from the Northern Territory south to southern Australia, including New South Wales but not Victoria, except for the Murray River drainage basin in the north (Figure 4-10). Figure 4-10 is a compilation of distribution maps for *N. ampullaroides, N. essingtonensis, N. hanleyi, N. kingi, N. sublineata, N. suprafasciata, N. tricincta, N. unicolor*, and *N. waterhousii*. The figure also includes the distribution of all *Notopala* species, including undescribed species, throughout Australia given in Ponder, Hallan, Shea, and Clark (2016e).

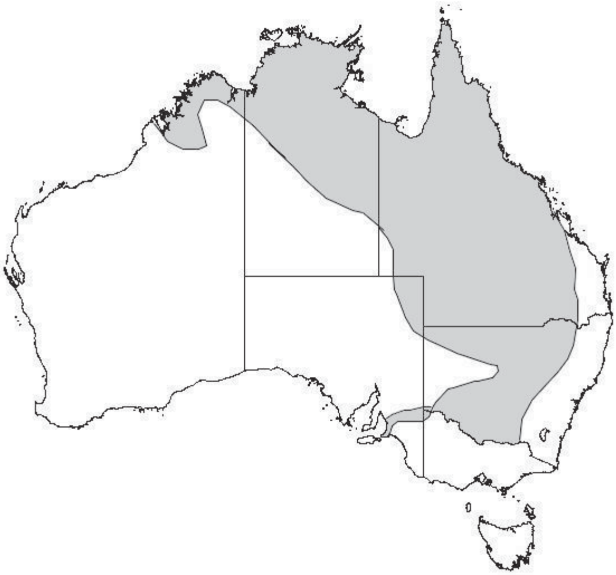

Figure 4-10. Distribution of *Notopala* species (Viviparidae) in Australia.

F. New Zealand

Hutton (1882) listed five freshwater prosobranchs, but viviparids are not on the list. Likewise, Ponder (1964) lists several freshwater prosobranchs for New Zealand, but none are viviparids.

G. South America

Orbigny (1854) examined molluscs from South America in the British Museum and recorded several *Paludina* species, but they are all synonyms of the *Paludestrina* species. Parodiz (1969); Starobogatov (1985); and Strong, Gargominy, Ponder, and Bouchet (2008) reiterated Prashad's (1928) observation that the Viviparidae occur nearly worldwide in temperate and tropical regions that, except as fossils, are absent in South America. Prashad (1928) reported two fossil viviparids in South America, *Viviparus wichmanni* Doello Jurado, 1927 from the upper Cretaceous of Rio Negro (Argentina) and *Paludina araucana* Philippi, 1887 from the Tertiary of Chile. These two records indicate that the viviparids lived in South America from the upper Cretaceous to the early Tertiary. Zarges (2006) reported six families of freshwater gastropods in Chile, five pulmonate families and one prosobranch family, Hydrobiidae However, Araya (2015, 6, 7) lists two Caenogastropoda families, Ampullariidae and Thiaridae, both introduced into Chile in 2000 and 2007, respectively, but Viviparidae was not among them.

Rumi, Gregoric, Núñez, César, *et al.* (2006) and Rumi, Gregoric, Núñez, and Darrigran (2008) corroborated Prashad (1928) and others that Viviparidae were absent after their searches for freshwater gastropods in Argentina. Of the 166 species described for Argentina, 101 belong to 10 families of Gastropoda, but Viviparidae was not among them. Three years later, Núñez (2010) examined freshwater gastropods in eight provinces of Argentina and reported on the same 10 families as Rumi, Gregoric, Núñez, César, *et al.* (2006) and Rumi, Gregoric, Núñez, and Darrigran, (2008). Most noteworthy of their lists was the proportions of non-endemic species (species occurring in Argentina and other countries) in nine families: Ampullariidae Gray, 1824 (12 spp., 10 non-endemic (83%), 2 vulnerable; Thiaridae Troschell, 1857, 4 species, 1 non-endemic (25%), 3 endemic (occurring only in Argentina) and vulnerable; Cochliopidae Tryon, 1866, 14 species, 4 non-endemic (29%), the rest endemic, most being vulnerable; Lithoglyphidae Troschel, 1857, 22 species, 6 non-endemic (27%), 16 endemic, and most are vulnerable; Glacidorbidae Ponder, 1986, 1 species, vulnerable; Chilinidae Gray, 1828, 17 species , 5 non-endemic (29%), 12 endemic, and most are vulnerable; Lymnaeidae Rafinesque, 1815, 6 species, 2 non-endemic (33%), 1 endemic and vulnerable, 3 of sanitary importance; Planorbidae Rafinesque, 1815, 15 species, 12 non-endemic (80%), 1 vulnerable, 3 of hygienic importance; and Ancylidae Rafinesque, 1815, 4 species, 3 non-endemic (75%), 1 vulnerable; Physidae Fitzinger, 1833, 5 species, 3 non-endemic (60%), 2 endemic, both vulnerable.

The absence of Viviparidae in South America was debunked by Ovando and Cuezzo (2012). They found an established population of *Sinotaia quadrata* (Benson, 1842) in a river and reservoir in Argentina, representing the first report of a recent viviparid species in South America. Live specimens of *S. quadrata* were first located in October 2009 in the Grande de Punilla River, Punilla valley, Cordoba Province in central Argentina. However, the species was likely introduced in 2010 or earlier, based on length-class analyses. The record increases the total number of invasive gastropods in Argentina to six. Ferreira, Paz, Rumi, Ocon, *et al.* (2017)

examined the species' ecological preferences and found it to be tolerant to a wide range of environmental variables, including moderately to heavily polluted streams; with its high fecundity and morphological plasticity, they predict the species could quickly colonize neighboring streams.

As for other countries in South America, Leão, Almeida, Dechoum, and Ziller (2011) did not list any viviparids in their list of invasive molluscs of Brazil. Birckolz, Salvador, Cavallari, and Simon (2016) updated the checklist of freshwater gastropods in Brazil but did not list any Viviparidae. Latini, Resende, Pombo, and Coradin (2016) found five native families of pulmonate gastropods and six families of prosobranch gastropods (Ampullariidae, Pleuroceridae, Thiaridae, Cochiliopidae, Lithoglyphidae, and Pomatiopsidae), but not Viviparidae. Pilsbry (1897, 1898), Pilsbry and Rush (1896), Arechavaleta (1900), and Gregoric and de Lucıa (2016) did not list any viviparids for Uruguay. The only prosobranch family found by Marcal and Callil (2008) in the Paraguay River was Hydrobiidae. Peru also lacks viviparids (Angrand 1846; Haas 1947). Lasso, Martínez-Escarbassiere, Capelo, Morales-Betancourt, *et al.* (2009) listed 14 families of freshwater gastropods in Venezuela, none of which were Viviparidae. Surinam has several species of Ampullariidae, but no viviparids (Vernhout 1914a). Only Ampullariidae (*Pomacea*) are reported as Colombian prosobranchs (Pilsbry 1935, 88). I could find no information on freshwater gastropods in other South American countries, specifically Bolivia, Ecuador, and Guyana.

1. Summary of Distribution of Viviparidae in South America

Only one established population of the viviparid *Sinotaia quadrata* occurs in Argentina (Figure 4-11). CMS and JMS are currently absent in South America.

Figure 4-11. Location of *Sinotaia quadrata* in Argentina, South America.

H. Caribbean and West Indies Islands

Included in this chain of islands are Cuba, The Bahamas, the Turks and Caicos, Puerto Rico, Dominican Republic, Jamaica, Aruba, Bonaire, Curacao, St. Martin, and St. Eustatius. One endemic viviparid occurs in Cuba, *Viviparus bermondianus* (Orbigny, 1842) in the Zapata Peninsula (Perera and Valderrama 2010). The species was not found in 2010 and has perhaps disappeared (Perera and Valderrama 2010). Five species of introduced freshwater gastropods also occur in Cuba, two thiarids and two ampullariids. Vernhout (1914b) recorded freshwater molluscs for Puerto Rico, Dominican Republic, Jamaica, Aruba, Bonaire, Curacao, St. Martin, and St. Eustatius. No viviparids occur in these islands. Clench (1955a) listed land and freshwater molluscs from Turks and Caicos, the Ragged Islands, and islands on the Cay Sal Bank, but most are land molluscs; none are viviparids. The same is true for the Cayman Islands, West Indies (Clench 1955b).

1. Summary of Distribution of Viviparidae in Caribbean and West Indies Islands

Only one endemic viviparid occurs in Cuba, *Viviparus bermondianus*, in the Zapata Peninsula (Figure 4-12). No viviparids occur in the other islands. CMS and JMS are currently absent in the Caribbean and West Indies Islands.

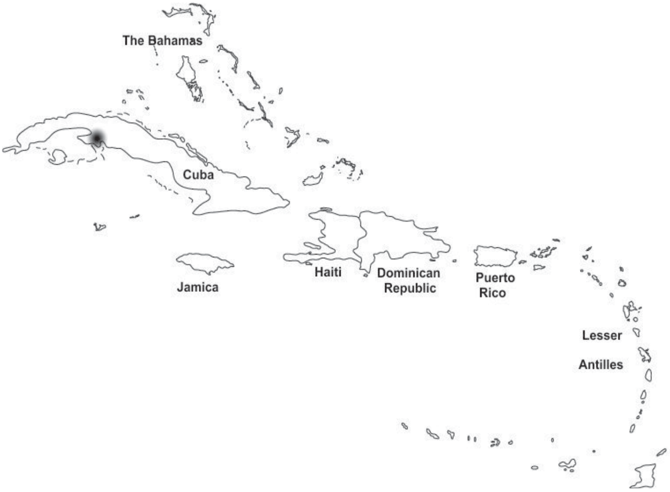

Figure 4-12. Location of *Viviparus bermondianus* in Cuba of the Caribbean and West Indies islands.

I. Central America

Mexico falls in the north of Central America, which consists of eight countries: Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama (Fischer and Crosse 1878).

Binney (1865) described a new species, *Viviparus inornata*, from "near Chapotilo, Mexico" (49). Martens (1890–1901) could not verify the site and pronounced the orthography of this word as likely incorrect. A friend informed him that there is a "Rancho named Chapotilo, near Sinaloa, in N.W. Mexico, a Hacienda Chapotilo at Cerralvo, in Nuevo Leon, near the Rio Grande del Norte, and a Rancho Chapotita in Michoacan, S.W. Mexico" (426) and thought the most probable locality was in N.E. or N.W. Mexico. Fischer and Cross (1878) did not report *V. inornata* from Mexico, yet they did report it later (Fischer and Crosse 1900), citing W.G. Binney's record from near Chopatilo (note spelling compared to Martens, above), Mexico. Still, they did not know in which state of Mexico the town of Chopatilo was located. They suggested that the "name was misspelt by the traveler who sent this Paludine to our learned colleague Mr. W. G. Binney" (291). Clench and Fuller (1965) recommended that *V. inornata* be considered a tentative synonym of *Viviparus georgianus* (Lea 1834) because it resembled unbanded and atypically green specimens from northern Florida. Moreover, they could not locate Chopatilo on any map and suggested that the locality given by Binney (1865) was in error. Thompson (2011), in his annotated checklist and bibliography of the freshwater snails of México and Central America, advocated that this synonymy is unlikely because "the weakly impressed suture that characterizes *Viviparus inornatus* differs strikingly from the much more deeply impressed suture of *Viviparus georgianus*" (24-25). Czaja, Meza-Sánchez, Estrada-Rodríguez, Sáenz-Mata, *et al.* (2020) and Thompson (2011) believed the location to be Nuevo Leon, Mexico.

Czaja, Meza-Sánchez, Estrada-Rodríguez, Sáenz-Mata, *et al.* (2020) presented an updated checklist of native Mexican freshwater gastropods with data on their general distribution, hotspots of endemicity, threats, and, for the first time, their estimated conservation status. The list contains 193 species, representing 13 families and 61 genera. Of these, 103 species (53.4%) and 12 genera are endemic to Mexico, and 75 species are considered local endemics because of their restricted distribution to minimal areas. Using the NatureServe Ranking, 9 species (4.7%) are possibly or presumably extinct, 40 (20.7%) are critically imperiled, 30 (15.5%) are imperiled, 15 (7.8%) are vulnerable, and only 64 (33.2%) are currently stable. With 61 species in 21 genera, the Cochliopidae are the most diverse family, followed by the Planorbidae (37 species) and Pachychilidae (31).

Pachychilus is the most species-rich genus with 30 species. Despite the high number of imperiled species (84), only seven species (3.6%) are listed as endangered by the Mexican Secretariat of Environment and Natural Resources. In addition, they identified three hotspots and two potential centers of gastropod endemicity. Czaja, Meza-Sánchez, Estrada-Rodríguez, Sáenz-Mata, *et al.* (2020) list *V. inornatus* as a local endemic with a NatureServe Rank of Critically Imperiled in Mexico.

Naranjo-García and Castillo-Rodríguez (2017) performed a recent inventory of the introduced and invasive molluscs in Mexico. They found 56 exotic, invasive molluscs, consisting of 15 brackish and marine species, 10 freshwater species, and 31 terrestrial species. Of these, 36% were introduced from Europe, 18% from Asia-Australia-New Zealand, and 46% are of cryptogenic origin, coming from different regions of the planet. Of the freshwater gastropods, four were prosobranchs represented by three ampullarids (Apple Snails, *Pomacea* species) and one thiarid (Trumpet Snails, *Tarebia*). Using data from Czaja, Meza-Sánchez, Estrada-Rodríguez, Sáenz-Mata, *et al.* (2020), who found 103 freshwater gastropod species, the percentage of exotics in Mexico is 3.9%, compared to 53.4% endemics. USGS (2020a) records two locations for CMS in Mexico, Calle Rosa, Los Mochis and Lengüeta Arenosa off All Saints Bay.

In Summary, Mexico has a great diversity of freshwater gastropods with 103 species and 12 genera endemic to the country; 75 species are considered local endemics. Only one local viviparid endemic, *Viviparus inornatus*, occurs in Mexico and is currently listed with a NatureServe Rank of critically imperiled. CMS occurs at two locations in Mexico (Figure 4-13). Guatemala, El Salvador, Costa Rica, Panama, Belize, Honduras, and Nicaragua appear to lack viviparids.

1. Summary of Distribution of Viviparidae in Central America

Mexico has a great diversity of freshwater gastropods with 103 species and 12 genera endemic to Mexico, 75 species are considered local endemics. Only one local viviparid endemic, *Viviparus inornatus*, occurs in Mexico (Figure 4-13) and it is currently listed with a NatureServe Rank of critically imperiled. CMS is found at two locations in Mexico (Figure 4.13).

Figure 4-13. Distribution of the endemic viviparid, *Viviparus inornatus* (black dot) and the Chinese Mystery Snail, *Cipangopaludina chinensis* (stars), in Central America.

J. North America

Last—but certainly not the least—is the distribution of Viviparidae in North America. One striking observation that arises from examining the distribution of viviparids in the rest of the world is that North America seems to be more of a recipient of exotic freshwater gastropods than a donor of its native freshwater gastropods to other countries. The only native viviparids in North America are *Viviparus sensu strictu* (often abbreviated as *s. s.*, *s. str.*, *sens. str.*, or *sens. strict.*), *Tulotoma*, *Campeloma*, and *Lioplax* (Binney 1867; Goodrich 1942a, b; 1944; Clench and Fuller 1965). Of these, *Viviparus* alone occurs in other parts of the world, and the other three subgenera are characteristically North American (Gill 1863; Prashad 1928; Clench 1962; Clench and Turner 1955; Clench and Fuller 1965). For example, Gill (1863) cited *Methano*, a synonym of *Campeloma*, and *Lioplax* and *Tulotoma*; Binney (1865) described *Methano decampi* as a member of the Viviparidae.

There is a high level of endemicity in many countries with much lower levels of exotics. For example, Mexico has 3.9% exotic vs. 53.4% endemic freshwater snails; only one, *Pomacea diffusa*, was of US origin (see discussion under Central America). Endemicity in Australia is due to the existence of only two types of aquatic habitats, springs associated with the Great Artesian Basin and long-term permanent streams in the coastal areas of southeast Australia and Tasmania. Hydrobiids are characteristic of these habitats and are almost entirely endemic, with only a few species like *Potamopyrgus antipodarum*, the New Zealand mud snail, native to New Zealand but widely invasive in other countries.

Strong, Gargominy, Ponder, and Bouchet (2008) classify global hotspots of freshwater gastropod diversity in four main categories: "1. *Springs and groundwater*. Springs, and sometimes the small headwater streams fed by them, are inhabited by taxa that are typically not found in larger streams or rivers. 2. *Large rivers and their first- and second-order tributaries*. 3. *Ancient oligotrophic lakes*. 4. *Monsoonal wetlands* and their associated rivers and streams" (158). Of these four categories, hydrobioids are endemic in all of them; endemicity of hydrobioids range (# species:# endemic) from 12:9 to 220:200 in springs and groundwater and 24:15 to 147:114 in ancient eutrophic lakes. Strong, Gargominy, Ponder, and Bouchet (2008) did not give ranges in the remaining categories, but Hydrobioids represent 16:5 in large rivers and their first- and second-order tributaries. Five families occur in monsoonal wetlands. Viviparidae are endemic in ancient oligotrophic lakes (e.g., Lake Victoria, Australia) and monsoonal wetlands (e.g., Northern Australia) (Strong, Gargominy, Ponder, and Bouchet 2008).

The viviparid diversity between the US and Canada is very different, even though the range in freshwater habitats is quite similar, at least within the temperate zone. The following descriptions explore the distribution of Viviparidae in both countries, focusing on the Chinese and Japanese mystery snails. In previous definitions, the search for CMS and JMS included the synonymy of *Paludina*, *Vivipara*, *Viviparus*, and *Cipangopaludina*. However, the search for synonyms of the two mystery snails in North America was made more accessible by the lists of synonymies in Burch (1982) and several other publications cited herein.

1. United States

The Viviparidae occur throughout the eastern half of the United States. As stated earlier, three genera— *Campeloma, Lioplax* (both of subfamily Lioplacinae), and *Tulotoma* (subfamily Viviparinae)—occur in North

America, the latter two genera being endemic to the United States (Burch 1982). *Viviparus* also occurs in the US, but no species are endemic to the country. Two introduced species represent *Cipangopaludina*. Details of distributions are given for only the Viviparinae (i.e., *Tulotoma*, *Viviparus* and *Cipangopaludina* species).

a. Lioplacinae

Campeloma is represented by eight species (Burch 1982), listed alphabetically below:

- *crassula*, distributed from the midwestern United States in the Great Lakes-St. Lawrence and Mississippi drainages
- *decampi*, restricted to northern Alabama
- *decisum*, the most widely distributed *Campeloma* from the northern states of New York and Michigan, south to Texas, Louisiana, Mississippi, Alabama, northern Georgia, and Virginia
- *floridense*, found in eastern Florida
- *geniculum*, occurring in northwestern Florida, southwestern Georgia, and southeastern Alabama
- *C. limum*, found in Atlantic drainage from North Carolina to Georgia
- *C. parthenum,* a southern species found in Ochlockonee River drainage in southern Georgia and northern Florida
- *C. regulare*, confined to the Alabama-Coosa drainage

Clench and Turner (1962) recognized only four species of *Lioplax*, but Burch (1982) recognized six species, listed alphabetically below; the distribution of all species except *L. talquinensis* can be found in Clench and Turner (1955):

- *L. cyclostomaformis*, ranging from Coosa-Alabama-Tombigbee River system in Georgia and Alabama to Texas River
- *L. pilsbryi choctawhatchensis*, distributed in the Choctawhatchee, Escambia, Flint, and Suwannee River systems, Florida and Georgia
- *L. pilsbryi pilsbryi* restricted to the Chipola River, Florida
- *L. subcarinata*, in the Atlantic drainage (New York to South Carolina) and gulf drainage
- *L. sulculosa*, distributed in the Mississippi drainage (Minnesota to Arkansas and Ohio)
- *L. talquinensis*, in the Ochlockonee and Yellow River systems, Florida and Alabama

b. Viviparinae

A single species represents *Tulotoma*, the endemic *T. magnifica* Conrad, 1834, restricted to the Coosa-Alabama River system in Alabama (Clench 1962; Burch 1982; Hershler, Pierson, and Krotzer 1990). It was initially found in the Coosa River System of Alabama, ranging widely from Big Canoe Creek south to Wetumpka, above the confluence with the Tallapoosa River. Localities included numerous sites on the Coosa River as well as lower reaches of several large tributaries. However, the snail has since been recorded from only two localities in the Alabama River System: the main river in the vicinity of Claiborne (type locality for *T. magnifica*) and Chilatchee Creek, southwest of Selma (Hershler *et al.* 1990).

It was abundant when first described by Conrad in 1834. Still, all populations declined precipitously due to impoundments of the rivers by the construction of dams, pollution from municipal waste discharges, and dredging operations (Hershler, Pierson, and Krotzer 1990). The species was declared endangered in 1991, but a documented increase in the extent and size of *Tulotoma* populations in four of five locations, the Coosa River, Kelly Creek, Weogufka Creek, and Hatchet Creek, was reported after a five-year review conducted in 2008 (AFWS 2011).

Three species in the US represent *Viviparus*: *Viviparus georgianus*, *Viviparus intertextus*, and *Viviparus subpurpureus*.

i. Viviparus georgianus

Viviparus georgianus is distributed widely through several northern and eastern states (Tables 4-8, 4-9). Figure 4-14 is a compilation of distributions shown in Table 4-8 from Clench (1962) and Table 4-9 from Morningstar, Daniel, Larson, and Fusaro (2020) and Appendix B, *Viviparus georgianus*. Clench's (1962) lists were based on the availability of collections in several US museums. Table 4-9 gives updated occurrences for many states, except the District of Columbia, Illinois, Kentucky, and Tennessee, since Clench's (1962) lists.

ii. Viviparus intertextus

Viviparus intertextus occurs in river systems as far south as the Houston ship channel system west of Houston, Harris County, Texas, and as far north as Rainy Lake in Minnesota (Tables 4-10 and 4-11, Figure 4-15). Being primarily in river systems, most locations of *V. intertextus* are expected to extend downstream and laterally into neighboring states, especially in the

Mississippi River. According to Clench and Fuller (1965), *V. intertextus* is widespread in Mobile, Mississippi, and other Gulf drainages from Texas to Minnesota. Surveys report populations of *V. intertextus* common in the lowest, slowest sections of the Ohio and Wabash Rivers (Appendix B, *Viviparus intertextus*). The updated distribution given in Morningstar, Daniel, Larson, and Fusaro (2020) is listed by states rather than drainage systems, as in Clench and Fuller (1962), but the latter lists many more locations than the former. Either they provided no updated information, or many river/drainage systems were not examined by Morningstar, Daniel, Larson, and Fusaro (2020).

Table 4-8. Locations of *Viviparus georgianus* in the United States according to the River Systems and Drainage River System for states in each category, from Clench (1962).

River System	**Drainage System**	**State**	**Location**
Great lakes-St. Lawrence	Lake Michigan	Wisconsin	Sunset Lake
		Illinois	Chicago River; Owossa; Wolf Lake; Calumet River; Washington Park
	Lake Erie	New York	Lake Erie, Dunkirk; Oatka Creek.; Lime Lake
	Lake Ontario		
	Lake Champlain	Vermont	Lake Bomoseen
	St. Lawrence River	New York;	Claton, Jefferson County
Mystic, Charles, Neponset	Their drainages	Massachusetts	Fresh Pond; Little Pond; Muddy River, Boston Public Gardens; Sargent's Pond; Houghton's Pond
Connecticut	Connecticut River	Massachusetts	Forest Park, Springfield
Housatonic	Housatonic River	Connecticut	Lake Waramaug
Hudson	Hudson river	New York	Erie Canal @ Frankfurt & Mohawk; Glen Lake; Lake Central Park; Prospect Park
Delaware	Delaware River	New Jersey	Riverton
		Pennsylvania	Fairmont Park
Potomac	Potomac River	Maryland	Potomac River.@ Great Falls, Chesapeake Canal, Ohio Canal, & Washington
		Virginia	Hunter's Point @ Alexandria; Little Hunting Creek; Potomac River @ Mt. Vernon
Altamaha	Altamaha River	Georgia	Altamaha River @ Darien
	Ocmulagee River	Georgia	Oscewickee Springs @ Abbeville

St. Johns	St. Johns River	Florida	L. Jessup; Wekiva River; Lake Monroe; Lake Woodruff; Spring Garden Creek.; Silver Springs; Oklawaha River; Lake George; Lake George; Juniper Creek.
Withlacoochee	Withlacoochee River	Florida	Withlacoochee River near Dare & Dunnellon
Suwanee	Santa Fe River	Florida	Poe Springs; Santa Fe River; High Springs; Ichtucknee River
	Withlacoochee River	Georgia	Withlacoochee River @ Olympia & Blue Springs; Suwanee River @ Withlacoochee River, Santa Fe River & Oldtown, Dixie County.
Steinhatchee	Steinhatchee River	Florida	Steinhatchee River near Salem
Ochlockonee	Ochlockonee River		Lake Talquin
Apalachicola	Flint River	Georgia	Kiokee Creek; Creek. @ Albany; Keels Creek.; Spring @ Bainbridge; Paul Clark Spring; Sealey Spring; Shackleford Creek; Blue Spring
	Chipola River	Florida	Reedy Creek; Big Creek; Chipola River; Scott's Ferry; Dead Lake
	Choctawhatchee	Florida	Holmes Creek
Coosa	Coosa River	Alabama	Big Canoe Creek; Rock Creek
	Black Warrior River	Alabama	Sipsey River
	Tombigbee River	Mississippi	Tibee

Mississippi	Mississippi River	Illinois	Quincy
	Illinois river	Indiana	Bass Lake
		Illinois	Des Plains River; Kankakee River; Canal @ Utica, Peru; Lake Senachwine; Peoria Lake
	White River	Missouri	Current River
		Arkansas	Newport; Spring River
	Arkansas River	Arkansas	Fourche
	Red River	Louisiana	Frierson's Mill; Alexandria, Rapides Parish
	Wabash River	Indian	L. Maxinkuckee; Tippecanoe River; Foot's Grave Pond; Wabash River @ New Harmony
		Illinois	Mt. Carmel; Little Fox River
	Kanawha River	Virginia	Fish Hatchery @ Wytheville
	Green River	Kentucky	Bowling Green
	Cumberland River	Tennessee	Lebanon; Cumberland River; Stone's River
	Tennessee River	Alabama	Alabama Pond; Byrn Spring; Byrd Spring L.; Flint River; Swan Lake; Flint Creek.; Swan Creek.; Ditch near Mussel Shoals Canal; Creek. near Great Spring, Tuscumbia
		Tennessee	Shelbyville
	Ohio River	Pennsylvania	Pittsburgh, Allegheny County
		Ohio	Cincinnati, Hamilton County; Newton, Hamilton Co.
		Kentucky	Covington, Kenton County
		Illinois	Ohio River@ Elizabethtown

Table 4-9. Great Lakes region occurrences of *Viviparus georgianus*, the earliest and latest observations in each state/province. States are listed alphabetically (From Cordeiro 2018), and Morningstar, Daniel, Larson, and Fusaro (2020).

State	**Year of earliest observation**	**Year of last observation**	**Hydrologic Unit Codes (HUCs*)**
Connecticut	1962	1983	Housatonic
District of Columbia	1962	1962	Middle Potomac-Anacostia-Occoquan
Florida	2015	2018	Caloosahatchee; Florida Southeast Coast; Sarasota Bay
Illinois	1962	1962	Chicago; Little Calumet-Galien; Pike-Root; Lower Ohio Bay
Indiana	2008	2014	St. Joseph; Tippecanoe; Wabash
Iowa	1967	2006	Flint-Henderson
Kentucky	1962	1962	Middle Ohio-Laughery
Maryland	1962	2013	Gunpowder-Patapsco; Middle Potomac-Anacostia-Occoquan; Middle Potomac-Catoctin
Massachusetts	1916	2019	Charles; Lower Connecticut; Nashua; Westfield
Michigan	1980	2018	Au Gres-Rifle; Au Sable; Boardman-Charlevoix; Brule; Carp-Pine; Cheboygan; Clinton; Detroit; Fishdam-Sturgeon; Flint; Keweenaw Peninsula; Lake Huron; Lower Grand; Manistee; Manistique; Maple; Menominee; Michigamme, Muskegon; Ontonagon; Ottawa-Stony; Pere-Marquette-White; Raisin; Saginaw; Shiawassee; St. Joseph; St. Marys; Thornapple; Tiffin; Tittabawassee
Minnesota	2006	2018	Beartrap-Nemadji; Big Fork; Clearwater; Clearwater-Elk; Crow; Crow-Wing; Eastern wild Rice; Elk-Nokasippi; Kettle; Leech Lake; Long Prairie; Cloquet; Lower Minnesota; Mississippi Headwaters; Otter Tail; Pine; Platte-Spunk; Prairie-Willow; Red Lakes; Redeye; Rum; Sauk; Twin Cities
Missouri	2013	2013	Bourbeuse

New Hampshire	2017	2019	Merrimack River
New Jersey	1962	2018	Hackensack-Passaic; Lower Delaware; Rondout
New York	1914	2016	Cattaraugus; Chenango; Hudson-Hoosic; Hudson-Wappinger; Lake Champlain; Lake Erie; Lake Ontario; Lower Genesee; Lower Hudson; Mettawee River; Middle Hudson; Mohawk; Niagara; Northeastern Lake Ontario; Southwestern Lake Ontario; St. Lawrence; Oneida; Oswego; Raquette; Seneca; Southern Long Island; Upper Genesee; Upper Susquehanna
North Carolina	2015	2019	Upper Catawba; Upper Neuse
Ohio	1995	2014	Middle Ohio-Laughery; Tuscarawas
Pennsylvania	1962	2003	Conemaugh; Schuylkill; Upper Ohio
South Carolina	1995	2008	Cooper; Lake Marion
Tennessee	1962	1962	Lower Cumberland-Sycamore; Stones
Vermont	1962	2017	Lake Champlain; Mettawee River; Lake Champlain; Mettawee River; Richelieu
Virginia	1962	2017	Lower Potomac; Middle Potomac-Anacostia-Occoquan; Middle Roanoke
Wisconsin	1906	2019	Bad-Montreal; Baraboo; Beartrap-Nemadji; Black; Black-Presque Isle; Brule; Buffalo-Whitewater; Castle Rock; Door-Kewaunee; Duck-Pensaukee; Flambeau; Jump; Lake Dubay; Lake Winnebago; Lower Chippewa; Lower St. Croix; Manitowoc-Sheboygan; Menominee; Middle rock; Milwaukee; Namekagon; Oconto; Ontaganon; Peshtigo; Red Cedar; South Fork Flambeau; Upper Chippewa; Upper Fox; Upper Rock; Upper St. Croix; Upper Wisconsin; Wolf

*HUCs = Watersheds are delineated by USGS using a nationwide system based on surface hydrologic features. This system divides the country into 21 regions, 222 subregions, 370 basins, 2,270 subbasins, ~20,000 watersheds, and ~100,000 sub-watersheds. For more details, see Appendix A, USA, hydrologic unit codes.

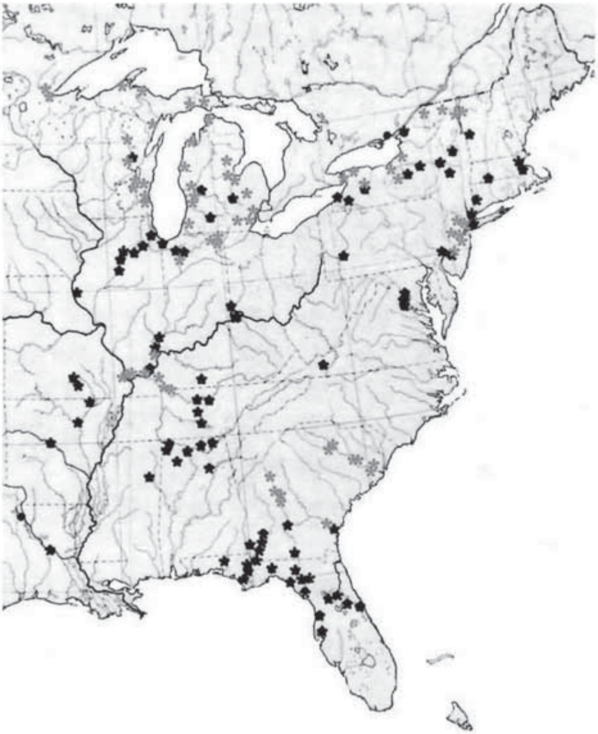

Figure 4-14. Distribution of *Viviparus georgianus* in the United States. Grey stars are from Clench and Fuller (1965); black stars are from Morningstar, Daniel, Larson, and Fusaro (2020).

iii. Viviparus subpurpureus

Viviparus subpurpureus has a much more restricted distribution in the US than the previous two *Viviparus* species. According to Clench and Fuller (1965) and Appendix B, *Viviparus subpurpureus* (a), (b), c) it is found in the Mississippi River system in northwestern Illinois, southeastern Iowa, northern Kentucky, the Neches and Sabine River systems in eastern Texas, the Sabine and Atchafalaya river systems in western Louisiana, and the Pascagoula River system in southeastern Mississippi (Table 4-12, Figure 4-16).

Table 4-10. Distribution of Viviparus intertextus in the United States, as reported by Clench and Fuller (1965).

River System	Drainage System	State	Locations
Houston Ship Channel	Houston Ship	Texas	Addics, near Houston
San Jacinto	San Jacinto	Texas	Cleveland, Liberty County
Liberty River	Liberty River	Texas	Dayton
Neches	Neches River	Texas	Naches River
Bayou Teche	Bayou Tech River	Louisiana	Bayou Tech near St. Martinville; Grand Coteau
Mississippi River	Mississippi River	Louisiana	New Orleans; Harahan near Houma; Terrebonne Parish
	Tennessee River	Arkansas	Samburg
		Illinois	Warsaw; Glancy's Lake; Rock Island; Lake Harmon; Rockford
		Iowa	Burlington; Muscatine; Davenport
	Minnesota River	Minnesota	Minneapolis; White Bear Lake
	Red River	Louisiana	Bayou Boeuf; Ouachita R; Alabama Landing; Alexandria; Frierson; Shrevport
	Wabash River	Illinois	Wabash River @ Mt. Carmel
	Illinois River	Illinois	Havana; Canton; Putman
	Iowa River	Iowa	Cedar River; Waterloo
	Pearl River	Mississippi	Conway's Slough
Coosa-Alabama	Coosa-Alabama	Alabama	Alabama River; Haley's Landing; floodplain in Tombigbee River

Altamaha River	Altamaha River	Georgia	Ohoopee R.; Little Ohoopee R.; Alligator Creek; Gum Swamp Creek @ McRae
Edisto River	Edisto River	South Carolina	Summerville
Santee River	Santee River	South Carolina	Pocotaligo River, Manning; Santee canal
Great-Lakes-St. Laurence	Lake Superior	Minnesota	Rainy Lake @ Rainy Lake

Table 4-11. Distribution of Viviparus intertextus in the United States, listed alphabetically by state. Data are from Morningstar, Daniel, Larson, and Fusaro (2020).

State	Location
Alabama	Coosa-Alabama River system
Arkansas	Eastern Arkansas
Georgia	Alabama River systems
Illinois	No location given
Iowa	Eastern Iowa, no location given
Louisiana	Bayou Tech system; Mississippi River
Minnesota	Minneapolis; White Bear Lake; Rainy Lake, Koochiching County
Mississippi	Pearl River system;
South Carolina	Edisto and Santee River systems
Tennessee	Northern Tennessee
Texas	Houston ship Canal, Harris County San Jacinto, Liberty, and Neches River systems

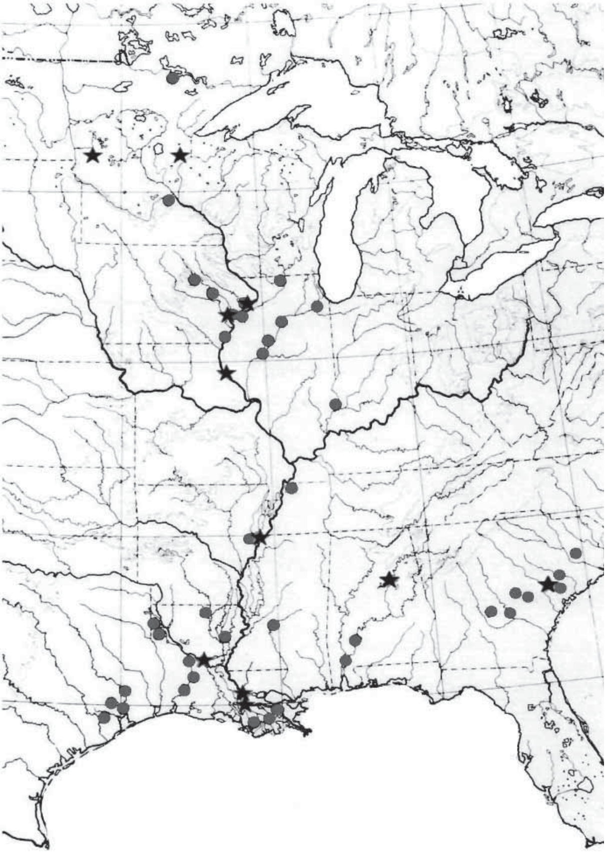

Figure 4-15. Distribution of *Viviparus intertextus* in the United States. Grey dots are from Clench and Fuller (1965); stars are from Morningstar, Daniel, Larson, and Fusaro (2020).

Table 4-12. Distribution of *Viviparus subpurpureus* in the United States, from Clench (1930) and Clench and Fuller (1965).

River System	Drainage System	State	Locations
Neches		Texas	Neches River, town Bluff
Sabine		Texas	Sabine River, Smith's Falls Camp; Cypress Creek
Atachafalaya		Louisiana	Atchafalaya River, South East of LeBeau
Mississippi	Mississippi River	Louisiana	University Lake; Lake Concordia;
		Mississippi	Big Black River; Mississippi River; Yazoo River
		Arkansas	Grand Lake
		Illinois	Mississippi River, Nauvoo
		Iowa	Mississippi River, Davenport; above McGregor
Red	Red River	Louisiana	Saline bayou @ US 84; Canal W of Krotz Springs; Tensas River; Black R.; Lake St. John; Old R. SE Jena; Lake Catahoula outlet; Little River; Ouachita River; Lake Bisteneau; Bayou Pierre
		Texas	Caddo Lake
		Arkansas	Bartholomew Bayou
		Oklahoma	Little River
White	White River	Arkansas	Indian Bay, Baytown
St. Francis	St. Francis River	Arkansas	St. Francis River
Ohio	Ohio River	Indiana	Wabash River
		Illinois	Ohio River, Elizabethtown; Wabash River; Little Wabash River; Saline River

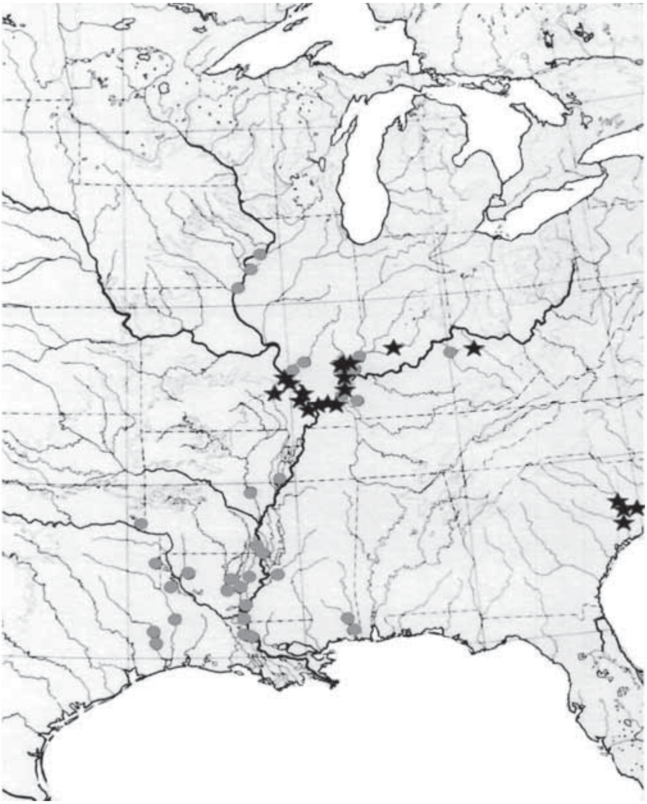

Figure 4-16. Distribution of *Viviparus subpurpureus* in the United States. Grey dots are from Clench and Fuller 1962; black stars are from websites (see text).

iv. Cipangopaludina chinensis

Cipangopaludina is represented by two species in the United States, *C. chinensis* and *C. japonica*. Considerable research has been done on Asian and European species of *Cipangopaludina*, especially by Lu, Du, Li, and Yang (2014) and Hirano, Saito, and Chiba (2015). Their studies have helped remove much confusion in the taxonomy of the two mystery snails. The taxonomic confusion with the North American *Cipangopaludina* began shortly after it arrived in the early 1890s on the Pacific coast. After Wood

(1892a) reported his finding of living specimens in a wooden bucket in a Chinese food market in San Francisco, his curiosity got to him and, through an interpreter, found out they were the first brought alive from Japan. Wood (1892b) reported that the specimens were collected in rice fields near Yokohama, Japan, and brought to America by sailors and then given to marketers in Chinatown, San Francisco (Stearns 1901). According to Wood (1892a) an interpreter told him that many of the Chinese (25,000 in Chinatown at the time) found them very good to eat; they threw them into boiling water, let them remain for a few moments, removed the operculum, separated the foot from the soft body, and added salt and pepper.

The taxonomic debate of North American CMS began after Stearns (1901) was sent a few specimens of *Viviparus*, when “a quite familiar Japanese form” was collected in a valley at Mount Hamilton in San José, California (91). A living specimen was sent to Dr. Pilsbry, who determined them to be *V. stelmaphora*, a synonym of *Viviparus malleata* Reeve. Sixteen years after Wood’s (1982b) report, Hannibal (1908) found among the freshwater molluscan fauna of the Artesian Belt between San José and San Francisco Bay a 2-cm high edible snail, a species introduced by the Chinese 15 or 20 years earlier. He sent the specimens to Dr. Dall, who identified them as *Viviparus lethycoides* Benson. Hannibal (1908) surveyed four ponds/lakes in the valley at Mount Hamilton, reported by Stearns (1901), and could not find any snails and concluded the location was incorrect. Hannibal (1911) again questioned the Mount Hamilton location and suggested the snails were probably collected in the Artesian Belt. He compared his *V. lecythoides* (**synonym of CMS**) snail with specimens from Nagasaki, Japan, and concluded his was also *V. malleatus* (**synonym of CMS**).

The name *V. malleatus* persisted for several years, from the early 1900s to the end of the 20th century. During this period, there was still some uncertainty, especially with Johnson (1915, 1916, 1918), when he used *V. malleatus* to describe the distribution of CMS in Massachusetts and *V. japonicus* in his updates (Johnson 1923). The change in species name was due to the classification of the freshwater Mollusca of North America, north of Mexico, by Walker (1918). In Walker’s (1918) synopsis, he listed *V. japonicus* referring to the same site, Muddy River, Brookline Massachusetts, cited by Johnson (1915a, b, 1916). Thus, for the first time, both *V. malleatus* and *V. japonicus* were listed as present in North America. Clench (1962) also listed both species in his Catalogue of the Viviparidae of North America.

Dundee (1974) and Clarke (1978) synonymized the two species because they could only find slight shell variations. However, Clench and Fuller

(1965); Stańczykowska, Magnin, and Dumouchel (1971); Jokinen (1982); Smith (2000); and Solomon, Olden, Johnson, Dillon, *et al.* (2010) considered the morphological (shell, radula) differences to be sufficiently large to retain them as separate species. David and Cote (2019) did genetic and morphological analyses on North American populations of both *C. japonica* and *C. chinensis* and found them genetically distinct but morphologically indistinguishable. These two species have no shell characters that can distinguish them morphologically where they co-occur in several lakes of New York. Van Bocxlaer and Strong (2016) state that the lack of shell variation might lead to inaccurate identifications by non-malacologists. They confirmed their suspicions by examining shell morphology, internal anatomy, histology, the radula, salivary gland, kidney, nerve ring, and reproductive organs. They found marked differences between *C. japonica* and other viviparids in these features, although *C. chinensis* was not among them. However, Hirano, Saito, and Chiba (2015) and Van Bocxlaer and Strong (2016) found *C. malleata* and *C. japonica* to be genetically distinct.

It took some time for the Chinese Mystery Snail to spread across the United States from the West Coast to the East Coast. Hannibal (1911) opined that CMS was originally transplanted somewhere between Alameda and Centerville, California (approximately 35 km between them), to supply Chinese markets in the San Francisco Bay area.

The chronology of distributions of CMS across states in the United States is fascinating for five reasons:

- First and foremost, the earliest record in the US is 1800 in Hawaii, as listed by Kipp, Benson, Larson, Fusaro, *et al.* (2019) and USGS (2020a) (Table 4-13). But Devick (1991) could not verify the year and recorded it as 1800?; perhaps the date should be recorded as the 1800s; the specific year is unknown, but presumably before 1892. If it is earlier than 1892, the record is significant for two reasons; one replaces the earliest published record by Wood's (1892) in San Francisco, California (Table 4-13).
- Second, it is improbable to be 1800 because Cuvier (1800) was the first to recognize Mollusca as a taxon, under Testacée (see his Fifth Table). Also, Cuvier (1849) first recognized *Paludina* as a member of the Family Trochusidae (see his Table 2.1), suggesting the introduction to Hawaii had to be between the 1850s and 1892.
- Third, if Hawaii is the first occurrence of CMS, it may have been on the Oahu and Kauai islands. It took 22 years (i.e., from 1892) to record the first observation outside of California—1914 in Massachusetts on the East Coast, that is, for it to travel coast to

coast in the US. Thus, it is unknown how long CMS was in Hawaii and Massachusetts before it was reported in each state. Speculation of dispersal times and vectors are discussed in Chapter V., Dispersal.

- Fourth, Colorado, Delaware, Oklahoma, Utah, and Vermont have not recorded CMS since it was first reported in 1965 (Table 4-13).
- Fifth, besides the five states with no records since 1965, the records for several states are likely low, with some states not being resurveyed since 1996 (Connecticut), 1997 (Hawaii), 2009 (Kentucky, the only year a survey was performed), 2012 (West Virginia), and 2015 (Illinois) (Table 4-13).

Table 4-14 shows the numbers of occurrences recorded for CMS in 36 states in the US. Wisconsin has the most detailed distribution of all the states, with 1,166 records, based on the sources given in the caption of Table 4-13. Minnesota and Illinois have also been well surveyed, with 212 and 200 records, respectively (Table 4-14). Some reasons for the differences in numbers of records among states are discussed in Chapter V. Dispersal.

Table 4-13. Years of earliest and latest records of *Cipangopaludina chinensis* in 39 states of the United States, listed chronologically by year of earliest record. The data are mostly from iNaturalist, with distribution notes from Wood (1892a); Stearns (1901, 1908); Hannibal (1908, 1911); Clench 1940; Clench and Fuller (1965); Dundee (1969, 1974); Branson 1977; Clarke (1978); Jokinen (1982, 1984); Cohen and Carlton (1995); Michelson (1970); Freas (1950); Sytsma, Cordell, Chapman, and Draheim (2004); Stewart (2006); Evans and Ray (2008); Pyron, Beugly, Martin, and Spielman (2008); Waltz (2008); Chaine, Allen, Fricke, Haak, *et al*. (2012); Haak, Chaine, Stephen, Wong, *et al*. (2013); Haak, Stephen, Kill, Smeenk, *et al*. (2014); Howell (2014); Miller and Sytsma (2014); Kipp, Benson, Larson, and Fusaro (2016): Vinsel and Tiemann (2016); Kipp, Benson, Larson, Fusaro, *et al*. (2019); Panther Pond Association (2019); iNaturalist (2020; and Kipp, Benson, Larson, and Fusaro (2020).

State	Year of the earliest record	Year of the last record	State	Year of the earliest record	Year of the last record
Hawaii	1800*	1997	Utah	1965	2020
California	1892	2020	Vermont	1965	2020
Massachusetts	1914	2020	Washington	1965	2020
New York	1920	2020	New Hampshire	1973	2020
Iowa	1943	2020	Illinois	1974	2020
Minnesota	1944	2020	Maryland	1974	2020
Michigan	1947	2020	Nebraska	1974	2020
Pennsylvania	1957	2020	Wisconsin	1974	2020
Arizona	1965	2020	Connecticut	1983	2020
Colorado	1965	1965	Virginia	1993	2020
Delaware	1965	2020	Kansas	2001	2018

Florida	1965	2020	Missouri	2002	2019
Indiana	1965	2020	Idaho	2008	2018
Maine	1965	2020	Oregon	2008	2020
New jersey	1965	2020	Kentucky	2009	2009
North Carolina	1965	2020	West Virginia	2011	2020
Ohio	1965	2020	Tennessee	2018	2020
Oklahoma	1965	1965	Alabama	2010	2020
Rhode Island	1965	2020			
Texas	1965	2020			

1800*: Date listed as 1800 by Kipp, Benson, Larson, Fusaro, *et al.* (2019) and USGS (2020a), but Devick (1991) lists the date as 1800? for *Viviparous chinensis*. See text for details.

Table 4-14. Numbers of occurrences recorded for *Cipangopaludina chinensis* in 41 states of the United States from May 2018 to July 2020, listed in descending order. Data are from the same sources as given in the caption of Table 4-13.

State	**No of Locations**	**State**	**No of Locations**
Wisconsin	1,199	Kansas	14
Minnesota	264	Iowa	12
Illinois	222	Nebraska	12
New Jersey	93	South Carolina	12
California	91	Idaho	10
New York	87	Vermont	9
Ohio	87	Arizona	8
Massachusetts	78	Florida	7
Michigan	77	Oregon	6
Pennsylvania	73	Rhode Island	6
Virginia	65	Utah	5
Indiana	46	Hawaii	4
Maine	44	Kentucky	4
Washington	34	Oklahoma	3
New Hampshire	30	Delaware	2
Connecticut	27	Louisiana	2
Maryland	26	Tennessee	2
North Carolina	19	Alabama	1
Texas	18	Colorado	1
West Virginia	17		
Missouri	16		

Figure 4-17 shows the distribution of CMS up to July 31, 2020, in the United States. The plots are based on the latitudes and longitudes provided in iNaturalist (2020) and USGS (2005; 2020a); the coordinates were copied and pasted into Google Earth Pro to find the locations. Alaska is not shown because Viviparidae is absent. Viviparids are present in Puerto Rico, but CMS is absent, as discussed in Section 7. Caribbean Islands and West Indies. Guam is included in Southeast Asia, section *f) Southeastern Asia* of this chapter, but it lacks viviparids. Hawaii and its islands are magnified to acknowledge the occurrences in four of the islands; from the bottom to top, they are Hawaii, Molokai, Oahu, and Kauai. The plots are based on the same sources given in the caption of Table 4-13. Many plots represent several occurrences because some locations are close together or the same locations were examined in one or more periods.

Figure 4-17. The distribution of the Chinese Mystery Snail, *Cipangopaludina chinensis* (grey dots), in the United States, up to July 31, 2020. See text for sources of data.

v. *Cipangopaludina japonica*

Wood (1892a) first reported JMS in the United States, and again the same year (Wood 1892b). However, Stearns (1901) sent one living specimen to Dr. Pilsbry, who determined it to be "*V. stelmaphora* Bgt. (= *V. malleatus* Reeve.)," both synonyms of *C. chinensis* (91). Hence the earliest record of JMS in the US is not 1892, but 1911 (Table 4-15); the USGS (2020b) record #52288, is from the Coalinga Oil Fields in California (Hannibal 1911). The following two earliest records are from Michigan at the Sparks [Foundation County] Park lagoons, Jackson Co. and Ohio in Lake Erie; both sites are in the Lake Erie watershed. The most recent record is from a pond adjacent to the Connecticut River at Brattleboro, Vermont, reported on June 8, 2020.

The Japanese Mystery Snail has a much more restricted distribution in the US than the Chinese Mystery Snail, with 23 states having JMS (Table 4-15) and 36 states with CMS (Table 4-13). Most occurrences of JMS are in North Carolina (25), probably because of more significant yearly search efforts from 2004 to 2017, with many years having repeat surveys (Table 4-16). The annual search effort was similar for Pennsylvania, Wisconsin, and

Virginia, and the numbers of occurrences were also identical, with 21, 18 and 15 events, respectively. The differences may be partly due to the total number of searches for several years, with Pennsylvania having 19 surveys, Wisconsin with 18 surveys, and Virginia with 12 surveys (Table 4-16). The number of JMS occurrences in the US is not reflected in Figure 4-18 because many locations are superimposed.

Table 4-15. The years of earliest and latest records of the Japanese Mystery Snail, *Cipangopaludina japonica*, in 23 states of the United States, listed chronologically from the earliest record. The numbers of counties, localities, and drainages surveyed over the period are given in Table 4-16. The data are from USGS-NAS (2020b) and iNaturalist (2020), with addenda in Wood (1982a, b); Hannibal (1911); Haas (1939); Clench and Fuller (1965); Wolfert and Hiltunen (1968); Jokinen (1982, 1992); Mills, Leach, Carlton, and Secor (1993); Bury, Sietman, and Kams (2007); Evans and Ray (2008); Pyron, Beugly, Martin, and Spielman (2008); Howell (2014); Perez, Segrest, Campos, Minton, *et al.* (2016); Van Bocxlaer and Strong (2016); Vinsel and Tiemann (2016); USWFS (2018); David and Cote (2019); NCWRC (2019); iNaturalist (2020); and Kipp, Benson, Larson, and Fusaro (2020).

State	**Year of the earliest record**	**Year of the last record**
California	1911	2020
Michigan	1937	2020
Ohio	1940	2020
Indiana	1965	2020
Massachusetts	1965	2020
Oklahoma	1965	1965
Florida	1994	1994
South Carolina	1996	2017
New England	1998	1999
Alabama	2003	2003
North Carolina	2004	2020
Kansas	2005	2013
Wisconsin	2007	2020
Minnesota	2007	2020
Missouri	2007	2020
Mississippi	2007	2007
Virginia	2007	2020
Pennsylvania	2011	2020

Delaware	2013	2013
Georgia	2013	2013
Maryland	2014	2020
Texas	2015	2020
New York	2016	2020
Maine	2020	2020
New Hampshire	2020	2020
Vermont	2020	2020

Table 4-16. Numbers of occurrences of the Japanese Mystery Snail, *Cipangopaludina japonica*, in the United States, listed in descending order of numbers of localities and years searched, with numbers of repeats in parentheses. Data are from the same sources as given in the caption of Table 4-15

State	**No. of occurrences**	**Years (repeats)**
North Carolina	25	2004(3), 2005, 2006, 2010(4), 2011(5), 2012(2), 2013(3), 2014(3), 2017(3)
Pennsylvania	21	2012, 2013, 2015, 2017, 2018(2); 2019(7); 2020(6)
Wisconsin	18	2007(8), 2010, 2011, 2012(2), 2014(3), 2015, 2016(2)
Virginia	15	2007, 2012(2), 2013, 2014, 2017, 2018(3); 2020(3)
Ohio	8	1940, 1945, 1963, 1965, 1980, 2015, 2016, 2019
South Carolina	7	1996, 1997, 2003, 2006, 2008, 2015, 2017
Indiana	5	1965, 2007, 2008(3)
Kansas	4	2005, 2007(2), 2013
Maryland	4	2014, 2015, 2020(2)
New York	4	2016, 2017, 2018(2)
Michigan	3	1937, 1965
Massachusetts	2	1965, 1968
Nebraska	2	1998, 1999
Oklahoma	2	1965
Texas	2	2015, 2020
Alabama	1	2003
California	1	1892

Delaware	1	2013
Florida	1	1994
Georgia	1	2013
Minnesota	1	2007
Mississippi	1	2007
Vermont	1	2020

Figure 4-18. Distribution of the Japanese Mystery Snail, *Cipangopaludina japonica* (black dots), in the United States, as of August 2020.

2. Canada

Only one viviparid is native to Canada, the Pointed Campeloma, *Campeloma decisum*. The species occurs in southern Manitoba, southern Ontario, and Nova Scotia (Clarke 1981; Burch 1989).

Teo species of viviparids have been reliably recorded in Canada, the Banded Mystery Snail, *Viviparus georgianus*, and the Chinese Mystery Snail, *Cipangopaludina chinensis*. The Japanese Mystery Snail, *Cipangopaludina japonica*, has not been reliably recorded in Canada, but several images on iNaturalist (2022) suggest the species is present in Ontario and Quebec. For example, photos, 142389865 from Reesor Pond, Markham, ON, 115567589 from a pond in Hamilton, ON, and 148147186 from Yomaska River, QC have 7 whorls, deeply impressed sutures, angled shoulders, and malleations evident on the upper whorls. Unfortunately, all photos have some or all rights reserved and authors could not be contacted for specimens for verification.

a. Viviparus georgianus

Bousefield (1955) reported *Viviparus viviparus* in eastern Canada (Quebec), but Clench (1962) examined the specimens and identified them as *Viviparus georgianus*. He found the following characters on Bousefield's specimens, "The shell, approximately one inch in height and three-quarters of an inch in width, is typically cream-colored and marked by three brown or purplish-brown spiral bands; occasional specimens are uniformly purplish-brown" (266). The species was introduced to Ontario and Quebec in 1867; Clench (1962) himself collected specimens from the Richelieu River, two miles south of Iberville, Quebec. The species has a discontinuous distribution in the Great Lakes-St. Lawrence River system, namely the Grand River and Ottawa River in Ontario and the Richelieu and Ottawa River in Quebec (Clarke 1981).

b. Cipangopaludina chinensis

In Canada, the Chinese Mystery Snail is distributed in the southern parts of six provinces: British Columbia (BC), Alberta, Ontario, Quebec, New Brunswick, and Nova Scotia. The first occurrence of CMS was in BC in 1894; Pilsbry (1894) noted that "Rev. Geo. W. Taylor reports the appearance of *Paludina Japonica* Mart. in the Chinese Market at Victoria, BC" (143). He adds that the occurrence of this species in the San Francisco markets was noted by Mr. W. M. Wood, which Stearns (1901) had verified to be CMS. In addition, only CMS has been found in BC since then (Figure 4.19).

Of the six provinces with CMS, Ontario has the most significant number of observations with 165; Quebec has 13; Nova Scotia has 9; New Brunswick has 4; British Columbia has 3; Newfoundland has 1 (Table 4-17). Figure 4.19 shows the distribution of CMS in Canada. Southeastern Ontario has the densest distribution of CMS; many of the observations shown are superimposed because of the proximity of locations, and some locations have multiple yearly observations.

Figure 4-19. Distribution of the Chinese Mystery Snail, *Cipangopaludina chinensis* (grey dots), in Canada, shown as stars.

It is noteworthy that two records for BC are in the same area of Victoria on Vancouver Island, where CMS was first recorded by Pilsbry (1894). Only one record of CMS has been recorded on the mainland of BC at Harrison Mills; the snails were intentionally planted in a nearby pond by a Chinese boss of millworkers at a sawmill for some epicurean dish (LaRoque 1948).

The single record for Alberta is in McGregor Lake, an off-stream storage reservoir created in 1920 (University of Alberta 1990). Five areas were surveyed just above the dam on both shores; three of the five areas have CMS, the densest populations being at along the east shore from the dam to 50.553161°, -112.905654°, with smaller numbers from this point to 50.545385°, -112.880530°. The west shore from the dam to 50.555272°, -112.919371° also has large numbers of CMS (Nicole Kimmel, email, July 14, 2020).

The first record of *Cipangopaludina chinensis malleata* was in the Great Lakes, sometime between 1931 and 1942 from the Niagara River, which flows into Lake Ontario (Mills, Leach, Carlton, and Secor 1993; USGS 2018). The following several records are from lakes in Peterborough and Hastings counties in 1996, including Stoney Lake and Moira Lake. Nearly all records are from cottagers (iNaturalist 2020), hence clumps of locations in "cottage country," especially Muskoka and Haliburton. The furthest west and north record is Fort Francis (48.604432°, -93.423096°) (Figure 4.19). The numbers of records per year increased from 2018 to 2020 to 67 (Table 4-17).

Most locations in Quebec are in the Ottawa River and St. Lawrence River watersheds. Bucci (1974) reported the first northern location of CMS in a small lagoon in the public park at Cartierville, Montreal Island, in 1974. Tornimbeni, Galvez, Triffault-Bouchet, Gaëlle, *et al.* (2013) describe the 2009 location (Table 4-17) for Saint Augustin Lake in Quebec City.

Several records are from the maritime provinces, with nine in Nova Scotia, four in New Brunswick, and one in Newfoundland (Table 4-17). McAlpine (2016) describes 13 locations in the three maritime provinces (New Brunswick, Nova Scotia, and Newfoundland).

c. *Cipangopaludina japonica*

JMS has likely established itself in Canada as of July 31, 2020. Perhaps the species is in Canada but has been misidentified as CMS. The differences in shell features between CMS and JMS are subtle. There is wide variation in shell characters of both species among populations (see Chapter VI. Biology, A. External Morphology), making it difficult to distinguish between species. The species is most likely in Lake Erie on the Ontario side because it was recorded in the lake in 1940 in Sandusky Bay, Ohio (USGS 2020b). Also, see comments under 2. Canada, p. 135-6, with respect to many images in iNaturalist (2022).

Table 4-17. Summary of years of data for records of *Cipangopaludina chinensis* in Canada, with repeats shown in parentheses. Provinces are ordered by the greatest number of years of observations. Sources of information are OFHA Database (2009), Tornimbeni, Galvez, Triffault-Bouchet, Gaëlle *et al.* (2013), Brady (2015), McAlpine (2016), EDDMaps (2020), iNaturalist (2020), and USGS (2020a).

Province	Years of Observations (repeats)
Ontario	1996(5), 1997, 2003, 2006, 2008, 2009, 2011, 2012(6), 2013(11), 2014(6), 2015(6), 2016(9), 2017(8), 2018(12), 2019(29), 2020(67)
Quebec	2020(13)
Nova Scotia	1955, 1963, 1990, 2005, 2008, 2014, 2015, 2020(2)
New Brunswick	1999, 2000, 2014(2)
British Columbia	1948, 2019, 2020(2)
Newfoundland	1983

K. Summary of Distribution of Viviparidae in North America

Two subfamilies of viviparids occur in the United States, Lioplacinae and Viviparinae. Two genera represent the Lioplacinae, *Campeloma* with eight species and *Lioplax* with six species. *Campeloma* is native to both the US and Canada, and *Lioplax* is endemic to the US but absent in Canada. The Viviparinae is represented by three genera, *Viviparus*, *Tulotoma*, and *Cipangopaludina*. *Tulotoma* is endemic to North America but found only in the US, not Canada; *Viviparus* occurs in most parts of the world, and *Cipangopaludina chinensis* and *Cipangopaludina japonica* are introduced in both the US and Canada. CMS is widely distributed in the US and Canada but omnipresent only in Southwestern Ontario; it has a limited distribution in BC, Alberta, Quebec, and the maritime provinces. Table 4-18 shows the global distribution of *Cipangopaludina chinensis* (CMS) and *Cipangopaludina japonica* (JMS).

Table 4-18. Summary of the global distribution of Viviparidae, CMS, JMS, *Viviparus* species, and *Bellamya* species.

Continent	**Subcontinent**	**CMS**	**JMS**	***Viviparus* spp.**	***Bellamya* spp.**
Europe	Northern	Denmark		Norway, Sweden, Estonia, Latvia, Lithuania, Denmark	
	Western	Netherlands, Belgium		Ireland, United Kingdom, Iceland, France, Switzerland, Belgium, Netherlands, Germany, Austria	
	Eastern	Russia		Poland, Czech Republic, Hungary, Slovakia, Serbia, Bulgaria, Romania, Moldova, Ukraine, Belarus, Georgia, Armenia, Azerbaijan, Russia	
	Southern			Italy, Croatia, Montenegro, Albania, Greece	
Asia	Northern	Russia		Russia	
	Western			Iran	
	Central			Turkey,	
	Eastern	China, South Korea, Japan	China, Japan	China, South Korea, Japan	
	Southern	India			Afghanistan, Pakistan, India, Bangladesh
	South-Eastern	Burma, Vietnam, Cambodia, Philippines		Burma, Vietnam, Thailand, Cambodia, Philippines, Malaysia, Indonesia, Sumatra, Java	Burma, Vietnam

Africa				Egypt, Africa	Africa
Australia				Australia	
New Zealand				Absent	
South America	Argentina			Argentina	
Caribbean Islands				Cuba	
Central America	Mexico	Mexico		Mexico	
North America	US Canada	US Canada	US	US Canada	

CHAPTER V

BIOLOGY

A. Introduction

This chapter examines the external morphology and internal anatomy of Viviparidae, emphasizing CMS and JMS, referring only to closely related species when information on CMS and JMS is lacking. Most of the biological descriptions are on the internal anatomy of the major systems, including the process of torsion and the digestive, respiratory, excretory, reproductive, circulatory, muscular, and nervous systems. Illustrations are used whenever possible, using images made for this chapter and images from websites and the literature with permissions.

Figure 5-1 provides a diagrammatic overview of the discussions on the biology of CMS and JMS. The external anatomy components are in boldface, and the internal anatomy is in italics. The chapter begins with descriptions of the external morphologies of CMS and JMS. Shell morphology is prefatory because its features are the most used in the identification of the two species. Like the radula and soft anatomy, other body features are also helpful for identifying species but require invasive techniques to isolate the diagnostic characters. All the internal organs compose the visceral hump that is wound around the central columellar pillar. The organ systems are distributed throughout the visceral hump, and their relative positions are not as shown in Figure 5-1.

B. External Morphology

There are two apparent components to the external morphology of prosobranch gastropods: the shell and the operculum. The columella is mostly internal but exposed in the upper aperture wall and somewhat external. For large-bodied viviparids like CMS and JMS, both the shell and operculum are defenses against predators. When the animal is relaxed, other exposed features are the head, tentacles, eyes, and foot.

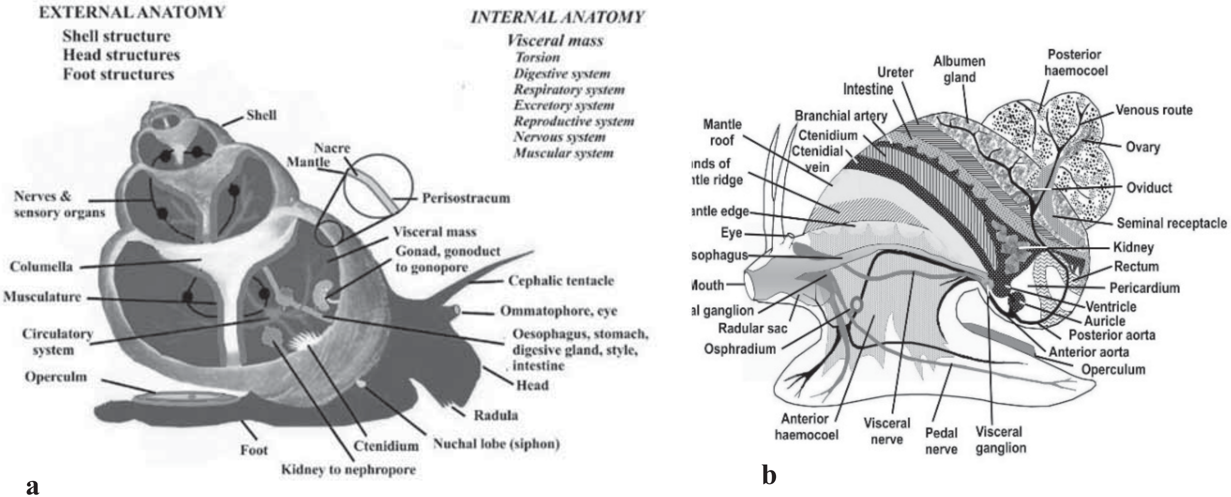

Figure 5-1. (a) Diagrammatic overview of the external and internal anatomies of prosobranch snails as preamble to discussions of the organ systems of the Chinese and Japanese mystery snails. (b) Disposition of major systems and organs of *Viviparus viviparus*, redrawn from Erlanger (1891b).

The head and foot are also part of the external morphology, at least when they are exposed. The head includes the neck with its urinary, reproductive, and anal openings; cephalic tentacles; and eyes. These will be discussed after the “hard parts” of the snails (shell, spire and body whorl, operculum).

1. Shell and Mantle

The shell is composed of calcium carbonate crystals (aragonite) held together in an organic matrix. The inner calcareous layer is enveloped on the outside by the periostracum, discussed in the next section.

The shell is secreted by the mantle, which is a projecting fold of body wall that lines the body whorl of the shell. Hyman (1967, 188-190) gives an excellent and well-illustrated description of the mantle of *Viviparus*. The following paraphrases his account of Neumann’s (1928) studies of *Paludina vivipara* and *P. ceylonica*. The mantle encircles the neck region of the snail, being broad dorsally and reducing rapidly in width around the sides of the neck until ventrally it forms a slight ridge. Posteriorly (i.e., the spire region), the mantle is continuous with the wall of the visceral mass. In addition to its shell-secreting function, the mantle has glandular and sensory actions. It is covered on both sides with the epidermis. On the dorsal surface, it is continuous with that of the visceral mass. On the ventral mantle surface, the epidermis is continuous with the anterior part of the snail’s body. The mantle interior consists primarily of connective tissue, muscle fibers, nerves, and blood lacunae. The mantle epidermis is a one-layered epithelium composed of cells varying from cuboidal to tall columnar (Figure 5-2). On the inner or ventral surface of the mantle, the epidermal cells are interspersed with gland cells.

The ventral mantle epidermis of *Viviparus* is also richly provided with mucocytes, which are transformed from epidermal cells; the transformation of an epidermal cell begins by the vacuolization of the cell, followed by the appearance of granules in the vacuoles and eventual fusion of the into a mucus mass (Figure 5-2a). The dorsal mantle epidermis is generally a cuboidal or columnar epithelium without special differentiations (Figure 5-2b). In *Viviparus* it is thrown into folds near the supramarginal ridge and tubular glands. The gland cells in the folds are believed to function in the secretion of the outer calcareous layers at the mantle edge. The inner calcareous layers are secreted by the entire dorsal surface of the epidermis throughout the snail’s life.

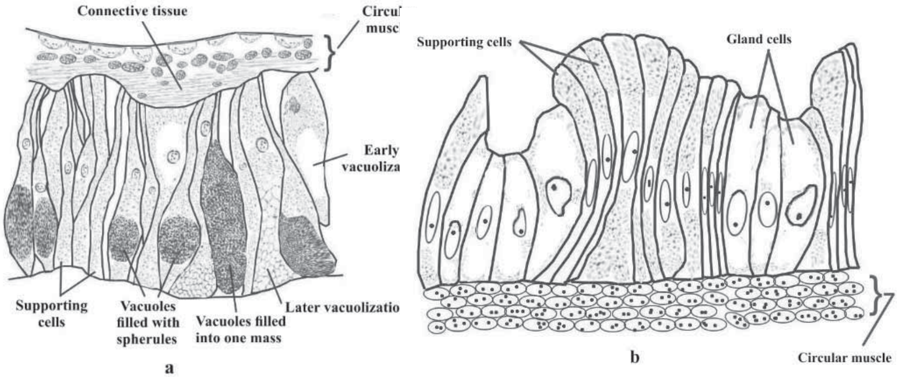

Figure 5-2. Cross section through the (a) ventral epidermis and (b) the dorsal epidermis of the mantle of *Viviparus*. Redrawn from Neuman (1928), (a) from Figure 21 and (b) from Figure 20, both in Plate 5.

A cross-section cut across the calcareous nacre and the growth lines in the viviparids reveal one crossed lamellate layer between two prismatic layers (Figure 5-3a). A cut parallel to the growth lines shows one prismatic layer between two crossed lamellate layers (Figure 5-3b). Aragonite layers are generally lamellate and common in most freshwater molluscs, including bivalves (Mackie 2007). Shells with a crossed-lamellar and prismatic structure are considered an adaptation to high resistance to abrasion due to their high hardness factors; abrasion resistance is considered desirable property in actively burrowing species (Taylor and Layman 1972).

Between the mantle and the rest of the snail body is the pallial mantle cavity. On its under surface, the roof of this cavity is a group of structures called the pallial complex. The complex comprises one or two gills; one or two osphradia; one or more glandular areas, called the hypobranchial gland; and terminal parts of the digestive, excretory, and reproductive systems (Hyman 1967). In *Viviparus*, the hypobranchial gland is composed entirely of granular cylindrical cells (Hyman 1967).

The shells of both CMS and JMS are highly variable regarding shape and surface features. Figures 5-4 and 5-5 show the essential features of the shell and operculum of CMS and JMS, respectively. There are four views of the shell: the front, or apertural view (Figures 5-4a, c and 5.5a); the rear, or abapertural view (Figures 5-4b, d and 5.b); the view from the top, or the apical view (Figure 5-6b, d); and the basal, or umbilical view (Figure 5-8). In living specimens, the apertural view shows the operculum and umbilicus, which is where the upper lip of the aperture joins the body whorl.

The gastropod shell has several features that are used for the identification of species, including its color, the number of whorls, type of nuclear whorl, type of sutures, type of umbilicus, shell height to shell width ratio (H:W), shell ornamentation, shell shape, spiral angle, apical angle, aperture shape, aperture lip configuration, and the operculum. Shell shape, spiral angle, and apical angle are discussed next under 2. Spire and Body Whorl. Figures 5-4 to 5-13 illustrate features of CMS and JMS in the following discussion. Many of the images are extracted from photographs of the two species in iNaturalist (2020).

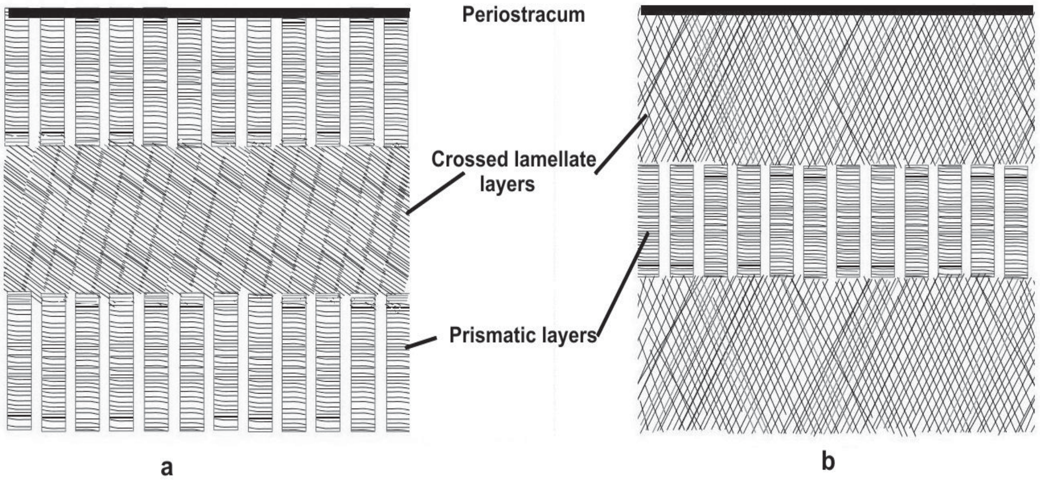

Figure 5-3. Aragonitic nacre showing a diagrammatic (a) cross section across the growth lines, and (b) parallel to the growth lines. Redrawn from Hyman's (1967) Figures 64A and 64B.

The difficulty of distinguishing certain genera of molluscs by their shells alone and on the anomalies concerning environmental influences is a “shell game” and has been long recognized (Gray 1835) as problematic. So it should not be surprising that considerable controversy exists regarding the distinction between CMS and JMS based on shell features. Some believe that there is no distinction and only one species, *Cipangopaludina chinensis*, occurs in North America, and they synonymize *C. japonica* with it (e.g., Dundee 1974; Clarke 1978, 1981), or refer to JMS as a morph of CMS (Jokinen 1982). Clench and Fuller (1965), who first described and illustrated differences in shell morphology between the two species, convinced many that both CMS and JMS occur in North America (e.g., Wolfert and Hiltunen 1968; Burch 1982; Taylor 1981; Jokinen 1982, 1984, 1992; Bury, Sietman, and Kams 2007; Perez 2016; USGS 2018; Kipp, Benson, Larson, and Fusaro 2020). Clench and Fuller (1965) distinguish between the two species (CMS, 404, 406; JMS, 401, 402)) using the following bulleted shell characteristics (in “quotes”), with my rebuttals or agreement following, based on Figures 5.4 to 5.13.

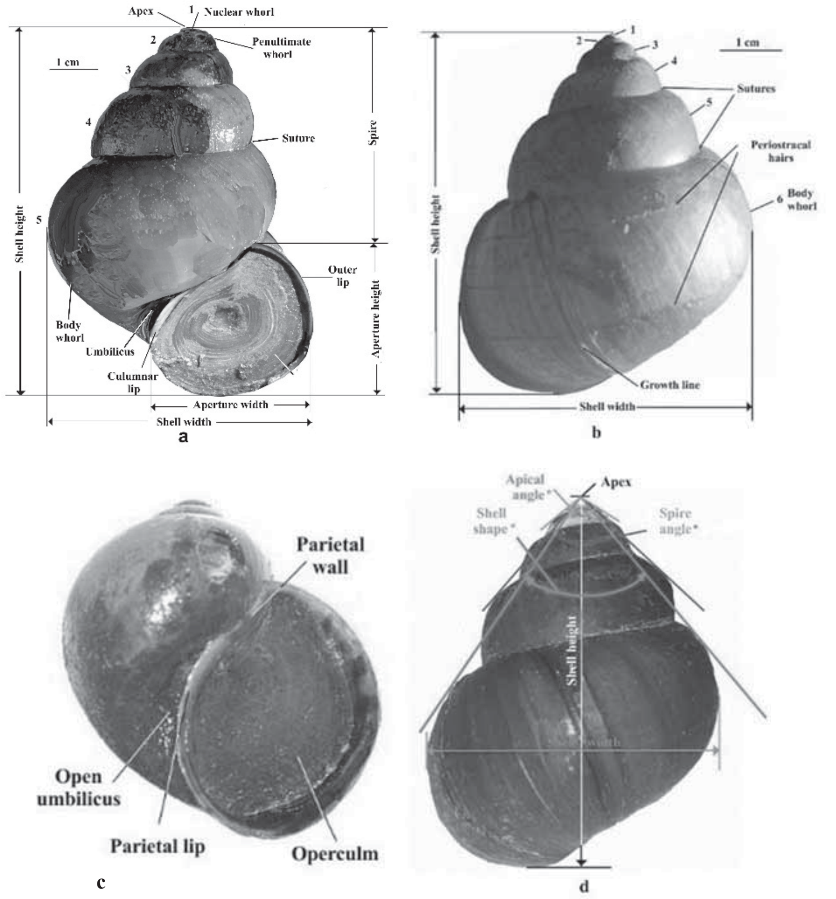

Figure 5-4. Chinese Mystery Snail: (a) Apertural view showing five whorls, aperture, operculum, umbilicus, and shell dimensions. (b) Abapertural view showing six whorls, periostracal hairs, and shell dimensions. (c) Umbilicus is open to parietal wall. (d) shell dimensions and angles illustrated (see text for details). (a, b, d) are GLM images; (c) extracted from photo 2764764 by Hyuntae Kim, Appendix C.

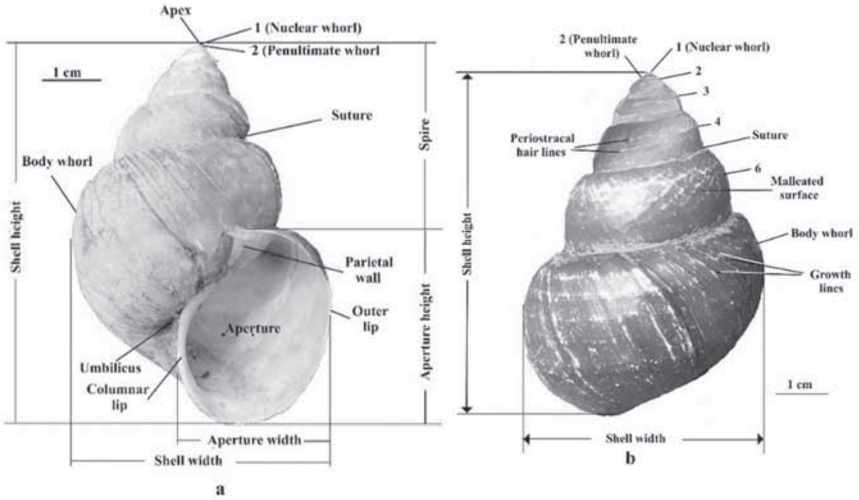

Figure 5-5. Japanese Mystery Snail. (a) Apertural view showing seven whorls, aperture, operculum, umbilicus, and shell dimensions. (b) Abapertural view showing seven whorls, periostracal hairs, malleated surface, and shell dimensions. Images are courtesy of Brian Watson.

a. Chinese Mystery Snail (refer to Figures 5-4a-d, 5-6 to 5-10, and 5-13)

- “Shell globose in outline, with some variation in size, large specimens reaching about 60 mm (~ 2.4 inches) in height”. Specimens likely attain a height of 7 cm based on a 6.7-cm high specimen reported by “kenkneidel” in iNaturalist (2020). Burch (1982) describes viviparids as subglobose to turreted and globosely conic as having a shell shape of 70^o angle, with many CMS having $70\text{-}75^o$ angles, e.g., Figure 5-4b, d; Figure 5-4d has a spire angle of $\sim 85^o$.
- Height:width ratios of four specimens range from 1.28-1.46, mean = 1.35 (Clench and Fuller 1965, 406). A random selection of specimens examined on iNaturalist have shell height:width ratios of 1.4, 1.15, 1.31, 1.24, 1,35, 1.22, 1.4, 1.15, 1.31, 1.24, 1.35, 1.27, 1.16, 1.17, 1.20, 1.17 = 16.27/13 = Mean of 1.25 (St. Dev. = 0.083) based on personal specimens and specimens in iNaturalist (2020). David and Cote (2019) found 1.0 to 1.1 for CMS from the Adirondacks, New York. Chiu, Chen, Lee, Chen, et al. (2002) found H:W ratios of 1.29, 1.20, 1.35, 1.30, 1.33 for CMS from four lakes in Taiwan and one in Japan. Range in H:W ratios is between 1.0 and 1.4.
- “Small, round umbilicus covered in part by the reflected parietal lip”. Umbilicus in Figure 5-4a is small, pinched, and closed at the junction with body whorl, but the umbilicus in Figure 5-4c opens onto the parietal wall.
- “Thin in structure, rather strong and smooth”. Some have pronounced rest rings on the body whorls, e.g., Figure 5-10.
- “Color a uniform light to dark olive-green, without any bands”. Color is varied (see Figures 5-6 and 5-7): some brownish, some blackish (Figure 5-8), some with rust-colored deposits on many whorls (e.g., Figure 5-10).
- “Whorls 6 to 7, strongly convex and generally with a very slight shoulder”. Five whorls occur on specimens with truncated apex and the nuclear whorl (protoconch) depressed within the penultimate whorl, e.g., Figure 5-7a. Those with six whorls often have the protoconch raised, e.g., Figure 5-6; if protoconch is elevated to a point, seven whorls are usually present, e.g., Figure 5-6g. Most whorls are strongly convex (Figure 5-6e-h).
- “Spire moderately extended and produced at an angle of 65° to 70°”. Some have angles between 70 and 85^o. Spire is mostly pointed (Figures 5-6a-h).

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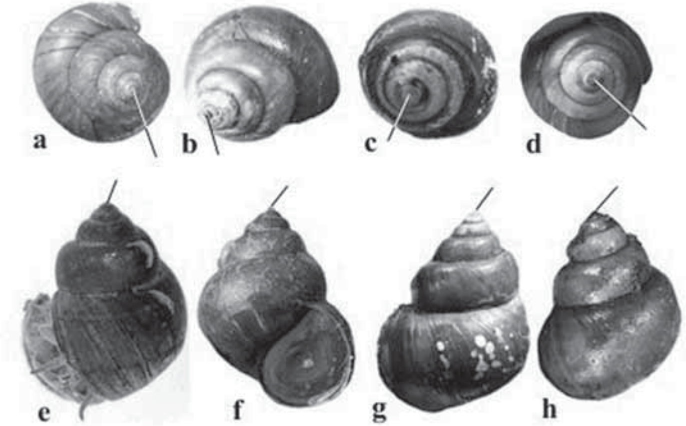


Figure 5-6. Chinese Mystery Snail with an elevated protoconch. (a-d) Apical views of the protoconchs. (e-h) Abapertural and apertural (f) views of the apex. Arrows are pointed to the protoconchs. All images are extracted from iNaturalist, April 15, 2021. (a) extracted from photo 64525033, by Threelark; (b) extracted from photo 91446580, by Andrew Sebastian; (c) extracted from photo 88941454, by Elissa Totin; (d) extracted from photo 33156571, by Mathew; (e) extracted from photo 5663472, by Hyun-tae Kim; (f) extracted from photo 41028454, by Marcus Rosten; (g) extracted from photo 92633223, by Elliot Greiner; and (h) extracted from photo 92618707, by Andrew Sebastian. See Appendix C for sources.

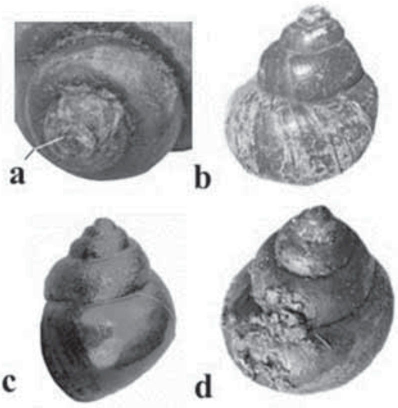


Figure 5-7. Depressed protoconchs of the Chinese Mystery Snail. (a) apical view. (b-d) abapertural views. (a) extracted from photo 49557225, by Alexis Williams; (b) extracted from photo 17466617, by Robert T. Jackson; (c) extracted from photo 2734482, by Hyun-tae Kim; and (d) extracted from photo 5663472, by Hyun-tae. See Appendix C for sources.

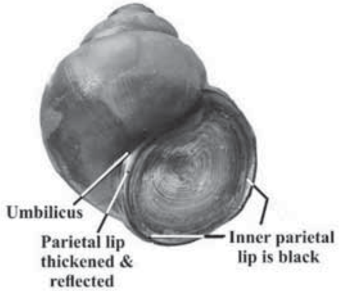


Figure 5-8. Chinese Mystery Snail with characteristic black inner lip margin and thickened parietal lip. Image courtesy of Jamie Delaney.

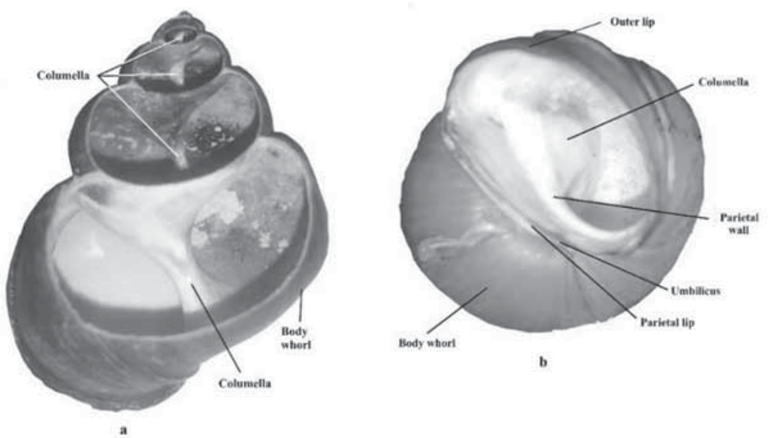


Figure 5-9. Columella of the Chinese Mystery Snail. (a) Abapertural cut out of the shell exposing the columella. (b) Umbilical view of columella. GLM images.

Figure 5-10. Growth rest rings on Chinese Mystery Snail in abapertural view. Shell extracted and modified from photo 92302990, by Andrew Sebastian. See Appendix C for source.

- “Aperture is subovate and virtually holostomatous”. Aperture is entire (holostomatous) and somewhat horizontally subovate (e.g., Figure 5-4a).
- “Outer lip very slightly reflected; parietal lip slightly reflected and thickened, especially over the umbilical area”. Columnar lip (= parietal lip) is thickened and reflected in Figure 5-8.
- “Entire lip and a short distance within the aperture, colored black”. Best visible in empty shells or with operculum withdrawn into the shell (Figure 5-8). Not present on all specimens.
- “Columella narrow and arched”. Arched mainly between body whorl and spire, thick in body whorl, thin in the spire (Figure 5-9a); the base of the columella is visible in umbilical view (Figure 5-9b).
- “Suture deeply indented”. See Figures 5-4a, b, 5-6, and 5-9a.
- “Sculpture consisting of fine growth lines, spiral lines, and fine to moderate malleation over the entire surface”. Many have heavy growth rest lines (e.g., Figure 5-10). Malleations are not common.
- “Occasional specimens show older reflected lips as fairly strong axial ridges; others may have one or more spiral threads developed into slight carinae”. The ridges are likely developed during growth resting periods (Figure 5-10).
- “Operculum corneous, thin, with concentric growth lines, and a sub-marginal nucleus”. The nucleus appears more subcentral than sub-marginal, deeply indented (e.g., Figures 5.4a, 5-6f, 5-8, 5.13a-d). In CMS, the opercular pad is larger than its base on the dorsal foot surface (Lu, Du, Li, and Yang 2014). Zhang and von Rintelen (2021, 9) examined the opercular characteristics of 38 species and 25 viviparid genera and characterized the CMS with “a concentric inverted-comma-shaped operculum by the following combination of characters: regular growth lamellae on the exterior surface, relatively small inner operculum region and a large nuclear region with a sandpaper-like layer (sometimes partly absent).”

b. Japanese Mystery Snail (refer to Figures 5-5a, b and 5-11 to 5-13).

- “Shell somewhat extended, varying in size, large specimens reaching 65 mm (~ 2½ inches) in length”. Some hobbyists claim shells can be as large as 75 mm (3 inches) in height.
- “Rimately umbilicate” (refers to a narrow umbilical opening that is partially closed by the expansion of the anterior columellar lip;

see Burch 1982), as in Figure 5-5a. Shell relatively thin in structure, strong and smooth.

- "Color olivaceous green to dark brownish-green, without banding". Some specimens are coated with algae or rust-coloured deposits; colors range from brown and dark green to black.
- "Whorls 7 to 8 strongly convex, with a smoothly rounded shoulder and a moderate carina below the suture, often with faint carinae above and below the periphery". Carinae are more pronounced in upper whorls of the spire; shoulders are more angulate below the sutures of the spire (Figures 5-11, 5-12). Post-birth juveniles show strongly angulated, early whorls; subadults show an angulated base of the body whorl (Van Bocxlaer and Strong 2016). Nuclear whorl is bulbous (Figures 5-11, 5-12a) in juveniles, curled in adults (e.g., Figure 5-12b).
- "Spire extended and produced at an angle of some 50^o to 55°". Some have up to 65^o angle.
- "Aperture subovate. Outer lip thin. Parietal lip consisting of a thin glaze". Aperture is somewhat vertically subovate (Figure 5-5a).
- "Outer columella narrow and arched". Clearly visible in images examined.
- "Suture deeply indented. Sculpture of fine to coarse growth lines and a few fine spiral threads". Many specimens exhibit faint malleations, particularly on the earlier whorls. Malleations are pronounced in Figure 5-5b as if tapped with a hammer diagonally between faint carinae.
- "Operculum corneous, thin, with concentric growth lines and a sub-marginal nucleus". Nucleus is deeply indented. Compare opercula of CMS in Figures 5-13a–c to those of JMS in Figures 5-13d–f; the operculum appears more vertically oriented in JMS than CMS.
- Has "a height:width ratio of about 4:3, which indicates a degree of globosity roughly equal to the of the more globose *V. chinensis malleatus*". A random selection of specimens in iNaturalist (2020) examined have shell height:width ratios of 1.38, 1.33, 1.31, 1.38, 1.44, 1.39, 1.52, 1.50, 1.36, 1.48 = 14.09/10 = Mean of 1.41 (St. Dev. = 0.072), compared to 1.33 (4:3) in Clench and Fuller (1965, 404).

Several other studies have examined the utility of shell characters for distinguishing CMS from JMS, including Smith (2000); Chiu, Chen, Lee, and Chen (2002); Van Bocxlaer and Strong (2016); and David and Cote (2019). Smith (2000) analyzed shell characters (and radulae and soft anatomy, discussed later) and found the shape of the spire and the presence of carination to be the principal shell characters distinguishing the two species. Still, they apply only to specimens 35–45 mm in shell height. Below 35 mm shell height, both species have a carina on the body whorl. Smith (2000) attributes the source of the differentiation in the two species to the allometric growth pattern described by Jokinen (1982), wherein the shell width in JMS increases at a slower rate than in CMS. Hence JMS has a sharper spire. However, while the regression slopes for each species are significantly different ($P < 0.05$), they are only slightly different and primarily undetectable to the human eye. While Smith (2000) found limitations in using adult shell morphology to distinguish between CMS and JMS, he did find the morphology of the intra-uterine juvenile shell with three distinguishing features: (a) differences in the position of the embryonic whorl (nuclear whorl or protoconch), (b) presence of periostracal hairs encircling the shell whorls, and (c) presence of carinae in the body whorl.

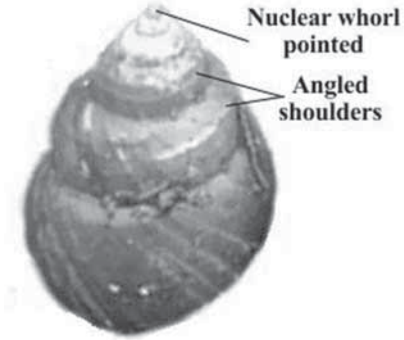


Figure 5-11. Abapertural view of Japanese Mystery Snail with pronounced angulate shoulder on spire (whorls 1–6). Image extracted and modified from photo 7266575, by Judy Gallagher. See Appendix C for source.

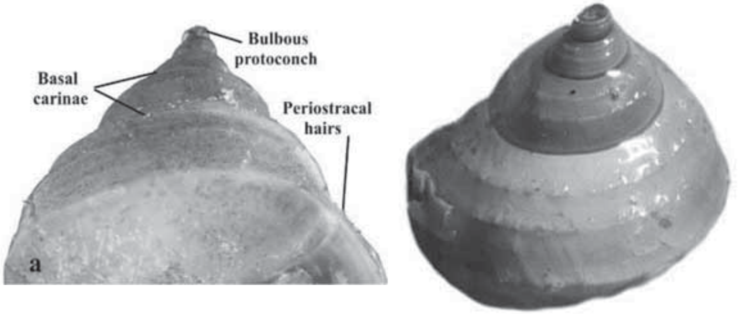


Figure 5-12. (a) Nuclear whorl bulbous in a juvenile Japanese Mystery Snail. (b) Protoconch curled in adult shell. (a) extracted and modified from image 16406 of Robert Aguilar of SERC; and (b) extracted and modified from photo 47691926, by Steven Bodzin, see Appendix C for source.

Pace (1973) and Brandt (1974) recognized the ambiguities associated with using simple descriptions of morphological characters or biogeographic information to distinguish CMS from JMS. Chiu, Chen, Lee, and Chen (2002) took a robust approach and examined the overall performance of morphological variations in the shell and operculum to illustrate the significant shell characters in delineating the two species. They used morphometric measurements and multivariate statistics of specimens from different geographic regions that comprise the distribution of subspecies or species of *Cipangopaludina*. For CMS, the essential taxonomic characters are spire height, shell width, and shell shape. But these traits can be confounded by intrinsic and extrinsic factors. The primary inherent cause of taxonomic confusion in gastropods is allometric growth, especially during the juvenile stage. The gross morphology of juvenile shells of some species of viviparid snails is so similar that they can only be separated using scanning electron micrographs of shell morphology and shell structure of bristles and lobes formed on embryonic and juvenile shell stages. Chiu, Chen, Lee, and Chen (2002) examined four populations of CMS in Thailand: wetlands and barrier lakes in a volcanic area characterized by low pH and soft water as well as two from reservoirs with higher pH and calcium content. They attributed extrinsic environmental conditions to induce variations in the shell shape of snails, such as low-calcium (< 2 mg Ca/L) and acidic environment ($pH < 5.8$); both states had shorter spiral portions that they explained as a constraint of growth. Dissolved apical pieces of shells were also commonly observed in specimens from the low pH lakes.

Controversy also existed with shell sexual dimorphism in *Viviparus* species. Differences in sizes were documented for *Lioplax subcarinata occidental* by Van Cleave and Chambers (1935) and *C. chinensis* by Chiu, Chen, Lee, and Chen (2002). Many attributed the more considerable size differences in female *Viviparus* to differences in reproductive age and selection of larger females for increased brood size and brood viability (Van Cleave and Lederer 1932; Jokinen, Guerette, and Kortmann 1982; Brown, Varza, and Richardson 1989; and Jakubik 2006). Brown, Varza, and Richardson (1989) found females twice as large as males in *Viviparus subpurpureus* and *Campeloma decisum*. For *V. subpurpureus*, Minton and Yang (2011) found differences were most pronounced in the inflation of the body whorl and the width of the aperture in female. They proposed these morphological differences may be adaptations for brooding due to female brooding their young in the pallial oviduct located on the right side of their body. However, Falniowski, Kozik, Szarowska, Fialkpwski, *et al.* (1996), in their shell analyses of both sexes in five European *Viviparus* species (*V. acerosus*, *V. ater*, *V. contectus*, *V. hellenicus*, and *V. viviparus*) concluded no significant shape differences between the sexes. They concluded that there was no shell sexual dimorphism in *Viviparus*.

Lu, Du, Li, and Yang (2014) analyzed shell features and anatomy of several systems to separate 18 species of *Cipangopaludina*, including *C. chinensis*, in China, and reduced the diversity to 11 species and 2 subspecies. Their analyses indicated that body whorl depth, shell width, aperture width, and aperture length were the main variables separating species of *Cipangopaludina*. Forty specimens of CMS that Lu, Du, Li, and Yang (2014) analyzed had a pointed apex, six to seven whorls, narrow sutures, a narrow or closed umbilicus, no sculpture except growth lines and axial undulations, a subcircular aperture, and a whitish-blue inner lip and a black or brown outer lip. The specimen illustrated has an H:W ratio of 1.32. Young specimens from the brood pouch had up to four whorls, a smooth protoconch, and three primary rows of chaetae (periostracal hairs) on the last whorl and two on other whorls. The operculum occupied the entire shell aperture. The center was brown and the outer parts were greenish. Then, there was a sub-central nucleus located closer to the inner margin as well as concentric growth lines that occupied about two-thirds of the opercula area.

Van Bocxlaer and Strong (2016) examined Japanese and North American specimens of JMS. They found the early teleoconch (the portion of a shell formed immediately after the protoconch stage) with a bluntly angular basal carina and two periostracal ridges with long hairs (e.g., Figure 5-12a). There was some variation in the apical angle of the teleoconch. Numerous fine growth lines became more prominent with age, giving the adult shell a fine network texture.

In agreement with Van Bocxlaer and Strong (2016), subadult shells of JMS have a pronounced basal angulation that becomes less conspicuous with age; early whorls usually display two prominent ridges that lie close together, whereas later whorls do not (Figure 5-11). As in Figure 5-11, the sutures become more deeply impressed, the shoulder more rounded, and the whorls more inflated as the shell grows. In both Japanese and American specimens that Van Bocxlaer and Strong (2016) examined, they found seven similarities:

(1) A high spire

(2) A spiral angle ~84° in juveniles and ~74° and ~68° in adult females and males, respectively

(3) The shape of the adult aperture was large and ovate, narrower adapically, with a well-rounded base

(4) A parietal callus but not very pronounced

(5) An open umbilicus

(6) An operculum that was corneous, sub-pyriform, thick, slightly translucent, brown, thicker and darker at the parietal and columellar margins than at the outer margin

(7) Concentric growth lines, faster at the outer margin, resulting in a subcentral nucleus (e.g., Figure 5-13f–i)

Figure 5-13 compares shells and opercula of both CMS and JMS. Shells and opercula are shown for both sexes of JMS. No images could be found for both sexes of CMS. Only two female and three male shells with opercula are shown. Opercular dimensions are similar for both sexes of JMS and similar to CMS. While more specimens need to be examined for both sexes of both species, the opercular dimensions are not likely a diagnostic feature of use to separate the species.

David and Cote (2019) used genetic evidence to confirm the presence of the Japanese Mystery Snail, *Cipangopaludina japonica* in northern New York. They examined some shell morphometrics for both CMS and JMS. They concluded that using conchological comparisons, both species were virtually indistinguishable from each other. For *C. japonica*, the number of whorls ranged from five to seven, all with relatively low angulations. The aperture possessed a thin operculum with concentric growth rings; both *C. japonica* and *C. chinensis* collected from the Adirondacks were almost indistinguishable conchologically, with the only variable character being a slightly more extended spire in some *C. japonica* specimens. In addition, *C.*

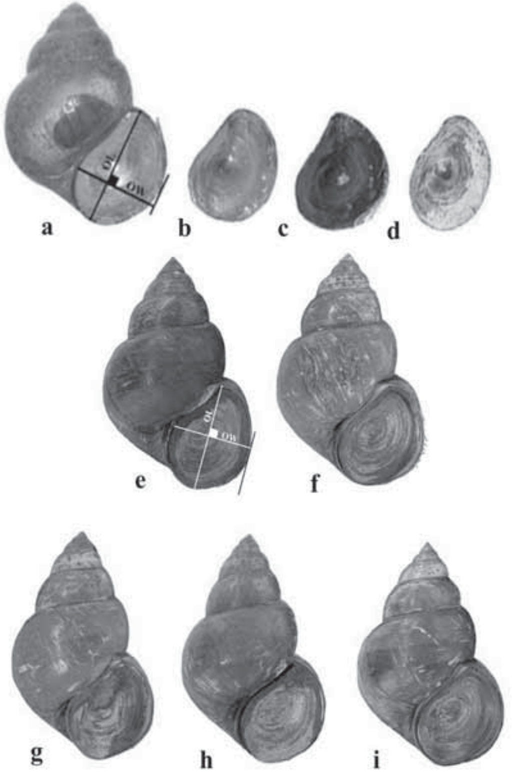
japonica had a marginally higher SL/SW ratio (1.2–1.3) than *C. chinensis* (1.0–1.1). They concluded that using conchological comparisons both species were virtually indistinguishable from each other. Although *C. japonica* appeared to have a slightly more elongated spire than *C. chinensis*, this trait still appeared highly plastic even within *C. japonica*.

2. Periostracum

The periostracum, made of a protein called conchiolin, gives the snail its color and texture. Besides acting as a substrate for mineralization and crystal growth, the periostracum also has a protective function. Chiu, Chen, Lee, and Chen (2002), in their study of four populations of CMS in Thailand, each in different levels of calcium and pH, found that specimens had deposited a thicker periostracum than in snails of populations in lakes with high pH (pH > 7.0) and high calcium (> 20 mg Ca/L). The mantle edge is where growth and secretion of the calcareous (aragonite) nacre occur and the periostracum's conchiolin.

Many images of CMS in iNaturalist (2020) have conspicuous rows of periostracal hairs, some so heavy that they are bristle-like (e.g., Figure 5-14d). In specimens with periostracal hairs, the numbers of rows of hairs range from one to three on the body whorl and one to two on the bottom spire whorls. Shells in Figure 5-14a–c are from the same pond but have different shell heights, a = 42.4 mm, b = 39.3 mm, c = 30.3 mm, indicating the hairs are gradually lost with age. The size of the shell in Figure 5-14d is not known.

Kessel (1933) examined the microscopic structure of the periostracum in larval shells of *V. viviparus* and *V. fasciatus*. The periostracum of the larvae consists of three longitudinal ridges, which run parallel with the whorls, and arising from bulges, are hairs (called appendages by Kessel) of various thicknesses (Figure 5-15, modified from Figure 1 of Kessel (1933)). Between the longitudinal ridges of hairs are parallel rows of varying thickness spaced at fairly regular intervals. The lighter ridges have shorter hairs than the darker rows (Figure 5-15). The ridges of hairs are only found on the embryonic periostracum of *V. viviparus*, while that of *V. fasciatus* has tiny hairs only visible on microscopic examination. Perpendicular to the ridges of hairs are thin, longitudinal whitish bands that divide the periostracal surface into large and small rectangles (Figure 5-15, shown within the large and small circles). According to Kessel (1933), the field of the periostracal surface that Biedermann (1901) interpreted was impressions of mantle epithelial cells in the periostracal groove. Kessel (1933) found faint to no traces of this sculpture in the periostracum of older shells. Kessel



Shell & operculum dimensions
(H/W):
(a–d)
Cipangopaludina chinensis
(a) 6.51/4.90;
OL/OW:
(a) = 1.37
(b) = 1.32
(c) = 1.25
(d) = 1.43

(e–i)
Cipangopaludina japonica
(e-f) Females:
H/W; OL/OW
(e) 6.75/4.67;
1.26
(f) 6.80/4.61; 1.38

Figure 5-13. Opercula of each of the Chinese Mystery Snail (a–d) and Japanese Mystery Snail (e–i). OL = operculum length, OW = operculum width at right angles to OL. Side bar gives dimensions of shell and opercula. (a) extracted from photo 2764764, by Hyuntae Kim; (b) extracted photo 33329610, by Quinten Wiegersma; (c) extracted from photo 41028454 by Marcus Rosten; and (d) extracted from photo 30220864, by David McCorquodale. (e–i) images courtesy of Dr. Bert Van Bocxlaer. See Appendix C for sources of images (a)-(c).

(1933) believes the lack of the periostracal sculpture in older shells is explained by the environmental factors because specimens of *V. viviparus* raised in undisturbed aquaria kept rows of hairs for a longer time.

The purpose of the periostracal hairs and bristles is speculative. They are not found on all specimens in a population, suggesting it is not an intrinsic trait, but it may be an individual trait, like hairiness on humans; nor are they found on specimens from many populations, suggesting it is not a species' inherited trait. The periostracal hairs occur on different age classes within a population, but some have one row (Figure 5-14a, Figure 5-16, column C), some have two rows (Figure 5.14b, Figure 5-16, column G), some have three rows (Figure 5-14c, Figure 5-16, column E), and some have none (Figure 5-16, column B). The specimens in Figure 5-16 are from a fishpond that went anoxic one winter, and many specimens, including all those in Figure 5-16, died, but at least three survived, and a new generation appeared. The female shown in Figure 5-14b has two rows of periostracal hairs. The two males have none. Perhaps the bristles are offensive to predators, although only juveniles would likely be prey items to ducks and fish. Perhaps they aid in trapping filamentous algae that are grazed by other snails (e.g., Figure 5-14e) because they cannot graze shell-attached algae on their shell. Shell-attached algae are a nutritious food source and often contain substantial amounts of omega-6 fatty acids that enhance the growth of CMS (Fujibayashi, Ogino, and Nishimura 2016).

One other purpose may be that the rows of hairs act as Velcro strips that aid in dispersing hirsute snails. Most modern birds have pennaceous feathers, stalks with vanes containing a high number of flattened barbs connected with barbules, much like in Velcro strips. Prum and Brush (2002) describe the pennaceous portion of a feather vane with distal barbules oriented toward the tip of the feather and the proximal barbules oriented toward the feather base. The hooked pennulae of the ends of the distal barbules extend over the upper surface of the vane (Prum and Brush 2002), which may offer an opportunity for hirsute snails to attach to the feather and be transported elsewhere. The snails would likely withdraw into their shells, leaving the operculum to prevent desiccation over long-distance dispersal (LDD) while the hairs keep the snails attached.

The periostracal hairs do not appear to be as common in JMS. Jokinen (1982) suggests their function is likely intra-uterine to stabilize the snail's position in the uterus, but this does not explain the bristles on adults (see Figures 5-14c, d). The scarcity of periostracal hairs on JMS may explain the limited distribution relative to CMS.

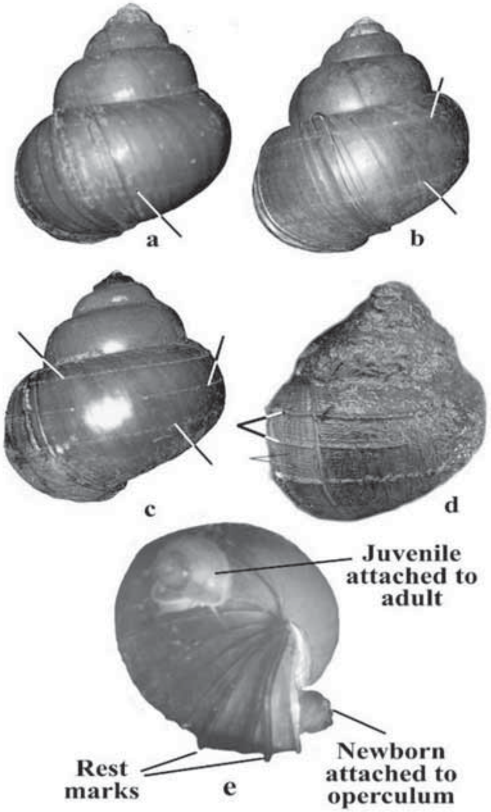


Figure 5-14. Chinese Mystery Snail with heavy rows of periostracal hairs (a) one row, (b) two rows, (c) three rows and (d) large arrows show thick rows of bristles, small arrows fine rows of hairs, all indicated with lines; (e) juvenile snail grazing on shell of mother. (a-c, e) GLM images; and (d) photo 41028439 by Marcus Rosten, see Appendix C for source.

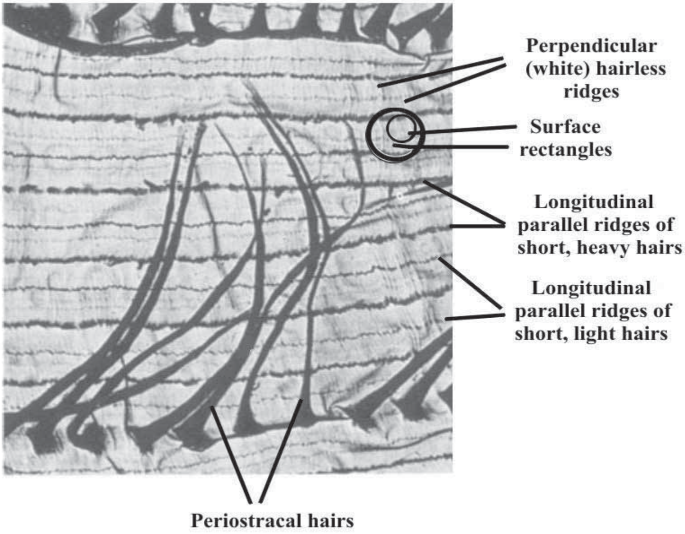


Figure 5-15. Surface sculpture of the embryonic periostracum of *Viviparus viviparus*. Extracted and modified from Figure 1 of Kessel (1933). Circles enclose two sizes of squares delimited by perpendicular and longitudinal ridges.

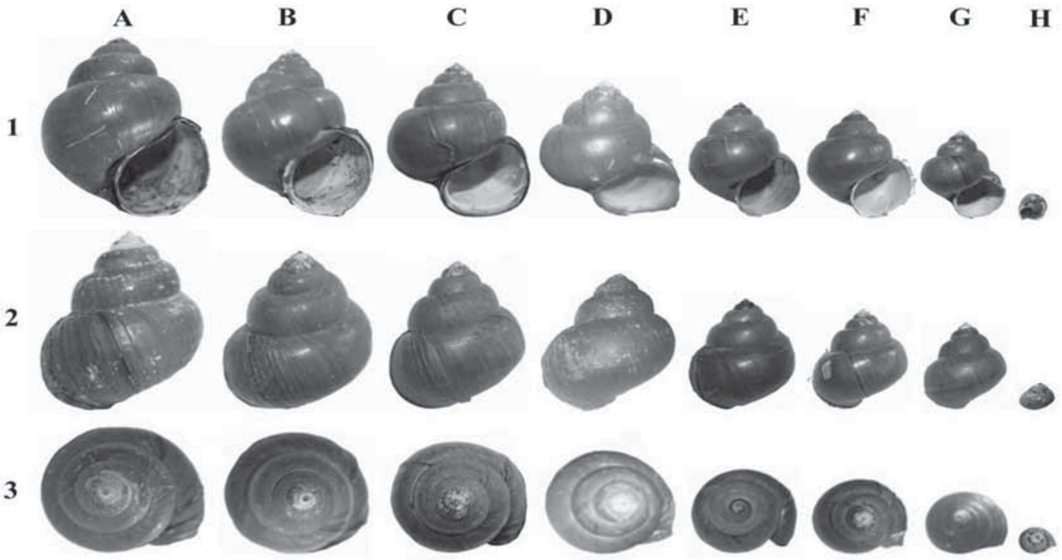


Figure 5-16. Range in size classes of the Chinese Mystery Snail that perished from anoxia in a fishpond (see text). Apertural views in top row (1), abapertural views in middle row (2), and apical views in bottom row (3). Each column of snails (A to H) has the same dimensions in height/width (cm) for 1 to 3. A: 45.0/37.3; B: 42.4/35.7; C: 39.3/33.6; D: 35.8/32.0; E: 30.3/27.4; F: 29.4/25.5; G: 27.5/23.7; and H: 9.4/9.3. GLM images.

3. Spire and Body Whorl

The spire consists of all the whorls, except for the body whorl. The top whorl is the nuclear whorl, or protoconch, which is the first whorl of the embryonic shell and represents the apex. Each spire whorl represents a rotation of 360°. When the aperture opens on the right with the apex up and the aperture facing you, the shell has dextral (clockwise) coiling; when the aperture opens on the left, it has sinistral (counterclockwise) coiling. In freshwater snails, only one family, Physidae, has counterclockwise coiling, although in some dextral families (e.g., Viviparidae), reversed whorls occur, such as in *Campeloma crassulum* (Bickel 1966).

The shell shape, spiral angle, and apical angle are illustrated in Figure 5-4d. Shell shape is used here as the angle formed between two lines drawn from the largest diameter of the body whorl through the apex. The spiral angle is often defined as the angle formed by imaginary lines tangent to the spire. Imaginary lines can be subjective, and Figure 5-4d shows the spire angle as the angle formed between two lines running from the outermost surface of the bottom spire whorl (usually 5th) through the apex. The apical angle is the angle formed between two lines running from the outer surfaces of the penultimate whorl through the apex.

4. Neck

The neck forms the floor of the mantle cavity. In JMS, the neck is modified on the right into a tall, broad cervical lappet or nuchal lobe near the urinary pore on the right (Van Bocxlaer and Short 2016). In the Viviparidae, the right nuchal lobe is curved and serves as a siphon (Hyman 1967). Nerves innervate the nuchal lobes from the pleural ganglia. Other openings on the right of viviparids are the anus and the female gonopore at the right side of the mantle cavity, just behind the thick, muscular mantle edge. Otherwise, the neck is a muscular conveyor shaft for conveying food from the mouth to the stomach and nerves and blood from the visceral mass into the head.

5. Head

The head of viviparids is bilaterally symmetrical and bears a pair of mobile and contractile cephalic tentacles that are long and slender in females. The right cephalic tentacle of males is modified into a penis with a terminal gonopore. As such, the right tentacle of males is shorter and thicker and more curved than the right one. The outer base of and fused with each cephalic tentacle is a short peduncle (ommatophore) that bears a terminal eye (Figure 5-17a). The head is prolonged beyond the base of the tentacles into a contractile snout that bears a ventral mouth (Figure 5-17a). In CMS, the snout is cylindrical with a flat anterior margin, and the length of the tentacles is about 1.3 times longer than the snout length. The ommatophore is short, located between the basal and middle third of the outer surface of each cephalic tentacle (Lu, Du, Li, and Yang 2014). The mouth is located on the ventral side of the head (Figure 5-17a). The radular complex is extruded beyond the mouth opening to rasp food from substrate surfaces. The radula is discussed under Internal Anatomy, section a) 2.

6. Foot

The foot is a muscular mass on the ventral part of the body best visible when it is fully extended (Figures 5-17a, b). The anterior part of the foot is called the propodium; the middle part, the mesopodium; the posterior part, the metapodium. It has a highly glandular organization with ciliated epithelial cells alternating with mucocytes. The sides and dorsal surface of the foot are covered with non-ciliated, cylindrical epidermal cells, occasionally interspersed with mucocytes (Hyman 1977).

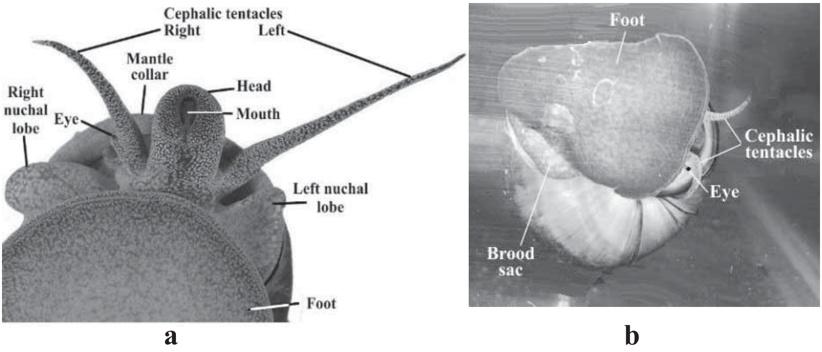


Figure 5-17. Ventral views of the Chinese Mystery Snail. (a) foot, head, tentacles, nuchal lobes extended, extracted and modified from photo 5663950, by Hyun-tae Kim, see Appendix C for source; (b) foot, brood sac, and tentacles of a female CMS, GLM image.

In CMS, the foot is a broad, muscular organ that forms the ventral part of the body and merges dorsally with the head and visceral mass (Figure 5-17a). In JMS, the foot is a broad, muscular mass with a long, shallow pedal gland along the anterior portion of the foot (propodium) (Van Bocxlaer and Strong 2016). The posterior end of the foot bears an operculum on its dorsal surface (Figure 5-1).

7. Operculum

Three morphogenetic types of opercula are recognized in gastropods: 1) multispiral (or a flexiclaudent variety), as in Valvatidae, which is secreted when the operculum is not in a closed position and fits by flexing into the whorl; (2) paucispiral, as in Amnicolidae; (3) concentric, as in Viviparidae. The latter two types (rigiclaudent varieties) grow in the aperture-closed position and fit snugly into the whorl (Checa and Templado 1998). Checa and Templado (1998) state that concentric opercula evolved several times from spiral opercula, both of which broaden the spectrum of shells using opercula for protection.

In viviparids, the operculum is first visible on brood-sac embryos and is situated above the foot and at the posterior end of its body. The dorsal surface of the metapodium secretes it. It consists of chitinous (but not chitin) layers in all viviparids (Hyman 1967). The aperture is sealed by the operculum, or trap door, which may be at the aperture or slightly withdrawn into it. The operculum is brought into the shell to close the aperture by the contraction of the columella retractor muscle to which it is attached. The insertion point usually leaves a single scar upon the inner operculum around the nucleus (Hyman 1967). In viviparids, the operculum is oval with concentric lines of growth and subcentral to a sub-marginal nucleus (Figure 5-13). It is somewhat flexible and sits on an opercular pad that is larger than the operculum in CMS (Lu, Du, Li, and Yang 2014). The soft pad likely provides a seal behind the operculum when pulled tightly into the aperture.

The operculum has three essential functions in gastropods: (1) it allows snails to resist desiccation during periods of drought and dry weather; (2) it protects the inner calcareous layer from erosion by acidic inputs (e.g., pH depressions during spring spate events in circumneutral waters), toxic chemicals, and short-term anoxia; and (3) it is protection against predators, like leeches (Kelly and Cory 1987). The operculum of CMS and JMS is composed of relatively thick corneous protein (conchiolin), is yellow to brownish, and when detached, it is usually somewhat translucent. The operculum grows in size as the shell grows such that it remains in proportion to the apertural dimensions.

8. Summary of the External Morphology

To help distinguish between JMS and CMS using external morphology, Table 5-1 lists the characteristics that, used in combination, may help separate the two species. The table is based on information in Clench and Fuller (1965); Burch (1982); Jokinen (1982); Smith (2000), Lu, Du, Li, and Yang (2014); Chiu, Chen, Lee, and Chen (2002); Van Bocxlaer and Strong (2016); and David and Cote (2019). It appears the most valuable characters to separate the two species are adult shell shape, H:W ratio and angle of the spire, number of whorls, and periostracal hairs on spire vs. body whorls.

Table 5- 1. Utility of some external morphology features to distinguish between the Chinese and Japanese mystery snails.

External Morphology	**Chinese Mystery Snail**	**Japanese Mystery Snail**	**Useful?**
Shell shape	Usually pointed apex; sub-globose to globose; shell height up to ~6.7 cm (2.6 in.)	Pointed apex; extended; height up to ~6.5 cm (2.6 in.)	Yes, for adults only
Shell spire	Acute, H:W ratio ranges from 1.13 to 1.40, mean = 1.25	Acute, H:W ratio ranges from 1.31 to 1.48, mean = 1.41	Yes, for ratios between 1 and 1.30
Carinae	Spiral angulations often present but only on the upper whorls of the spire	All whorls often with spiral angulations or carinae, but all post-birth shells with distinct carinae on the base of the body whorl	Yes
Umbilicus	Narrow, open or pinched closed	Pronounced, open to closed	No
Shell structure	Thin but strong	Thin but strong	No
Shell color	Light to dark olive-green, some black	Light to dark olive-green	No

Whorls	Usually 6, some 5 or 7; nuclear whorl often depressed; spire whorls mostly rounded, some acutely rounded; some malleated	7–8, nuclear whorl bulbous; spire angulate with shoulders or carinae; some malleated	Yes, for whorl number
Periostracal hairs	Common, often 3 rows on body whorls, 1–2 on others, some bristle-like	Uncommon, usually fine hairs	Yes if present
Spire angle	Usually 65º–70º, maximum 85º	50º–55º, maximum 60º	Yes
Aperture	Subovate, entire	Subovate, Upper outer lip reflected	No
Operculum	Somewhat horizontally subovate; nucleus deeply indented	Somewhat vertically subovate; nucleus deeply indented	No

C. Internal Anatomy

This section examines the significance of the internal systems and their components in determining the potential of CMS and JMS to establish themselves under a range of ecological conditions. It is a preamble to the tolerances and requirements of the two species discussed in the next chapter. Much emphasis has been placed on the phylogeny of gastropods and has elucidated significant findings on their evolution under certain ecological conditions. Some systems have received more significant attention than others, with elaborate accounts of specific characters or components. The internal anatomical characters reviewed here include analyses of the radula in the digestive system; ctenidia (gills) in respiration and feeding: renopericardial (kidney) structures of the excretory system: sperm ducts, sperm, and spermatogenesis in reproduction; the nervous system; sense organs (tentacles, osphradia); and early development.

1. Torsion

The entire torsion process occurs in the larval stage, discussed in detail in Chapter V, B. Internal Anatomy, 1. Torsion, using *Viviparus viviparus*, which has received considerable study (e.g., Simroth 1881; Erlanger 1891a, b; Auerbach 1896; Butschli 1876, 1887; Taylor 1900; Drummond 1902; Anderson 1928; Wolper 1950; and Hyman 1967). This section deals with the effect of torsion on the configuration of the visceral mass and its components in prosobranchs, especially viviparids.

All prosobranchs undergo a process of torsion during embryonic development. The configuration of all the internal systems is directly or indirectly due to torsion, or the twisting of organ systems, especially the nervous system, into a figure eight. This torsion results in a 180° rotation of the shell and viscera relative to the head and foot of the veliger. Snails that have undergone torsion are referred to as "torted."

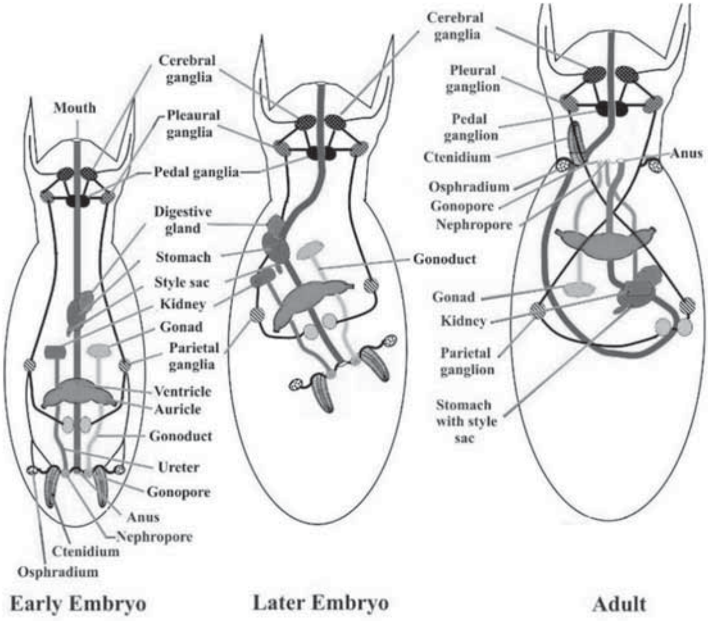
Spengel (1881, pp. 372–375) was the first to recognize this peculiarity in prosobranchs and coined the terms Streptoneura (from Greek *streptos* = twisted and *neûra* = nerves) and Euthyneura (from Greek *euthys* = straight and *neûra* = nerves). The terms embrace the classification of gastropods (see Table 2-4, in which Streptoneura is a subclass). Streptoneura expresses the condition of the 180-degree rotation of the visceral mass while head and foot remain fixed (Figure 5-18), and that of the Euthyneura remains untwisted. As Spengel (1881) pointed out, the Euthyneura condition is a character of the primitive mollusc (e.g., the freshwater bivalve *Margaritifera margaritifera*), which is the typical arrangement of the head and its mouth at the anterior end, and the anus, excretory, and reproductive openings at the posterior end. This primordial condition created a dilemma for spired gastropods, where most of the visceral mass is compressed posteriorly within the spire.

In the same year, Erlanger (1881a, b) gave an account of the coelom and its derivatives in prosobranch snails, which prompted renewed opinions/speculations by numerous people (e.g., Lang 1892; Plate 1896; Butschli 1887; Amaudrut 1898; Pelseneer 1898; Boutan 1899; Guiart 1901; Pelseneer 1911), attempting for an outcome of a theory for torsion. Drummond (1902) examined the various approaches using *Viviparus viviparus* and abridged her views into two classes: (1) those which view the present position of the pallial complex as a forward movement along the right side of the body, which resulted from greater growth of the left side of the body than of the right; and (2) those which consider the current position of the pallial complex is a ventral flexion, which is followed by a vertical rotation of the whole visceral hump upon the head. The latter is more probable because of the preponderance of the evidence showing a vertical displacement through 180°. A ventral flexion of all the organs contained in the visceral hump occurs in the course of ontogeny (Drummond 1902). She concluded from both comparative anatomy and embryology that the esophagus also underwent an actual twist.

The most accepted theory for the adaptive value of torsion appears to be proposed by Garstang (1928); it enables a veliger to retract its head and foot into the shell and subsequently seal the aperture with the operculum. He suggested that torsion evolved as a larval defense through a single mutation, although Pennington and Fu-Shiang (1985) showed that torsion does not function defensively. Garstang (1928) considered that the primitive posterior position of the visceral mass in the larva (see Figure 5-18, early embryo) is disadvantageous in that there is no place into which the vulnerable head, with its appendages, can be withdrawn. He claimed that it is the foot, not the head, that can safely withdraw into the shell, leaving the head, the essential part of the body, exposed to attack. Morton (1958) concluded that torsion, with the resulting forward-facing position of the mantle cavity, offers a great advantage to the adult because the point of entry of the inhalant pallial water current is brought to the foremost position in the forward-moving animal. Morton (1958) reasoned that the current could be tested by the pallial complex (osphradium, hypobranchial gland, gills), which, in association with the adult head's sense organs, presages the environment the animal is moving.

During torsion, the pallial complex undergoes a ventral flexion followed by a vertical rotation of the whole visceral hump upon the head (Figure 5-18, adult). When completed, the direct effect of torsion is to bring the mantle (pallial) cavity to the front of the larval body, thus enabling the head, with its all-important velum, to be safely withdrawn into it at the first onset of danger. The foot and its operculum on its posterior surface, which closes the entrance on contraction, follow (Garstang 1928).

The mantle cavity is in the anterior body whorl and receives the alimentary, renal, and reproductive openings. Lateral cilia create the respiratory current on both sides of the filaments on the axes of the paired ctenidia. The current passes between the filaments in the opposite direction to the flow of blood through the gills. The cilia cleanse the incurrent water and sort and envelope sediment in mucus secreted from hypobranchial glands on the roof of the mantle cavity. The osphradia, which tests incoming water quality, are located where the water current first impinges on the surface of the mantle cavity. The ctenidia, hypobranchial glands, and osphradia form an efficient unit of the pallial complex. The structures and functions of the pallial complex are discussed later under Chapter V, Biology; B Internal Anatomy; 3. Respiratory System. The anus and other openings discharge into the exhalant chamber dorsal to the ctenidia.



Early Embryo Later Embryo Adult

Figure 5-18. Process of torsion and its effect on configuration of major internal systems.

Yonge (1947) supported Garstang's theory on the origin of torsion because it was of immediate advantage to the larva and supported the selection of an original mutation and the nonexistence of partially torted or intermediate forms (Knight 1952; Ghiselen 1966). Although of advantage to the adult as well, the occurrence of torsion presented an immediate problem, that of hygiene, created by the discharge of excrement into the anterior mantle cavity. The hygiene was ultimately restored by the appearance of a marginal aperture; a subsequent withdrawal of the anus, which enabled the exhaled water carrying feces and excreta to bypass the head; sacrifice of the right ctenidium when the left to right respiratory current was established; and the rectum was extended to the margin of the cavity (Yonge 1947). The asymmetry of the pallial organs caused by the asymmetrical coiling of the shell probably followed torsion. The reproductive and renal organs are asymmetrical. The left gonoduct disappeared along with the left gonad, apparently preceding torsion; the right gonoduct opens into the renopericardial canal (Yonge 1947).

While the shell and operculum are the most obvious external features, the radula is the most available character complex in gastropods. In earlier studies, it has been used as a major character in higher classification, the opposite direction to the flow of blood through the gills. The cilia cleanse the incurrent water and sort and envelope sediment in mucus secreted from hypobranchial glands on the roof of the mantle cavity. The osphradia, which test incoming water quality, are located where the water current first impinges on the surface of the mantle cavity. The ctenidia, hypobranchial glands, and osphradia form an efficient sensory unit of the pallial complex. The structures and functions of the pallial complex are discussed later under Chapter V, Biology; B Internal Anatomy; 3. Respiratory System. The anus and other openings discharge into the exhalant chamber dorsal to the ctenidia.

While the kidneys and gonads were paired in the primordial gastropods, one of each organ and the associated pores were lost in the torsion process. Thus, the existing kidney of the prosobranchs corresponds to the definitive left kidney of other gastropods (Erlanger 1891a, b; Drummond 1902). “No gastropod exists with paired gills, auricles, and kidneys without also displaying a complete torsion of its mantle-cavity and shell through 180° from back to front” (Garstang 1928).

The question of how torsion evolved has been examined for many years, and Yonge (1947) summarized with five theories: (1) torsion occurred initially by stages in the adult; (2) torsion occurred in the embryo due to antagonism between the growth of the foot and that of the shell; (3) torsion occurred in the embryo essentially to meet the needs of the adult; (4) torsion occurred rapidly in post-larval life to meet the needs of adult life; and (5) torsion occurred rapidly in embryonic life to meet purely embryonic needs.

Knight (1952), Morton (1958), Ghiselin (1966), Penninton and Fu-Shiang (1985), and Edlinger (1988), among others, have since supported the theory that torsion evolved in a primitive mollusc. Guiart (1901) compared ontogeny and phylogeny and perceived the cause of torsion as not existing in the embryo but in the primitive mollusc. Garstang (1928, 87) capitulated that “the only mutation required to start the torsion in the assumed ancestral pre-gastropod larva was an asymmetry in the development of the retractor muscles, thus bending the head and foot round during contraction.” The ideal muscular arrangement for bringing about complete rotation would consist of a right-sided cephalic retractor with posterior attachment and a left-sided pedal retractor with an attachment in front of the other, the two crossing one another more or less at right angles (Garstang 1928). Hyman

(1967) believed that the asymmetrical pull of the muscles runs from the velar lobes to the larval shell. The muscular mechanism required may be difficult to prove because the torsion process is rapid, from six to eight hours in the primitive Top Snail, *Trochus* (Robert 1903), to two to three minutes in the less primitive limpet, *Acmaea* (Boutan 1885).

Torsion is an all-or-none process; it is either a complete 180º rotation or it does not occur at all. Most gastropods pass through the torsion process or tort. Garstang (1928), convinced by the evidence that the opisthobranchs (sea slugs and sea hares) also tort, believed that an evolutionary process of detorsion, or detort, also occurred. The anus, gill, and kidney, at first in their mantle-chamber, moved back along the right side of the body, reversing the original order of events in the 180º rotation.

Other gastropods do not tort or untort. Garstang (1928) argues that if 10 degrees are used as a reasonable range for each successive stable position in a series of adult rotations, there are 18 different positions in which some snail might reasonably be expected to terminate detorsion. All the unwinding snails have detorted without specific organs of the original left side with which they torted. According to Garstang (1928), every possible stage from complete torsion through partial to complete detorsion for more than the 18 grades is likely represented today by families, genera, and countless species.

2. Digestive System

All snails have a mouth, a buccal mass that houses a cartilaginous odontophore and underlies the radula, a pharynx, an esophagus, a stomach (gastric chamber) with a crystalline style, a digestive gland (liver), an intestine, a rectum, and an anus. The buccal mass consists of the odontophore, radula, and all the muscles associated with each. Thus, all organs are of interest. Some have been studied in detail for CMS and JMS, and the diagnostic features of these are examined in this section. Many other components are similar among prosobranch snails, especially viviparids, and these are reviewed for completeness of the system. The component of particular interest is the radula because it is the first structure that gathers food from the substrate. Viviparids also gather food from the water column using their ctenidia, a process described later under V.B.3. Respiratory System.

Differences in the digestive systems of viviparids, including CMS and JMS, exist and are described and nicely illustrated by Streneck and Watling (1982); Rao (1989); Ponder and (1997); Smith (2000); Katuno and Sasaki (2008); Lu, Du, Li, and Yang (2014); and Van Bocxlaer and Strong (2016), among others. Detailed descriptions of each of the systems, with illustrations, would require a tome. The studies mentioned above are recommended for those interested in the details. Emphasis is placed here on the components that distinguish CMS and JMS (and other Viviparidae) from other families of gastropods. The studies that reveal more striking differences are digestive, respiratory, excretory, reproductive, nervous, muscular, and physiological systems.

a. Radula

The shell and operculum are the most obvious external features, but the radula is also an available complex for study in gastropods. Earlier studies have used the radula as a major character in a higher classification, as reflected in names like Stenoglossa, Rachiglossa, Architaenioglossa, and Taenioglossa (Ponder and Lindberg 1997).

The radula of viviparids is of the taenioglossid type. It has seven teeth in each row: one middle (rachidian) tooth, flanked on each side by one lateral and two marginal teeth. They function like rakes, first scraping algae and then assembling the resultant mass. For CMS and JMS, the radula is used as a rake, generally to scour up microscopic, filamentous algae from a surface. Radular apparatus is present throughout the taenioglossids (Hyman 1967; Anistratenko, Ryabceva, and Degtyarenko 2013).

The mouth opens into a pocket-like buccal cavity, containing the radular sac, an evaginated pocket in the posterior wall of this cavity. The radula apparatus consists of a cartilaginous odontophore with its protractor and retractor muscles and the radula protractor and retractor muscles (Figure 5-19). The odontophore is movable and protractible. The radula itself is movable on its membrane over the odontophore. Through this action, the radular teeth become erect at the tip of the odontophore. The tip of the odontophore scrapes the surface while the teeth cut and scoop up the food and convey the particles through the pharynx and esophagus to the digestive tract. These activities continually wear down the forward teeth. New teeth are continuously generated at the posterior end of the buccal cavity in the radular sac. They are slowly brought forward to the tip by a slow forward advancing of the ribbon, replaced in their turn when they are sloughed off. The teeth of the radula are lubricated by mucus of the salivary gland. Food particles are trapped in the mucus, lubricating the progress of food into the pharynx and esophagus.

The radula is produced in the radula sac. A new basal membrane and new transverse rows of teeth are continually added at the posterior end throughout the snail's life. Teeth production is rapid, some species generating up to five rows per day. The radular teeth are produced by odontoblast cells in the radular sac. According to Ponder and Lindberg (1992, 142), “The radular teeth are typically not formed until shortly before hatching. They are secreted from transverse bands of odontocytes proliferated from odontoblasts in the distal end of the radular sac, bands of odontocytes separated by transverse bands of membranoblasts that produce the radular membrane.”

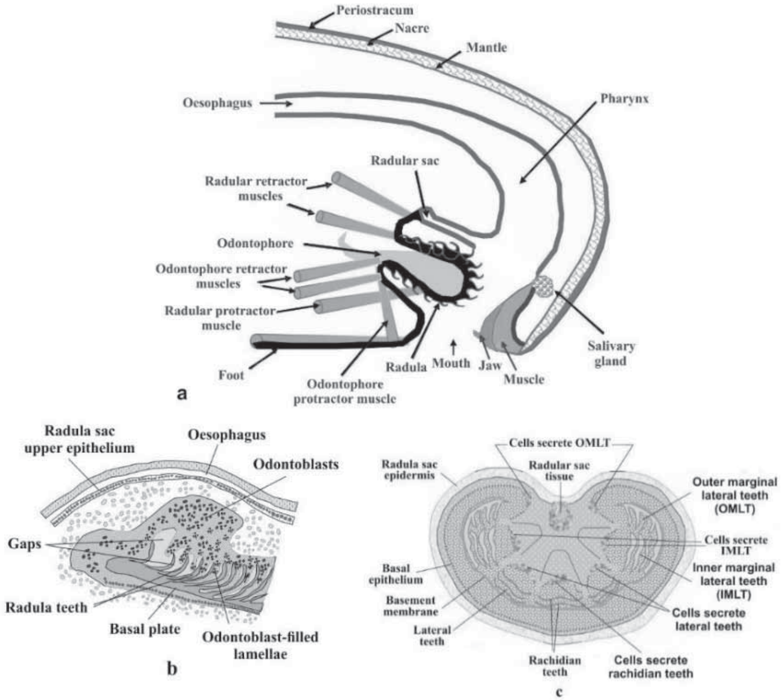


Figure 5-19. (a) Structures involved in the operation of the radula and odontophore in the mouth of gastropods. (b) Longitudinal section through the posterior end of an embryo of *Viviparus viviparus*, drawn from Figure 8 in Bloch (1896). (c) Cross-section through the radular sac of *V. viviparus*, drawn from Figure 16 in Rossler (1885).

Bloch (1896) describes the embryonic development of the radula of *V. viviparus* in detail, with illustrations. Figure 5-19b is a longitudinal section through the radula in its later development in *V. viviparus*. Bloch described tooth formation as an abundant secretion of chitin by cells deep in the lamellar-like extensions (Figure 5-19b). The radular sheath pushes the already formed parts forward in the upper part, where secretion does not yet take place as quickly, and lifting from the cell base takes place. The small teeth are separated separately and only fuse afterwards; Figure 5-19b shows a tooth that has just become detached from the odontoblasts, being carried away by the advancing basal plate. Figure 5-19c, drawn from Figure 15 in Rossler (1885), is a cross-section through the radular sac of *V. viviparus*; it shows a hemispherical bulge protruding from the posterior wall of the epithelial diverticulum, with the odontogenic cell groups corresponding to the seven-tooth plates typical of viviparids. The bulge creates the teeth of the middle row, while the adjoining groups take care of the separation of the somewhat smaller intermediate plates. The upper cell complexes are responsible for forming the narrower hook-like teeth attached to the radula's outer edge. These edge plates do not encompass the associated cell groups from the front like the other teeth but more from the side.

The radula has numerous longitudinal rows of chitinous and recurved teeth; each tooth is divided into three sections: a base, a shaft, and a cusp (Figure 5-20a). The tooth base is attached to the underlying cuticular ribbon, the number of teeth present depending on the species and may number more than 100,000. Thus, the greatest number of teeth per row is over 200 teeth, 100 on each side of the rachidian (Hyman 1967).

The arrangement of all radula teeth in a row has a formula; for taenioglossid radulae, the formula is 2 – 1 – R – 1 – 2 (Figure 5-20a). The diagnostic features for each species are the numbers of denticles on each cusp; the radular formula for the teeth and denticles on the left side is number of marginal teeth / number of cusps / number of lateral teeth / number of cusps, the rachidian (median) tooth / number of cusps and repeated for the right side. The shape and arrangement of the radular teeth adapt to the functional feeding capabilities of the species (Steneck and Watling 1982).

Figure 5-20b shows a transverse row of the radula of the Chinese Mystery Snail, drawn from Jokinen (1982). The two marginal teeth have seven denticles; the two inner lateral teeth have a large middle cusp and four smaller cusps on each side of it; the two outer lateral teeth have a large pointed middle cusp and three smaller cusps on each side of it; and the rachidian has a large rounded middle cusp and four smaller cusps on each side of it. The radula formula for the Chinese Mystery Snail reported by

Jokinen (1982) is 1/7, 2/9, 1/9, 2/9, 1/7. Lu, Du, Li, and Yang (2014) give a somewhat different description of CMS from China, the major difference being two lateral teeth (inner and outer) reported by Jokinen (1982) and two marginal teeth (inner and outer) reported by Lu, Du, Li, and Yang (2014). Lu, Du, Li, and Yang (2014) describe the rachidian as wide with rounded major cusps and four smaller triangular cusps on each side; the lateral tooth has a tongue-shaped major cusp and three minor denticles on each side; the inner marginal tooth has a tongue-shaped major cusp and three minor cusps and the outer marginal teeth with 10 almost equal-sized cusps. They did not provide a figure of the radular teeth. Lu, Du, Li, and Yang (2016) reported that the radula formula is 2/7-10, 1/7, 1/9, 1/7, 2/7-10.

Van Bocxlaer and Strong (2016) provide detailed images of the radula for JMS, a drawing of which is shown in Figure 5-20c. The two outer marginal teeth have slightly broader shafts than the inner marginals and are slightly bowed outwardly toward the base, with a broadly rounded cutting edge bearing eight cusps of more or less similar size and shape, but decreasing somewhat in size toward the outer edges; the two inner marginal teeth are more asymmetrical than the lateral teeth, with long slender shafts and a cutting edge with one large, rounded median cusp flanked by two inner and three outer smaller cusps; the two lateral teeth are similar in width but longer than the rachidian, somewhat asymmetrical, and with a more prominent central cusp than the rachidian, flanked by two very small cusps and six or seven larger cusps; the rachidian is flanked by tiny and larger inner cusps, and by one or two small and four larger outer cusps. Thus, for JMS, the radular formula is 2/8-11, 1/13, 1/16-18, 1/8-11, 1/13, 2/8-11.

Park, Jeong, Jung, and Chung (1997) report the same radular formula for each species as 1,10,11,1,11,10,1. However, based on their Table 2 of the cusp arrangements on the single rachidian tooth, the two inner laterals, two outer laterals, and the two marginal teeth that lack a middle cusp, their formulae are as follows: for CMS from three sites: 0/11, 1/6-10, 1/8-12, 1/10, 1//8-12, 1/6-10, 0/11; for JMS from one site: 0/11, 1/6-8, 1/8-12, 1/10-12, 1/10-12, 1/8-12, 1/6-8, 0/11. The difference between the two species was the number of cusps on the rachidian tooth, 1/10 for CMS and 1/10-12 for JMS.

Hickman (1980) summarizes the set of radula processes as (1) secretion by odontoblasts of new teeth posteriorly on new radular membrane; (2) anterior migration, shaping and hardening (tanning, mineralization) by superior epithelial cells anterior to the odontoblasts; (3) recruitment into the actively working portion (working bend) of the mechanism; (4) progressive breakage and wear; and (5) detachment at the anterior end coupled with anterior detachment and disintegration of the radular membrane.

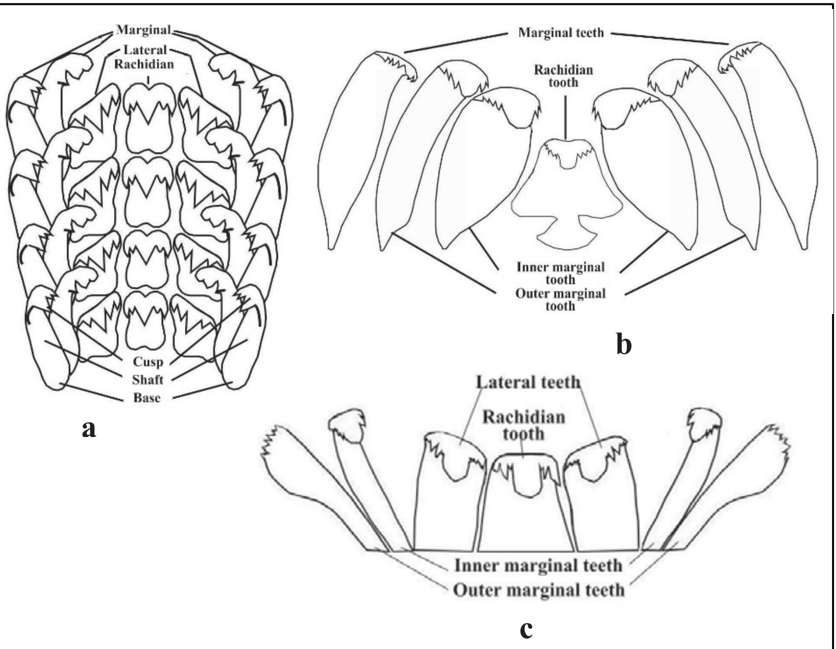


Figure 5-20. (a) Four rows of a taenioglossid radula, each tooth with a cusp, shaft, and base. (b) Radula of the Chinese Mystery Snail. Drawn from Figure 3 in Jokinen (1982). (c) Radula of the Japanese Mystery Snail, drawn from Figure 7 in Van Bocxlaer and Strong (2016).

b. Odontophore

Hickman (1980) and Katsuno and Sasaki (2008) describe the odontophore as "odontophoral cartilage" that consists of single or paired cartilages that are fused or unfused. The odontophore of CMS consists of a single pair of unfused cartilages (Katsuno and Sasaki 2008). The unfused pair is shown in Figure 5-21a, drawn from Katsuno and Sasaki (2008). While Figure 21a shows the two cartilages as mirror images of each other, side by side, the cartilages overlap each other as shown in Figure 5-21b, which was traced from a cross-section through the two plates shown in FIG. 6C of Katsuno and Sasaki (2008). Each cartilage is wrapped in a thin membrane and underlies the radular membrane. The odontophore controls the radula's eversion and retraction. The radula moves forward using a protractor muscle and backward by a retractor muscle. The numbers of muscles in a species depend on the type of feeding activity.

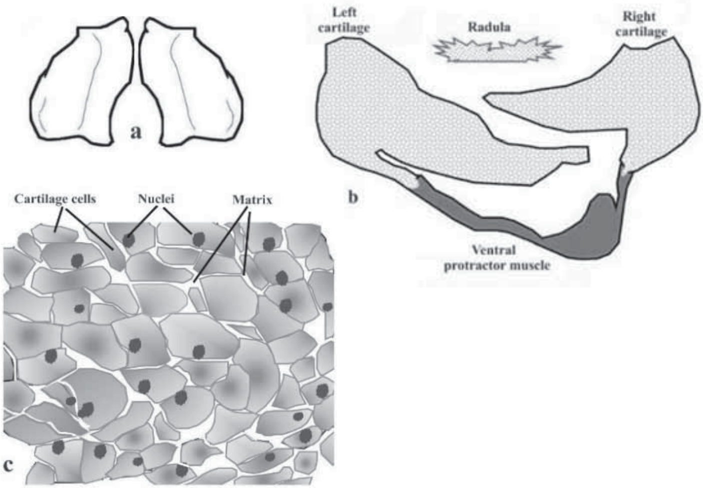


Figure 5-21. Odontophore structure of the Chinese Mystery Snail. (a) One pair of cartilages. (b) Orientation of left and right cartilages with respect to radula and the ventral protractor muscle. All figures are drawn from images in Katsuno and Sasaki (2008), a = FIG. 1D; b = FIG. 6C; c = FIG. 6D.

The cartilages are closest and are connected ventrally by a single-layered ventral approximator muscle inserting at the outer lateral side in CMS. The right cartilage overlies the left cartilage (Figure 5-21b). The cartilages are closest and connected ventrally by single-layered ventral approximator muscle inserting at the outer lateral side (Katsuno and Sasaki 2008). Most cartilages show similar histology with stiffened matrix and cartilage cells containing small nuclei that tend to be located close to the matrix. The odontophore of CMS has a thin matrix, cartilage cells, relatively large nuclei mostly in contact with the matrix; Figure 5-21c is a schematic sketch of FIG. 6D in Katsuno and Sasaki (2008), showing an enlarged view of odontophoral cartilage. The morphological characters (e.g., number, composition, histology, extent of overlapping) of the odontophore appears to be phylogenetically constrained, not ecologically constrained (Katsumo and Sasaki 2008), implying that the odontophore is similar in all Japanese Mystery Snails.

c. Feeding and Digestion

Having explained all the parts of the feeding apparatus, Graham (1973) describes feeding in prosobranchs as a rhythmical process comprising a series of events cyclically repeated. First, the snout is lowered to the substratum and several rasping cycles occur; at the end of a feeding, the snout is raised from the substratum. Graham (1973, 122) describes several phases for each cycle though all unite into one continuous movement: "(1) the mouth opens. (2) the odontophore is protracted and its tip is protruded through the mouth near the ventral lip. (3) the sub-radular membrane is pulled outwards over the tip of the odontophore so that a small number of rows of radular teeth are carried over the bending plane and erected. (4) the tip of the odontophore is moved anteriorly (dorsally) over the surface of the substratum. (5), whilst this is occurring, the sub-radular membrane and radular teeth are retracted over the tip of the odontophore and bending plane so that they close and rasp the substratum; (6) the odontophore is withdrawn. (7) the mouth closes. In addition, movements of the jaws (where present) take place so that they are pressed over the odontophoral tip or lifted free of it. (8) the food, which has been collected, is swallowed."

d. Esophagus

Both CMS and JMS display the effects of torsion, seen at the mid-esophagus region, where the continuation of the esophagus containing its dorsal folds and dorsal, ciliated food groove, is twisted into a figure eight. The anterior esophagus emerges from the dorsal posterior side of the buccal apparatus and forms a simple tube bearing the dorsal folds and dorsal food groove. The esophagus is commonly lined with short to tall ciliated columnar epithelium containing mucocytes, both of which aid in transferring food into the stomach. Side pouches and glandular expansions may or may not be present in viviparids, depending on the species (Hyman 1967).

In the Chinese Mystery Snail, the esophagus has a pair of dorsal, longitudinal folds, about 1.5 times of buccal mass length. It runs along the hypobranchial gland to the posterior of the columellar muscle, where it then turns right and passes upwards in the floor of the pericardial chamber. After it reaches the digestive gland in the upper part of the visceral hump, it curves around to open into the stomach (Lu, Du, Li, and Yang 2014). The esophagus is inserted in the posterior gastric extremity. It gradually enlarges and curves toward the left. The stomach abruptly expands, becoming almost as wide as its whorl, the posterior narrows without clear separation with the intestine (Lu, Du, Li, and Yang 2014).

According to Van Bocxlaer and Strong (2016), in the Japanese Mystery Snail, the esophagus walls between the dorsal folds bear fine, irregular longitudinal ridges. They describe the mid-esophagus as continuing posteriorly as a simple tube in a central position, slightly to the right of the food groove, with no side pouches or glandular elaborations. It deflects slightly toward the right at the posterior part of the mantle cavity to continue posteriorly along the columellar aspect, passing below the renopericardial complex; the posterior esophagus is finely longitudinally ridged and widens substantially just before opening ventrally to the posterior gastric chamber.

e. Stomach (Gastric Cavity, Gastric chamber)

The stomach wall is thin and non-muscular, the passage of food instead being performed by cilia. In viviparids the anterior part of the stomach contains an array of ciliated grooves and ridges that form a sorting area; it also contains two longitudinal ridges, the major and minor typhlosoles or ciliated furrows that direct currents into the intestine. The stomach has an anterior invagination, the style sac, that usually contains a crystalline style in viviparids (Figure 5-22a). The style sac is lined by a uniform layer of ciliated columnar epithelium (Figure 5-22b). The action of the cilia causes the style to rotate on its longitudinal axis, generally in a clockwise manner. As the style is formed, it is simultaneously rotated and pushed forward by powerful cilia of the style sac (Mackintosh 1925). Food from the esophagus is pulled into the stomach on a mucus string wrapped around the head of the rotating crystalline style (Figure 5-22a). An area of the body wall of the stomach is protected by a chitinous gastric shield secreted by epithelial cells of the stomach wall. In *Crepidula* the style substance consists principally of globulin and contains an amylolytic enzyme. According to Mackintosh (1925), the crystalline style and style-bearing region of *Crepidula* resemble in great detail those of certain bivalves in terms of the shape, proportions, and structure of the style sac, typhlosoles, and intestine; of the presence of a gastric shield; and the form, composition, and function of the style (see Figure 5-22b, a cross-section through the style sac of *Musculium* in Mackie 2007)).

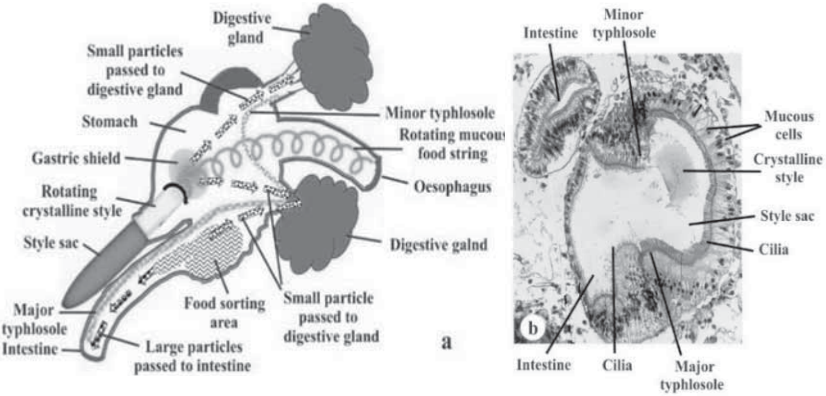


Figure 5-22. Food processing from the esophagus to the stomach in viviparids. (a) Rotating crystalline style brings food from esophagus to the crystalline style where enzymatic digestion occurs, and the large and small particles are sorted and passed to the digestive gland or the intestine. (b) Section through the gastric cavity and style sac showing the crystalline style (from Figure 1.24b in Mackie 2007).

In JMS the non-muscular, thin walls of the stomach have a prominent T-shaped ridge that separates a deep, concave, cuticularized style sac pocket (Van Bocxlaer and Strong 2016). The style sac is about 1.5 times the length of the stomach and forms a voluminous undivided sac. It bears two ventral typhlosoles that traverse its length. At the distal end of the style sac, the typhlosoles turn sharply to the left before continuing anteriorly through a 90° angle, with two shallow pyloric caeca elaborated between the curves. A crystalline style appears to be absent in JMS (Van Bocxlaer and Strong 2016).

Purchon (1977) attributes several functions to the crystalline style that are relative to the digestive process: (1) the style pulls food into the stomach faster than the action of cilia of the esophagus; (2) it stirs the general contents of the stomach and passes the particles to the sorting area where unsuitable particles are rejected and passed ultimately to the rectum; (3) it gently rubs the contents of the stomach against the gastric shield; and (4) the style slowly dissolves, releasing into the stomach the amylolytic enzymes that were secreted and incorporated into the substance of the crystalline style in the style sac. These enzymes initiate a preliminary phase of extracellular digestion in the stomach. The dissolution of the style acidifies and lowers the viscosity of the mucoid contents of the stomach.

The processing of the food in the stomach is illustrated in Figure 5-22a. The food sorting area separates larger particles for rejection through the intestine and passes on smaller ones to the brownish digestive gland (liver). The minor and major typhlosoles (Figure 5-22b) create currents that direct digestible food to the digestive gland and less digestible food to the intestine (Hyman 1967).

The stomach of CMS is located halfway posterior to the pallial cavity, the posterior half immersed in the thin-walled digestive gland, as shown in Figure 5-23a, which is drawn from Figure 2B of Lu, Du, Li, and Yang (2014). In JMS, the stomach occupies most of the body just behind the elongate pericardium, lying embedded in the lobes of the digestive gland. Figure 5-23b–d is derived from Figure 4B–D of Van Bocxlaer and Strong (2016). Figures 5-23c, d show the albumen gland emerging from the right, posterior stomach wall to form a ridge along its floor near the right of the esophageal opening. A single digestive gland duct opens to the gastric chamber floor about midway along the left side of the glandular pad. A transverse limb crosses the stomach floor in front of the esophageal aperture and bears the gastric shield and style sac to its right (Figures 5-23b, c). Two sorting areas are present in JMS. A larger one is developed in the left stomach floor and roof anterior to the esophageal opening and extends anteriorly to the intestinal tract; at the right is a smaller, narrower sorting area to the left of the gastric shield (Van Bocxlaer and Strong 2016).

In JMS, and not well described in the literature or shown in Figure 5-22, are several longitudinal folds in the stomach, but these are well illustrated by Van Bocxlaer and Strong (2016). They show two folds in the left side of the larger sorting area, a prominent outer longitudinal fold and a smaller inner one; two additional longitudinal folds border the larger sorting area on the right and extend posteriorly from near the proximal end of the major typhlosole; the two folds on the left side of the larger sorting area merge to form a single fold that crosses from left to right at the front of the esophageal opening and continues posteriorly to the right of the digestive gland duct. JMS has a small sorting area that extends posteriorly on the left side to the rear wall of the stomach. It has another longitudinal fold that emerges in the stomach floor at the level of the digestive gland duct. At the rear of the stomach, this longitudinal fold and those on the left side of the glandular pad curve around the base of the glandular pad into the roof, merging and terminating at the right posterior end of the glandular pad, behind the gastric shield (Van Bocxlaer and Strong 2016).

Within the stomach roof of JMS is a series of flattened finger-like ridges that extend from the prominent outer longitudinal fold to the left side of the main sorting area. The ridges begin as small undulations at the anterior tip of the longitudinal fold, gradually elongating and broadening, spanning the roof and extending onto the stomach floor behind the gastric shield at the right side of the glandular pad. At the left, anterior end of the main sorting area, the weak inner left longitudinal fold's expanded tip delimits a shallow gastric pouch. The division between the stomach and the style sac is demarcated by a constriction (Van Bocxlaer and Strong 2016).

f. Digestive Gland (Liver, Hepatopancreas, Midgut Gland)

The digestive gland of viviparids dominates the greater part of the visceral mass. The gland is lobulate, has numerous tubules or acini, and opens into the stomach by several ciliated ducts. The gland has granular cells (digestive cells) that are tall cells with bulging free ends and cytoplasm filled with granules and vacuoles and often contains fat droplets (Hyman 1967). Other cell types (e.g., calciferous cells with calciferous spherules) may be present but have not been reported in viviparids. Calcareous spherules have been reported in *Pomacea paludosa* in the mantle tissues, which function in regenerated shell formation. The calcium spherules in the digestive gland are reportedly utilized for normal shell formation and shell regeneration (Watabe, Meenakishi, Blackwelder, Kurtz, *et al.* 1976).

The digestive gland of JMS is a large yellow, brown, or greenish organ located in the visceral hump. It usually occupies about the 2.0–2.5 most apical whorls, with its anterior ~0.5 whorls supporting the right aspect of the stomach (Figure 5-23b–d) (Van Bocxlaer and Strong 2016). The digestive gland is divided into two lobes: a smaller anterior one, which borders the right wall of the gastric chamber, and a larger posterior one. The gland is drained by tubules that join the digestive gland ducts, which run along the columellar aspect of the visceral whorls. The ducts increase in size anteriorly and open to the stomach, one posteriorly, two anteriorly.

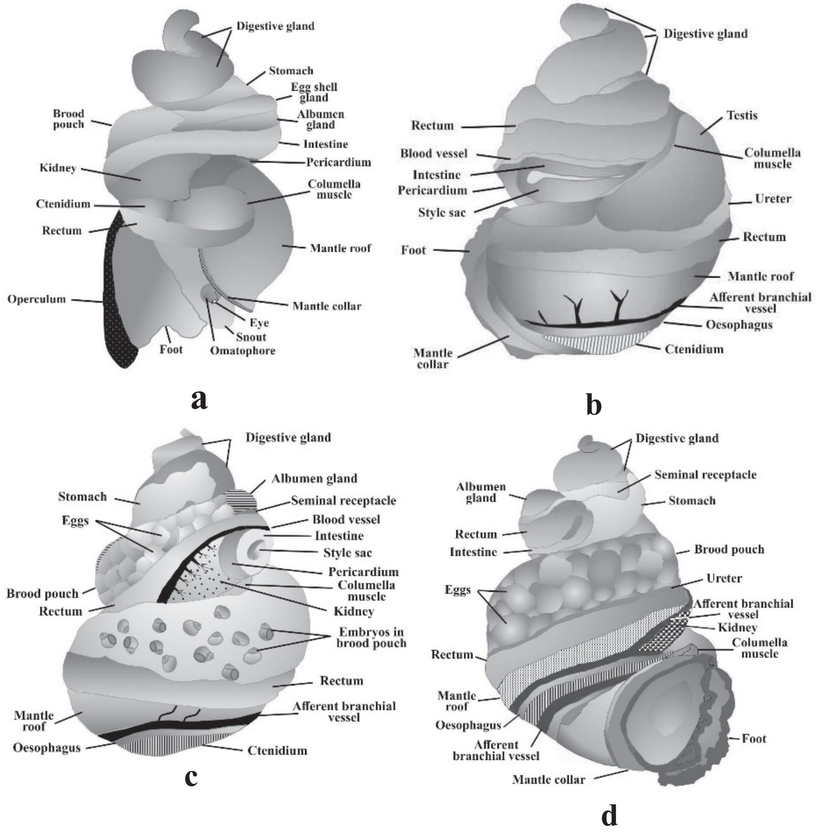


Figure 5-23. Anatomical configurations of: (a) a female Chinese Mystery Snail, left lateral view, drawn from Figure 2B in Lu, Du, Li, and Yang (2014); (b) a male Japanese Mystery Snail, abapertural view; (c) Japanese Mystery Snail abapertural view; and (d) apertural view. (b)–(d) drawn from Figures 4B–D in Van Bocxlaer and Strong (2016).

g. Intestine

The intestine is generally a slender tube leaving the stomach near the esophageal opening into the latter (Figure 5-22a, b). In the viviparids, the intestine usually makes some turns or coils before terminating at the anus. The anterior part of the inner wall of the intestine may bear a typhlosole. The epithelial lining typically consists of cuboidal to tall columnar ciliated cells interspersed with mucocytes or goblet cells (Hyman 1967).

The intestine of CMS forms a loop overlying the pericardial cavity (Figure 5-23a). When the intestine reaches the digestive gland, it turns sharply forward to continue on as the rectum. The rectum passes forward on the right of the mantle cavity to open at the anus lying just behind the mantle (Lu, Du, Li, and Yang 2014).

The intestine of JMS emerges from the anterior end of the style sac and curves ~180° to continue posteriorly overlying the pericardium and the right side of the style sac (Figure 5-23b). The typhlosoles of the style sac continue laterally into the intestine, with the major typhlosole present for half the length of the intestine. The intestine continues posteriorly, its posterior limit coinciding with the posterior wall of the pericardium, where it turns back on itself to widen into the much larger and more thin-walled rectum (Van Bocxlaer and Strong 2016).

h. Rectum

In JMS, the rectum is thin-walled and semi-transparent, making contents easily visible externally; posteriorly, the rectum borders the right dorsal side of the pericardium and at the anterior end of the pericardium, it enters the pallial cavity to continue dorsally at the right side of the mantle roof, left of the ureter and the testis/brood pouch (Figure 5-23b, c). The rectum is surrounded by a layer of connective tissue and is penetrated by blood vessels, including a rectal sinus; anteriorly, at the mantle collar, the rectum terminates in a free anal papilla; in the anterior part of the rectum, the feces are compacted into small, oval pellets rectum (Van Bocxlaer and Strong 2016).

3. Respiratory System

The respiratory system of viviparids embraces a gill (or ctenidium), a hypobranchial gland, and an osphradium. The gills of all operculate snails are assigned to a respiratory group called Pectinibranchiata (Latin Pecten = comb) owing to their comb-like (pectinate) gills (Taylor 1900). In the prosobranchs, gills can contain either one (i.e., monopectinate) or two rows (i.e., bipectinate) of lamellae. All viviparids are monopectinate.

a. Ctenidia (Gills, Branchiae)

The gills of viviparids function not only as respiratory organs but as food gathering and sorting organs. Lankester (1883) prefers to refer to the gills of molluscs, including viviparids, as ctenidia because of their dual role, an interpretation accepted here. In *Viviparus* the right ctenidium is lost with only a monopectinate ctenidium remaining (Yonge 1947). However, Taylor (1900) provides an illustration of the ctenidium of "*Paludina*" (*Viviparus*), taken from Lankester (1883) and drawn in Figure 5-24 here, that is bipectinate. According to Bernard (1890) and Yonge (1947), the ctenidia of *Viviparus* are monopectinate with large triangular lamellae suspended over a ciliated food groove extending across the floor of the mantle cavity. In all pectinibranchs, the ctenidial axis becomes fused with the mantle wall, which projects the filaments' single row. Lying parallel to this single row of filaments and ventrally is the osphradium. The fusion allows for the more efficient removal of sediment by an additional ciliary current on the floor in the inhalant region. In this, the heaviest particles are immediately rejected (Yonge 1947). Cilia on the ctenidium envelop digestible particles with mucus and pass them to the food groove. Some digestible food particles collected on the ctenidial filaments are directed to the tip and dropped into the food groove. Undigestible particles are wrapped into mucus balls and then expelled through the exhalant siphon without passing through the digestive tract. Because these balls are not true feces, they are referred to as pseudofeces (Figure 5-25). The filaments of viviparids are elongated, providing an additional surface for the frontal and abfrontal (rear) cilia, which change in function from cleansing to food collection to convey material to the mouth along the tips of the filaments (Yonge 1947).

Lu, Du, Li, and Yang (2014) describe the ctenidium of CMS as long and narrow, about the same length as a pallial cavity, anterior end at mantle border. Gill filaments are very tall and narrow, arched toward the right, and the apex is slightly pointed, close to food groove. The mantle edge of CMS is simple and thick. The oviduct occupies the right margin of the mantle cavity in females. The ureter runs along the right margin of the mantle cavity in males. The rectum is on the dorsal and left sides of the ureter. In females, at the right end of the mantle border are three openings. The most posterior and smaller one is the ureter pore. The anus is most anterior, and the female opening is larger and located between the anal and ureter openings.

Van Bocxlaer and Strong (2016, 243) examined the mantle cavity of JMS. They describe it as “long, usually somewhat shorter in males (~1.0 whorl) than in females (~1.5 whorls) and bounded posteriorly by the renopericardial system. On the mantle floor, slightly to the left of the midline, a conspicuous food groove extends from the posterior ctenidium to the head. A prominent ridge marks the base of the food groove and fuses anteriorly with the right nuchal lobe, forming a trough deflected around the cephalic tentacle and continues anteriorly toward the mouth. The monopectinate ctenidium is composed of elongate triangular leaflets and extends along the left mantle roof from near the mantle collar to the posterior end of the cavity. At the anterior-most third of the ctenidium, overlying the large efferent branchial vein lies the slender osphradium, which forms a ridge with distinct papillae along the side facing the ctenidial axis, likely representing vestigial “leaflets.”

An endostyle (a longitudinal, ciliated, grooved organ on the ventral wall of the pharynx and esophagus that secretes mucoproteins for filter feeders) runs along the length of the afferent axis of the ctenidium. Posteriorly, the endostyle wraps around the base of the ctenidium and is continuous with the posterior end of the food groove (Van Bocxlaer and Strong 2016).

b. Osphradium (Spengel’s organ, Olfactory organ)

Lankester (1883, 636) first described a patch of the epithelium of the body wall, near the base of each ctenidium, as “peculiarly modified and supplied with a special nerve and ganglion. This patch is Spengel’s olfactory organ, which tests the respiratory fluid, and is persistent in its position and nerve supply throughout Mollusca. We propose to call it the osphradium.”

Lankester and Bourne (1883) further added that the osphradium is distinguished from all other organs presumed to have the olfactory function, whether placed on the head, lips, tentacles, or elsewhere.

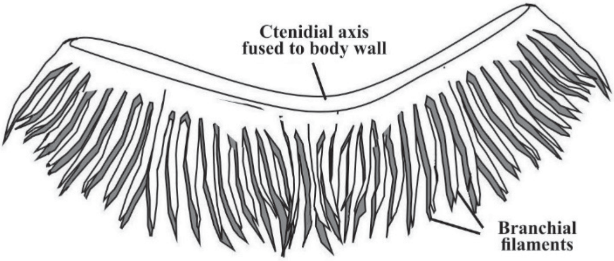


Figure 5-24. Pectinibranchiate ctenidium of *Viviparus*. Drawn from Fig 2E of Lankester (1883) and Figure 6 of Taylor (1900).

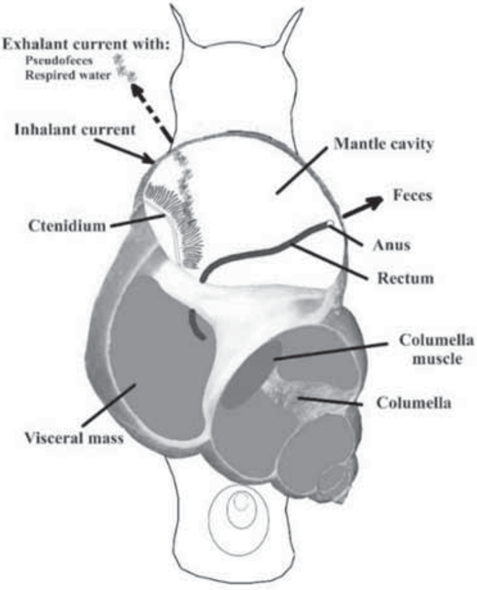


Figure 5-25. Role of the ctenidium in viviparids in which they function in respiration, collection and selection of suspended food items, and rejection of waste particles as pseudofeces.

Bernard (1890, 331-332) examined "les organs palleaux" of prosobranchs, mainly marine species, but also of *Paludina* (*Viviparus*), of which his research pioneered the study of the osphradium, "l'organe de Spengel," or Spengel's Organ, in Viviparidae. His research followed up on that of Lacaze-Duthiers (1872, 483) on pulmonates who reported an "organ in a constant position, easy to find in its vicinity, behind and above the inhalant siphon, at the height of the angle that the ctenidium forms when uniting with the mantle." The organ was referred to by many as the "organ of Lecaze-Duthiers."

Figure 5-26 shows the structure of the osphradium of *Viviparus* drawn from Bernard's (1890) Plate IX, Figures 39 and 40. Figure 5-26a shows in the connective tissue large numbers of nerve bundles that leave the central nerve and end up in the epithelium. The longest of the nerve bundles are immediately attached to the epithelial pits. Their length, position, and numbers vary greatly, often seen in the same section (Bernard 1890). The osphradial epithelium consists of ciliated cells and nerve cells (Figure 5-26b).

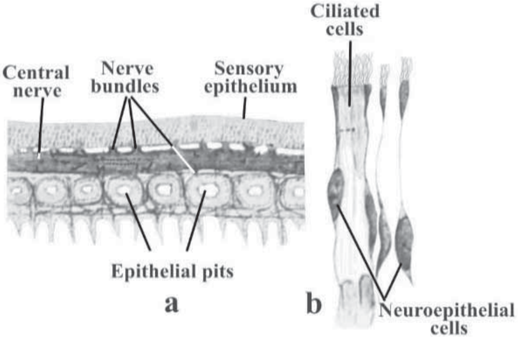


Figure 5-26. Structure of part of the osphradium of *Viviparus*, showing (a) the relationship between epithelial pits and nerve elements and (b) the presence of ciliated and neuroepithelial cells. (a) drawn from Figure 39 and (b) from Figure 40 in Bernard (1890).

Bernard (1890) did not find gland cells or ganglia in the osphradial epithelium in his study, but Wölper (1950) and Haszpruner (1985) found both structures in *Viviparus*. The structure of the osphradia found in both studies is similar (Figure 5-27a, b), although Wölper (1950) did not show gland cells in his illustration, drawn from Figure 5-27a. Wölper (1950) measured the osphradium in *Viviparus* as a bulge 2 to 4 mm long and about 1 mm wide on the left side in front of the ctenidium before inflowing respiratory water flows through the filaments. The epithelium of the osphradium is thicker than the surrounding epithelium and has numerous epithelial pits, which lie closely adjacent and are cylindrical. Above the epithelium lies a relatively thin cuticle about 2 to 3 µm thick. Wölper (1950) distinguished three types of cells in the epithelium of the osphradium: (1) epithelial cells with a cylindrical shape and of different widths, (2) round to smaller oval cells with nuclei having abundant granular chromatin and a visible nucleolus, and (3) gland cells that pass through the cuticle and appear somewhat lighter in the specimen than the surrounding epithelial cells (Figure 5-27a).

Haszprunar (1985) characterizes *Viviparus* as having an osphradial epithelium with sensory cells and having processes (= central zones) and laterally situated ciliated epithelium (= lateral zones); all epithelia are two-layered, and all lateral zones are formed as grooves (Figure 5-27c). The ctenidium and osphradium are innervated from the supra esophageal ganglion. However, Lindberg and Sigwart (2015) found the osphradium primarily innervated by a separate nerve from the left pleural ganglion (Figure 5-26d). Haszpruner (1987) considers the organ of Lacaze-Duthiers as homologous with the organs of Spengel, both now called osphradial sense organs.

The actual function of the osphradium is still speculative. Lacaze-Duthiers (1872, 491) did not specify a function of the pulmonate organ but concluded that it is “certainly aimed at the appreciation of some special qualities of the surrounding world, and these qualities are probably related to respiration.” Spengel (1881) first referred to these structures as “Geruchsorgan,” or olfactory organs. Bernard (1890) was as tentative, stating Lacaze-Duthiers’ and Spengel’s conclusions about the role of the organ are united or are simply a difference in the degree of detecting sensations, somewhat analogous to distinguishing the irritability of chemical substances in the state of gases or vapours by humans. Yonge (1947) believed the osphradium to be a mechanoreceptor that estimates the amount of sediment in the incoming water. Wölper (1950) used a

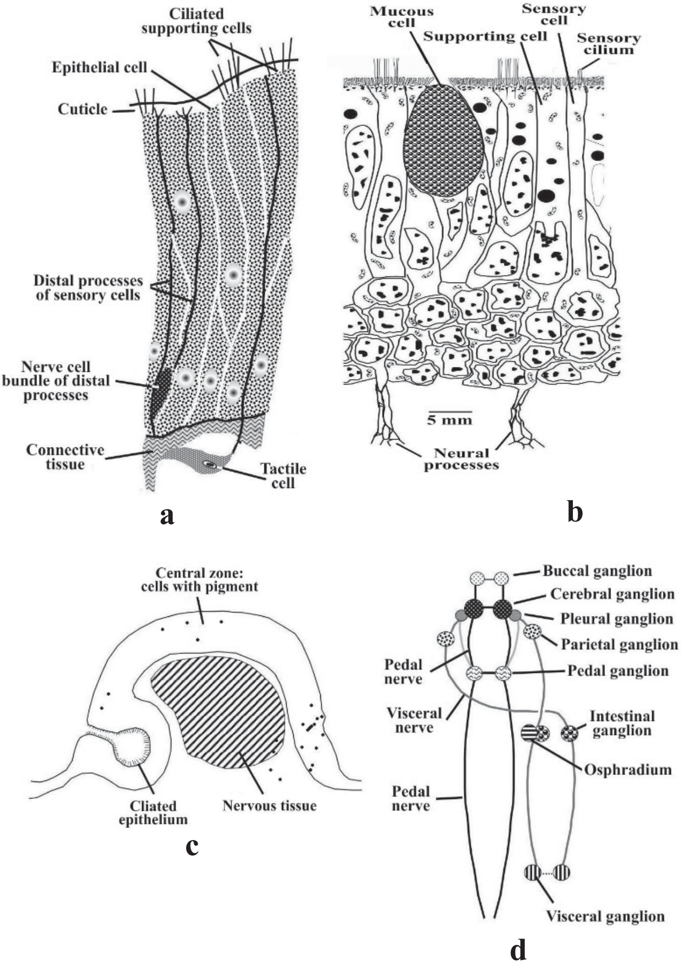


Figure 5-27. Diagrammatic osphradial structures of *Viviparus*, drawn from (a) Wölper (1950), Figure 6, Osphradial epithelium with ciliated cells; (b) Haszprunar (1985), Figure 5, Section of the osphradium; (c) Haszprunar (1985), Figure 7, Transverse section; and (d) Lindberg and Sigwart (2015), Figure 1, Generalized structure of the nervous system.

combination of experimental and anatomical work and suggested the osphradium has a possible role in reproductive biology. Haszprunar (1985) showed that the osphradium is a chemoreceptor that senses chemical irregularities in the incoming water and is not a mechanoreceptor. Haszprunar (1987) also suggested a chemosensory reproductive function by synchronizing gamete release in broadcasting taxa of molluscs. Lindberg and Sigwart (2015) review the various functions attributed to osphradia in gastropod and bivalve taxa. They gave other functions, including light sensors, which monitor photoperiod for reproductive control, detection of O_2 and CO_2, regulation of ciliary activity, locating prey, and those cited above, concluding that the osphradium is more of a chemoreceptor than a mechanoreceptor.

The osphradium of the Chinese Mystery Snail is ridge-like, very close to the ctenidium, and about the same length from the anterior tip of the osphradium to the mantle border (Lu, Du, Li, and Yang 2014).

In the Japanese Mystery Snail, Van Bocxlaer and Strong (2016) found the osphradium to be slender in the anterior-most third of the gill, overlying the large efferent branchial vein. It forms a ridge with distinct papillae along the side facing the ctenidial axis, likely representing vestigial leaflets.

c. Hypobranchial Gland

The hypobranchial (under gill) gland is a single highly glandular area of the epidermal lining of the mantle roof. In viviparids, the hypobranchial gland lies under the left ctenidium. Bernard (1890) provides descriptions and images of the hypobranchial gland in *Viviparus*; Figures 61–62 in Plate 12 of his analyses had to be enhanced for Figure 5-28 to illustrate the descriptions (translated from French). Figure 5-28a shows the location of the gland with the ctenidium partly removed. In *V. viviparus*, it is elongated and located along the ctenidium toward its base and opening into the branchial venous vessel (Figure 5-28b). Bernard (1890) describes its width as constant and approximately 1 mm; it has slight transverse folds at fairly regular intervals and extends down the ctenidium as shown by the gray bars in Figure 5-28a. Figure 5-28b is a cross-section that shows the gland is made up of a high epithelium that almost exactly covers the afferent vessel (blood sinus), which accompanies the gill from end to end (Bernard 1890). Transverse blood lacunae, regularly arranged, lead the blood from the afferent vessel to each of the ctenidial lamellae. The height of the epithelium decreases rapidly, and the gland attenuates as soon as it ceases to cover the afferent vessel (Figure 5-28b).

Bernard (1890) found only one row of cells in the basilar membrane, supporting the hypobranchial gland (Figure 5-28b). The nuclei are arranged at all levels, but along the straight edge that protrudes over the rest of the mantle, the nuclei are mainly peripheral tightly packed together. Toward the middle of the organ, the nuclei located in the middle region become more and more scarce; they are spherical and provided with a strong nucleolus and are most abundant near the base of the gland (Figure 5-28c).

The hypobranchial epithelium consists principally of cuneiform (wedge-shaped) ciliated cells, mucocytes, and neurosensory cells. According to Hyman (1967), the cuneiform ciliated cells generally occur between the gland cells, but in *Viviparus* the gland is composed almost entirely of granular cylindrical cells. Figure 5-28d shows all possible forms of ciliated cells, with the nuclei located at all levels. The attachment end is always slender. Many resemble neuroepithelial cells and, in many cases, could pass for nerve endings.

The hypobranchial gland of CMS and JMS are poorly described. Lu, Du, Li, and Yang (2014) found the hypobranchial gland to lie left of the gill margin of CMS. In JMS the hypobranchial gland is weakly developed (Van Bocxlaer and Strong 2016).

The principal function of the hypobranchial gland appears to be the secretion of mucin (Hyman 1967). Wanichanon, Laimek, Linthong, Sretarugsa, *et al.* (2004) believe the increased folding of the glandular epithelium into pleats increases the mucus-secreting surface area, and the quantity of mucus being discharged into the mantle cavity increases when the animal is irritated. They suggest the mucus thus produced and secreted is for protection and for clearing away debris from the anus and renal organs, keeping the ctenidia and mantle cavity clean. The irritations inducing mucin secretion are foreign particles from turbid water attaching to the gland's surface, the mucus cells releasing mucus to bind particles that will be brushed away by the ciliary action of the epithelial cells (Wanichanon, Laimek, Linthong, Sretarugsa, *et al.* 2004). It seems likely that the mucus enveloping pseudofeces also originates from the hypobranchial gland.

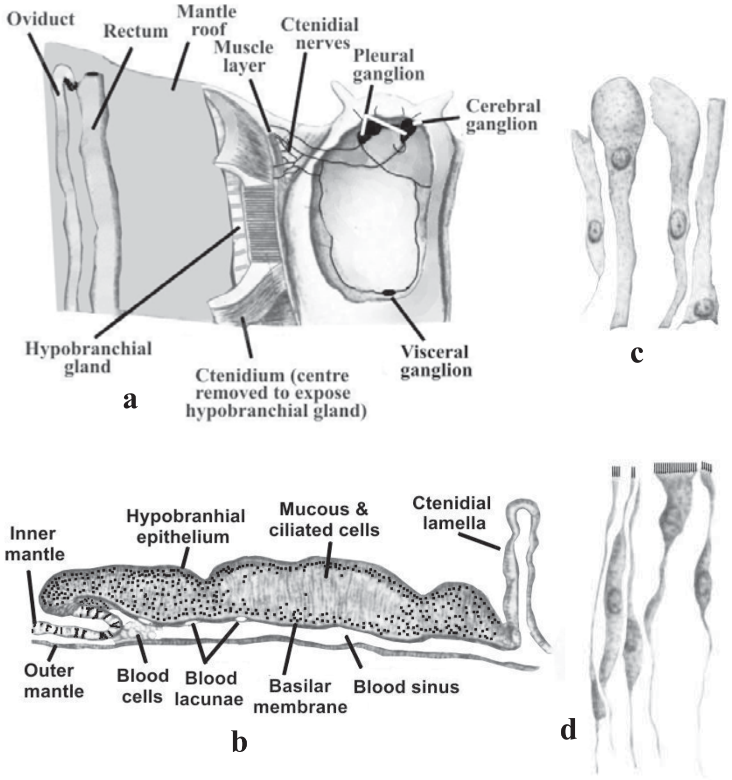


Figure 5-28. All figures are of *Viviparus* and revised for better clarity, all from Bernard (1890): (a) Location of the hypobranchial gland, with the middle of the ctenidium removed, from Figure 61; (b) a cross section through the hypobranchial gland, from Figure 62; (c) mucoid cells, from Figure 62a; (d) ciliated cells, from 62b.

4. Excretory System

The processes involved in urine formation are filtration of waste fluids and ions from the blood (hemolymph) and the secretion and absorption of some ions. The following subsections describe the principal organs of the excretory system, the processes of urine formation in viviparids, and excretion in CMS and JMS.

a. Kidney (Nephridium, Renal Organ)

The primitively paired nature of the kidneys persists in a more or less distinct form in the viviparids. Due to torsion, the right kidney, though briefly connected with the pericardium and mantle-chamber, has entirely lost its renal function (Taylor 1900). The ureter of the right kidney has become utilized as a genital duct; the left kidney and its canals still retain its wholly renal and secretory integrity. In *Viviparus*, the transitory right kidney has been detected during embryonal development, but its ureter persisting in the adult solely as a genital duct (Taylor 1900).

Perrier (1889) described the kidney's shape of *Viviparus* as a tetrahedron. Figure 5-29, from Perrier's (1889) Plate VIII, Figure 37, shows the relationship of the kidney to the ctenidium, heart, and genital structures; the body wall in Figure 5-29 is cut open, and the left half is folded back to expose the ctenidium, pericardium, and kidney. The top of the tetrahedral-shaped kidney is attached to the roof of the pericardium; its base is attached to the upper body wall behind the pallial cavity and to the right of the axis of the body (Figure 5-29). The top of the kidney below the floor of the pericardium and its other two surfaces are connected. One is connected with the pallial cavity and the other with the pericardium at the opening of the renopericardial canal.

The renal system is filled with a network of anastomosing channels in all directions and communicating with others (Figure 5-30a, b; Figure 5-31a). Within the kidney is a reservoir (also called sac and bladder) that stores products excreted by the kidney; between the reservoir and the ureter is a narrow orifice through which excretory products are passed to the ureter (Figure 5-30b). The renopericardial canal ends in this reservoir. The reservoir is surrounded by kidney tissue (Perrier 1889).

Perrier (1889) provides images of *Viviparus* showing the kidney containing numerous lacunae and projecting glandular lamellae (Figure 31a) overspread by a densely ciliate layer of secretory cells (Figure 31d). The secretory cells fill up the lumen (Figure 31b,c) of the organ and have a brownish fluid with concentrically formed concretions within the kidney cells and excretory vesicles.

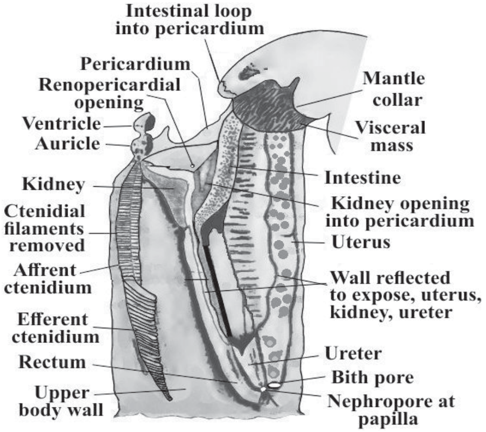


Figure 5-29. Overview of the pallial cavity of *Viviparus* showing the relationship of the excretory system to neighboring internal organs. Redrawn from Plate VIII, Figure 37 in Perrier (1889).

One theory of urine creation is that the secretory cell walls rupture and release the contents (Taylor 1900). The deoxidized and impure blood returning from its course through the body, laden with the waste products of the oxidation of the tissues, joins with some arterial blood from the lung and circulates within the kidney before reaching the ctenidium, thus constituting a portal circulation that partially purifies the blood by eliminating the nitrogenous waste matters in the form of urea, uric acid and calcium phosphate as well as any ammonia, creatine, or other substances (Taylor 1900). However, as discussed below, urine is now known to be created by ultrafiltration through the heart’s walls within the pericardium (see *d)* Urine Formation).

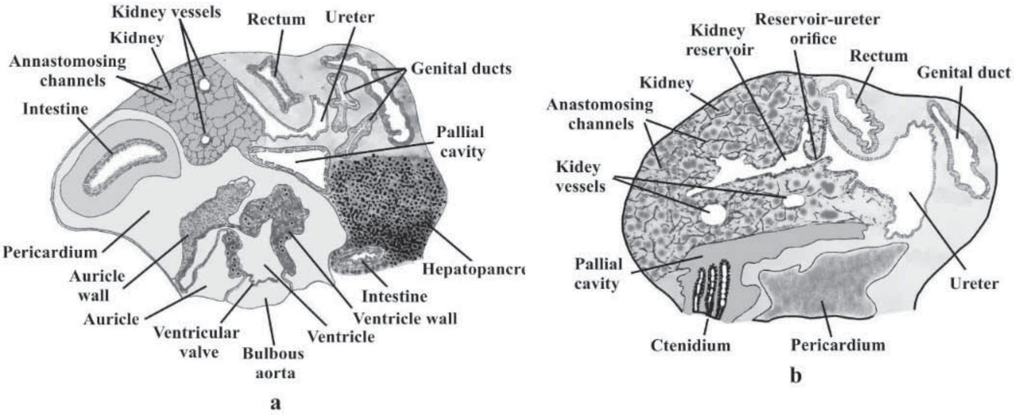


Figure 5-30. Sections of *Viviparus* showing kidney relationships with its components: (a) kidney in relation to ureter, pericardium, and heart; (b) kidney in relation to its reservoir and ureter through an orifice. (a) is drawn from Plate VII, Figure 38 and (b) from Plate IX, Figure 39 of Perrier (1889).

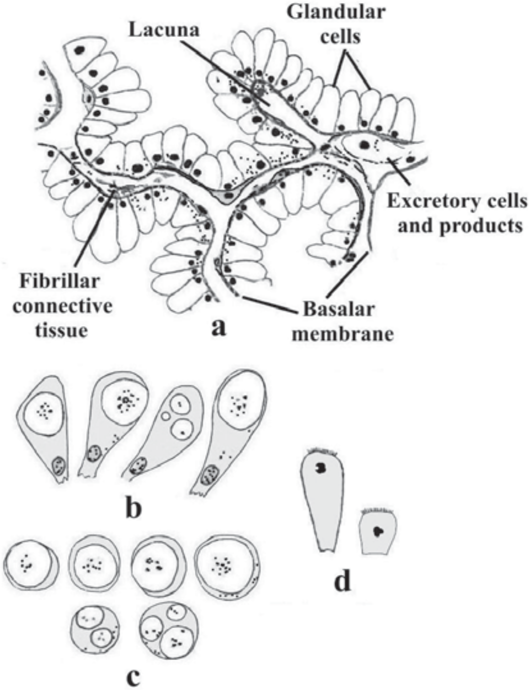


Figure 5-31. Kidney channels and cells of *Viviparus*: (a) anastomosing channels; (b) kidney cells; (c) excretory vesicles; (d) ciliated cells. All drawn from Plate IX in Perrier (1889); a from Figure 41; b, c, d from Figure 45.

Attached to the channels are connective cells with large basal nuclei (Figure 5-31a). The lacunae end in two large efferent vessels that meet at the anterior angle of the kidney and finally open at the afferent branchial sinus. All the connective cells are similar (Figure 5-31a); they are very small and very close together, and in the center of each is an excretory vacuole. The vacuoles (Figure 5-31b) have clear walls, and within them is a brownish liquid, which, according to Perrier (1889), constitutes urinary secretions. The rest of the cell is occupied by the nucleus' protoplasm, always at the cell base (Figure 5-31b). Perrier (1889) thought the excreted products were not deposited in all the points of the protoplasm but concentrated by some secretory activity; the vacuole increases more and more in size, the concretions forming inside it, and later, when the cell swells, the vacuole protrudes into the renal cavity. The vacuole then separates from the cell (Figure 5-31c) into the urinary chamber, while the cell itself continues to function. These cells are the only ones that are found throughout the entire kidney (Perrier 1889).

b. Pericardium

The pericardial cavity of viviparids comprises the chamber housing the heart. It forms an extensive coelom (body cavity) constrained by the coils of the intestine and the duct of the genital tract at the base of the visceral hump (Figure 5-30a, b). Within this coelom, it communicates with the kidney by the renopericardial canal (Figure 5-29). The pericardium is large; in an animal weighing 1 gram (wet weight without shell), it may contain 100 μL of liquid (Little 1965b).

In *Viviparus* the kidney lies to the right of the ctenidium, with its apex pointing anteriorly. Its opening into the ureter lies close to the renopericardial opening posterior-ventrally. This area is the only part of the kidney with a recognizable lumen, which narrows as it extends anteriorly and permeates the spongy walls like a series of narrow, blind-ending tubules. The tubules are often filled with yellowish excretory concretions, irregular in shape, molded and supported by the surrounding epithelium until they are large enough to be shed (Andrews 1979). Circulation of urine and expulsion of the concretions is achieved by spasms of muscular contraction rather than by ciliary activity (Andrews 1979).

c. Renopericardial Canal

The renopericardial canal of viviparids is short and muscular (Little 1965b). It is folded upon itself, forming a loop, connected proximally by the ciliated renopericardial funnel with the base of the pericardial cavity (Taylor 1900). At the distal end, the canal connects to the kidney reservoir or bladder at a papilla, which has a slit-like opening into the ureter, controlled by a sphincter muscle. The renopericardial canal opens into the bladder close to the papilla; the end of the renopericardial canal and the kidney papilla are very close together (Little 1965b). When the sphincter opens the papilla, urine flows into the ureter that runs through the pallial cavity. It opens to the outside, at the top of a papilla, situated between the rectum and the genital papilla (Figure 5-32). The renopericardial canal is surrounded by a rather heavy musculature. Internally, it is covered with a ciliated epithelium formed of rather large granular cubic cells that are vacuole-free, well defined, and non-excreting. At the renal opening of the canal are often rather long papillae, especially between it and the excretory pore (Figure 5-32). These parts are covered with the same ciliated cells that line the canal (Perrier 1889). Little (1965b, 49, 51) summarizes the activities of urine cycling through the pericardium as two phases: (1) “An expulsion phase” where the “kidney muscles contract, forcing liquid from the small spaces into the larger spaces, and thence into the large bladder; the bladder muscles probably also contract, and while the renopericardial canal stays closed the papilla muscle opens the sphincter of the kidney pore so that liquid is forced into the ureter”. (2) “An intake phase” where “the papilla muscle closes the kidney pore, kidney muscles relax, and the renopericardial canal opens. Positive pressure in the pericardium forces liquid into the kidney and re-expands it, aided by the tension exerted on the contracted kidney by surrounding organs; pericardial

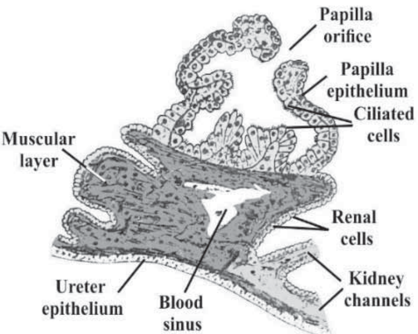


Figure 5-32. Papillae lining the entry of the renopericardial duct in the main urinary chamber of *Viviparus*. Drawn from Plate IX, Figure 42 in Perrier (1889).

fluid becomes distributed in the kidney spaces, in contact with the kidney cells."

a. Ureter

Leydig (1850) referred to the ureter by the name of Wasserbehdlter, or aquifer reservoir, in which he believed waste fluid enters the kidney and mixes with the blood, which entered through openings in the blood channels. However, Perrier (1889) showed no openings in the blood ducts, and the kidney vessel is a simple excretory duct (Figure 5-33a, b).

In *Viviparus* the ureter is a long tube that runs from the side of the kidney, initially under the rectum, then between the rectum and the genital duct, almost to the edge of the mantle (Figure 5-29), where an opening is controlled by a sphincter situated on a small papilla (Little 1965b).

There are very few kidney vessels in *Viviparus* (only two are shown in Figure 5-30a, b). They eventually empty into the kidney reservoir or chamber, which consists of large circular and oblique bundles of muscles, longitudinal muscles being absent (Perrier 1889). Any musculature may contribute to the stirring of fluid retained in the ureter (Andrews 1979). The ureter bears only shallow folds on its walls, running parallel to and just beneath the rectum to open on the anterior edge of the mantle skirt (Andrews 1979).

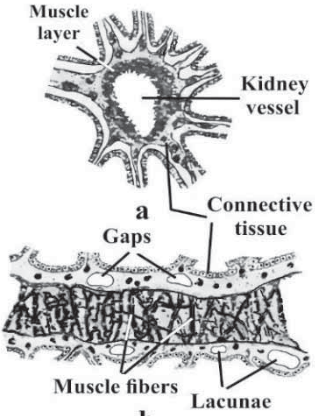


Figure 5-33. Sections of a kidney vessel of *Viviparus*: (a) Cross section; (b) Longitudinal section. Drawn from Plate IX, Figures 43 and 44 in Perrier (1889).

b. Urine Formation

In all aquatic molluscs, the initial process of urine formation is the filtering of blood through the wall of the heart into the pericardium; examples include the marine gastropod, *Haliotis*, (Harrison 1962); the freshwater bivalve, *Anodonta* (Picken 1937); the freshwater snail, *Viviparus;* and the branchial heart of the *Octopus* (Little 1965a, b). Next, the pericardial fluid passes to the kidney, where secretion and reabsorption modify it to form the final urine.

The urine of marine molluscs has the same concentration of salts as the blood, but its ionic composition is different. In freshwater molluscs, salts are reabsorbed in kidney tubes, and the final urine is more diluted than the blood. Therefore, it is a prerequisite for freshwater snails to dilute the blood to equalize the hydrostatic pressure between the two fluids, and in the process, waste fluids and products (i.e., urine) are created. In prosobranchs, most of the urine is formed by the left kidney (recall that the right kidney was resorbed during torsion). In viviparids (and other prosobranchs), the urine is formed by its ultrafiltration from the blood into the pericardium and is later modified by secretion and resorption (Picken 1937; Little 1965a, b; Potts 1967; Boer, Algera, and Lommerse 1973; Boer and Sminia 1976; and Andrews 1979).

Viviparids have an open circulation with the highest hydrostatic pressure found in the heart. The exact site of filtration is in the walls of the auricle that are thin and consist of podocytes that communicate with pedicels attached to the basal membrane (Figure 5-34) (Potts 1967; Boer, Algera, and Lommerse 1973; Andrews 1979; Ichimura and Sakai (2017); among others). Urine is produced by ultrafiltration when the formation rate is proportional to the excess hydrostatic pressure over the colloidal osmotic pressure (Little 1965b). Filtration is increased if the blood volume is increased either by the addition of blood or seawater to the circulation. The increase in filtration rate is associated with an increase in blood pressure (Potts 1967).

a. Ultrafiltration

Three processes are involved in the formation of urine: filtration, reabsorption, and secretion (Little 1965b). The initial step in urine formation in most freshwater molluscs is ultrafiltration of the hemolymph into the pericardial cavity. The kidney modifies the composition of this initial filtrate before being expelled to the ureter as urine (Little 1965b, 1967; Andrews and Little 1971, 1972). Ultrafiltration can only occur in systems where the hydrostatic pressure exceeds the colloidal (mainly proteins) osmotic pressure of the coelomic fluid (Picken 1937). The ultrafiltrate is ideally in equilibrium between the two solutions (blood and urine) that are separated by a membrane and contain little if any protein vital to the organism (Potts 1967). The creation of urine by ultrafiltration of blood impurities through the auricle of the heart could be colloquially termed auricular urination.

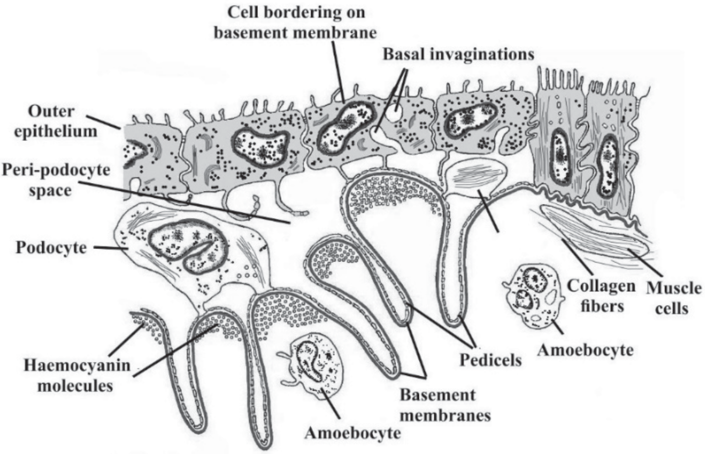


Figure 5-34. Schematic representation of the ultrastructure of the wall of the auricle of *Viviparus viviparus*. Drawn from Figure 8 in Boer, Algera, and Lommerse (1973).

Ultrafiltration in freshwater gastropods (and other invertebrates) are distinguished by a special cell type, the podocyte (Figure 5-35). These cells have many interdigitating feet, the pedicels, which are juxtaposed to a basement membrane; thin diaphragms bridge the slits between the pedicels. Boer and Sminia (1976) give a schematic drawing of the three-dimensional sieve present in the slits between the pedicels of podocytes of *V. viviparus*, drawn from Figure 5-35 in which their "teeth" appear to be more peg-like than tooth-like; the following description is a summary of their text. Holes of the sieve measure about 90 x 110 Å; knobs of opposite teeth almost touch, and all teeth of the same row are about 90 Å apart. Thus, a slit diaphragm has a sieve structure with holes measuring about 90 x 110 Å. The distance between the upper and lower diaphragm is about 60 Å. These two diaphragms appear as one distinct "zip-fastener" in their micrographs, indicating that the upper and lower diaphragm teeth lie perpendicularly above each other. The teeth of both diaphragms are shown in Figure 5-35 as sections perpendicular to the basement membrane and parallel to the long axis of the pedicels; the teeth of two opposite rows do not alternate but lie straight above each other.

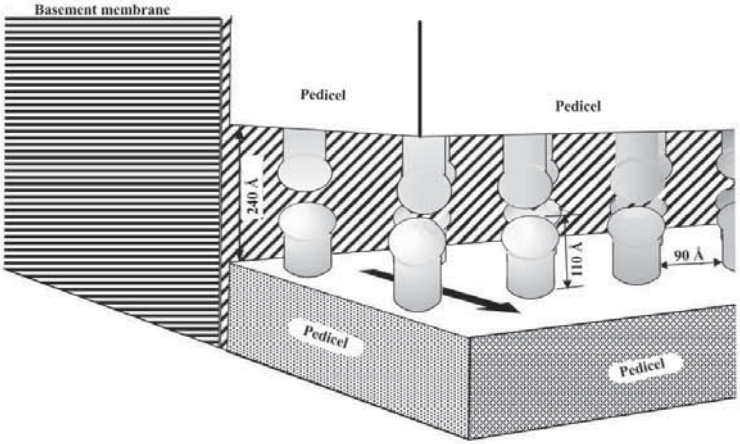


Figure 5-35. Schematic drawing of the three-dimensional sieve present in the slits between the pedicels of podocytes of *Viviparus viviparus*. Drawn from Figure 3 in Boer and Sminia (1976).

b. Secretion and Resorption

After ultrafiltration, the urine passes through the kidney, subject to other secretion and reabsorption processes. Perrier (1889) believed that secretion occurs from the pericardial glands located on the wall of the auricle, but Little (1965b) stated that secretion is likely to take place in the kidney. Some degree of ionic secretion and resorption occurs in *Viviparus*, where extensive salt resorption occurs, leading to passive water loss from the urine. The urine becomes hyposmotic to the blood (i.e., the total amount of solutes in urine is lower than that of blood.), and water tends to be lost from the urine, thus reconcentrating the solutes. In *Viviparus* the final volume of urine is between one-half and one-third of the initial filtrate, and between 80% and 90% of the total chloride is resorbed, although the final concentration is 30% of that in the blood. The pH of the pericardial fluid in *Viviparus* is identical to that of the blood (Table 5-1), as appropriate for an ultrafiltrate (Little 1965b). About 20 mM NaCl/L, and probably some water, are reabsorbed in the kidney; about 5 mM^{-1} NaCl, and probably a little water, are reabsorbed in the ureter (Little 1965b).

Table 5-2. Composition of medium, blood, and urine in *Viviparus viviparus* front stream water (Little 1965b) (mM/L ±S.E.)

Ion	**Medium**	**Blood**	**Pericardial fluid**	**Kidney-sac fluid**	**Final urine**
Na	2.5	32.5 ±0.8	32.0 ±1.5	13.0 ±1.7	9.0 ±1.7
Ca	3.3	5.8 ±0.6	4.8 ±0.2	2.5 ±0.5	1.5 ±0.02
Cl	8.0	29.0±1.0	29.0 ±1.2	13.0 ±1.1	10.0 ±1.2
Δ as NaCl	5.0	38.5 ±1.4	37.0 ±1.5	13.5 ±2.1	7.0 ±1.8
pH		7.71 ±0.05	7.70 ±0.05		

The kidney sac of *Viviparus* typically has a limited amount of secretion and resorption of ions. Still, it is the site of resorption of glucose and the secretion of para-amino hippuric acid and related compounds (Potts 1967).

Little 1965b examined the inorganic composition of the urine of *V. viviparus* and measured the rate of urine production. The rate of production of urine by *Viviparus* is between 0–25 and 0–91 µL/g/min. She attributed at least two factors that probably influence this rate: a change in blood pressure and a change in salt concentration of the external medium, which may act via external sensory receptors.

5. *Cipangopaludina chinensis* Excretory System

Lu, Du, Li, and Yang (2014, 517) describe the kidney of CMS as "triangular with four almost plane surfaces: 1) posterior surface toward pericardium; 2) left with a pallial cavity; 3) ventral right with ureter; 4) dorsal with the mantle." The dorsal length of the kidney's left plane is similar to the right ventral plane, and about two times longer than the posterior plane (Figure 5-36). This configuration emulates Perrier's (1889) tetrahedron. The nephrostome is a round, small pore located in the center basally inferior region of the ventral surface of the kidney (Figure 5-36). The ureter runs between the rectum and oviduct in females or the right pallial cavity edge in males, and the ureter pore just posterior to the anus or just posterior to the female pore (Lu, Du, Li, and Yang 2014).

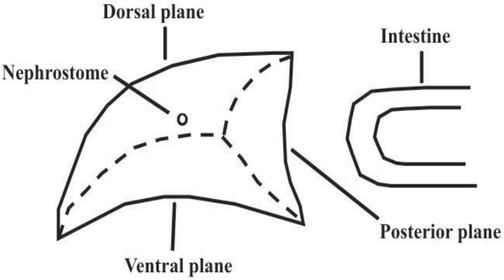


Figure 5-36. Shape of the Chinese Mystery Snail kidney and its relationship to the intestine. Drawn from Figure 2, CI in Lu, Du, Li, and Yang (2014).

6. *Cipangopaludina japonica* Excretory System

Like *Viviparus*, the kidney of JMS has thick spongy walls with a small lumen (Andrews 1979). This tetrahedral organ lies to the right of the ctenidium, with its apex pointing anteriorly. Its opening into the ureter lies close to the renopericardial opening posterior ventrally (Figure 5-37). This area is the only part of the kidney with a recognizable lumen. The lumen narrows as it extends anteriorly and permeates the spongy walls like a series of narrow, blind-ending tubules, often filled with yellowish excretory concretions, irregular in shape, sculpted, and supported the surrounding epithelium until they are large enough to be shed (Andrews 1979). The dorsal wall of the kidney is richly supplied with afferent and efferent renal veins. Fluid from the pericardial cavity passes to the kidney via the renopericardial canal, then to the ureter via the opening in the kidney (Figure 5-37). Van Bocxlaer and Strong (2016) found the kidney of JMS to be a compact, glandular mass of tubules with a small lumen at the rear of the mantle cavity that encloses the region where the ctenidium and endostyle curve into the food groove (Figure 5-38). The kidney typically has a curved tetrahedral shape bordered at its dorsolateral edges by two prominent blood vessels that converge at its anterior tip (Figure 5-37); the vessel at the right emerges from the rectal sinus, and at the left is the afferent branchial vessel.

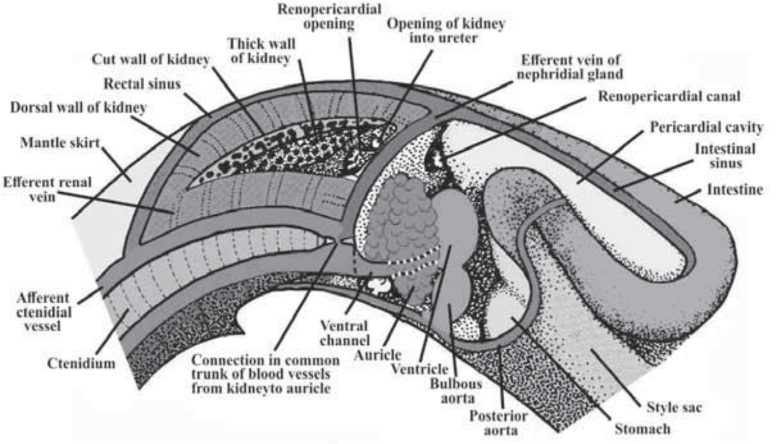


Figure 5-37. Structure and configuration of the kidney and its components in *Viviparus contectus* and *Cipangopaludina japonicus.* Drawn from Figure 1 in Andrews (1979).

A smaller efferent vein of the nephridial gland along the posterior border of the kidney also connects to the rear end of the afferent branchial vessel (Van Bocxlaer and Strong 2016). A small nephrostome opens dorsally at the right side, roughly at the posterior third of the kidney (Figure 5-38). It connects the main kidney chamber to a proximal expansion of the ureter lying between the kidney and the rectum. A small renopericardial duct at the right posterior side of the kidney (Figure 5-38) lies close to the nephropore. The ureter continues anteriorly as a tall and narrow uninterrupted chamber between the pallial gonoduct and the rectum. As described previously, the ureter opens anteriorly via the urinary pore located between the rectum and gonoduct. The slit-like urinary pore opens slightly behind the papillate anus, opening near the mantle edge (see Figure 5-29). Some reabsorption of ions occurs in the ureter, in which the final urine is stored (Andrews 1979).

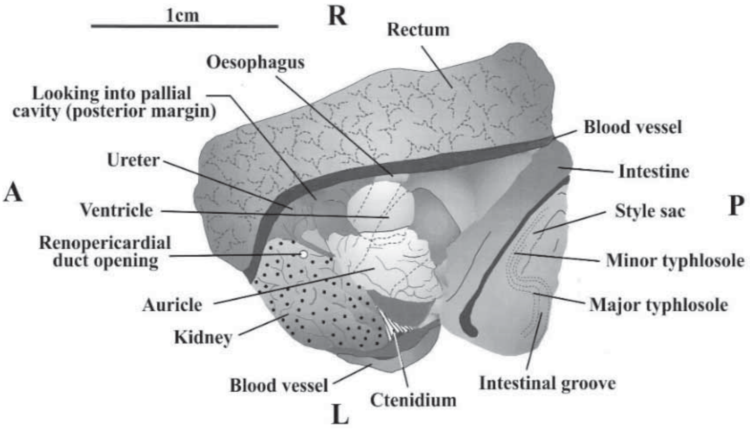


Figure 5-38. Schematic representation of a dorsal view of the pericardium of *Cipangopaludina japonicus*. A = Anterior, L = left, P = posterior, R = right. Redrawn from Figure 9 in Van Bocxlaer and Strong (2016).

Andrews (1979) examined the fine structure of the excretory system of *Viviparus contectus* and *Viviparus japonicus* (= *Cipangopaludina japonicus*) using scanning and transmission electron microscopy. She found that the primary urine is filtered through the wall of the auricle into a capacious pericardial cavity in which it is stored, in agreement with earlier investigators (e.g., Little 1965a, b; Boer, Algera, and Lommerse 1973; Boer and Sminia 1976). The auricle consists of a single-layered epicardium comprising podocytes and squamous cells overlying sheets of pedicels on lateral branches of the podocytes (Figure 5-39). Transverse bridges link adjacent pedicels and the diaphragms over the filtration slits; unlike Boer and Sminia (1976), who recognized two diaphragms, Andrews (1979) does not attribute the filter system of *Viviparus* as constituting a secondary filter. Instead, the epicardium of the ventricle is a transporting epithelium implicated in the resorption of glucose from primary urine.

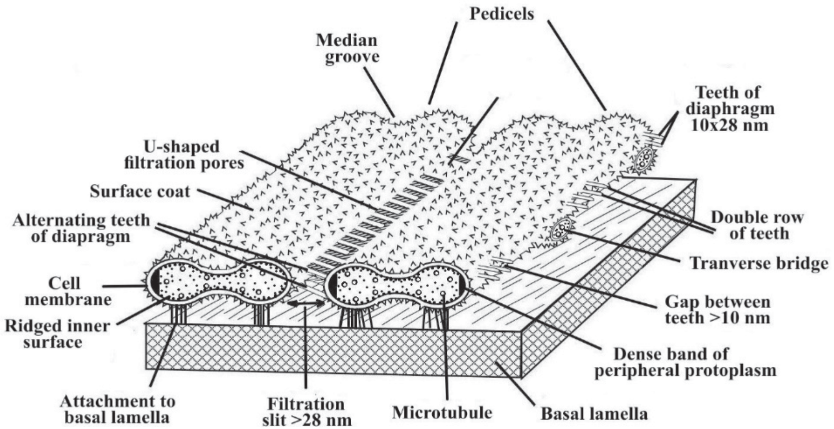


Figure 5-39. Schematic representation of a high magnification scanning electron micrograph of pedicels with closed filtration slits of *Viviparus contectus* and *Cipangopaludina japonicus*. Redrawn from Figure 8 in Andrews (1979).

7. Reproductive System

Vail's (1977b) gross dissection and histological studies of the reproductive systems of three species of viviparids (*Viviparus georgianus* of the Viviparinae, and *Campeloma geniculum* and *Lioplax pilsbryi* of the Lioplacinae) found many variations within males and females. Similar variations were reported by Lu, Du, Li, and Yang (2014) for *C. chinensis* and by Van Bocxlaer and Strong (2016) for *C. japonicus*, which suggests there is no standard reproductive system among viviparids. In males, these differences include relative size, location, and form of the testis, vas deferens, seminal vesicle, pallial vas deferens, prostate gland, and the copulatory tentacle. In females, these differences are in the relative size, location, and form of the albumen gland as well as the junction of the ovary with the oviduct and albumen gland duct, seminal receptacle, pallial oviduct, and vagina. In addition, a gonopericardial duct (canal from gonad to pericardium) is not present in all female viviparids. The following discussion focuses mainly on the reproductive systems of males and females of three species, *V. georgianus*, *C. chinensis*, and *C. japonicus*, using illustrations to demonstrate the differences among the species. Not surprisingly, *V. viviparus* has also received considerable study, especially on sperm morphology and development (e.g., Siebold 1836; Auerbach 1896).

a. Viviparus georgianus

Vail (1977b) examined several specimens of *V. georgianus* from Holmes Creek, Florida, and some of the following descriptions and illustrations are summaries of his studies on the species, beginning with males.

i. Males

Viviparids are sexually dimorphic, with the right tentacle modified as a penis in the males, the tentacle being much shorter than the right tentacle and distinctly curved.

i. Testis

In living specimens, the testis is a large, bright yellow to gold organ consisting of two separate parts connected by the vas deferens (Figure 5-40a–c). The posterior testis occupies the entire ventral and left lateral surfaces of the apical whorl, with the digestive gland abutting its dorsal and dextral surfaces (Figure 5-40a). The anterior testis extends from the columellar axis, from which runs the vas deferens to the dorsal midline surface of the body whorl, behind the posterior end of the mantle cavity (Figure 5-40b, c) (Vail 1977b).

a. Sperm (Spermatozoa)

The following descriptions examine only the external characteristics of the sperm of viviparids, not the details of spermiogenesis. The early literature is beneficial for more information on sperm morphology, whereas the more recent literature deals more with spermiogenesis.

Viviparid males possess two kinds of sperm in each animal, typical sperm and atypical sperm. Siebold (1836) examined *Paludina* (*Viviparus*) *viviparus* and described the two types, a typical hair-like type and a worm-like type (Figure 5-41a, b). His early studies of sperm dimorphisms prompted myriad studies, not only for *V. viviparus* (see Figure 5-41c, d from Auerbach 1898 as well as CMS, discussed later) but for many other prosobranchs. Some could not support the existence of both types, such as Kolliker (1847) and Paasch (1843), who could not find vermiform spermatozoa. Shortly after, Leydig (1850) confirmed both forms, although Duval (1884) disputed the origin of his vermiform type. Speyer (1855) described and illustrated both the “helically wound” (Plate II, Figure 18) and “worm-like” (Plate II, Figure 19) sperm, the latter with seven delicate tails. Auerbach (1896) and Erlanger (1898) also endorsed the existence of both types. Brunn (1884a, b), Brock (1887), Ishizaki and Kato (1958), Kohler (1888), and Giusti and Selmi (1982) examined numerous other prosobranch species and confirmed the existence of both kinds of sperm in all of them. However, the shapes of the two types often differed.

The flagellated forms of *V. viviparus* have a head, middle piece and tail, the head having a distinct corkscrew-like appearance and containing the nuclear material (Figures 5-41). The vermiform types have a terminal brush of flagella, which provides mobility to the sperm (Figure 5-41a–d). Siebold (1836) did not give magnifications to his images for Figures 5-41a, b, merely describing them as greatly enlarged.

Meves (1900, 1903) first described the differentiation between the two kinds of spermatozoa as occurring during the growth period of the spermatocytes. According to Meves (1900, 1903), spermatogonia cells undergo unequal growth and thus give rise to both the hair-shaped and the worm-shaped spermatozoa. On the advice of a colleague, Meves (1903) termed the two kinds of spermatozoa eupyrene (those that provide an ordinary amount of nuclear material) and oligopyrene (those with little nuclear material). Hence, the flagellated forms are eupyrene types, fertilizing females' eggs; the vermiform or worm-like forms are apyrene. Oligopyrene types are absorbed or digested somewhere in the female reproductive system (Reinke 1914; Hyman 1967). Meves (1903) demonstrated 12 flagella in the end piece of an atypical spermatozoon of *V. viviparus*.

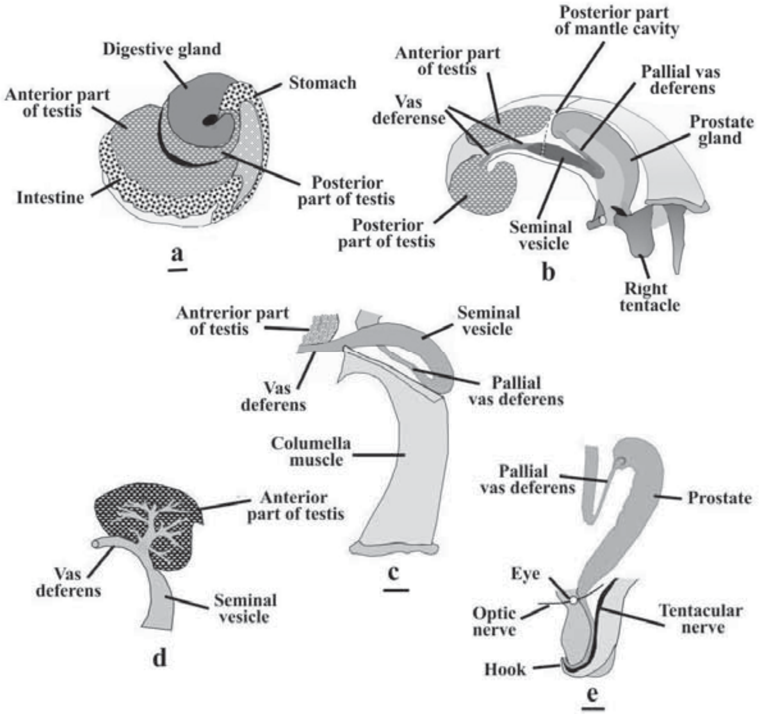


Figure 5-40. Reproductive anatomy of male *Viviparus georgianus*. All scales under a, c, e = 1 mm. (a) Dorsolateral view of intact apical and part of body whorl to show natural topographic locations; (b) schematic drawing of reproductive system in uncoiled animal with dorsal mantle removed; (c) connections of seminal vesicle; (d) dendritic pattern of ductules entering vas deferens from distal part of testis; and (e) prostate gland running through copulatory right tentacle. All are drawings of illustrations from Vail's (1977b) Figures 26–30.

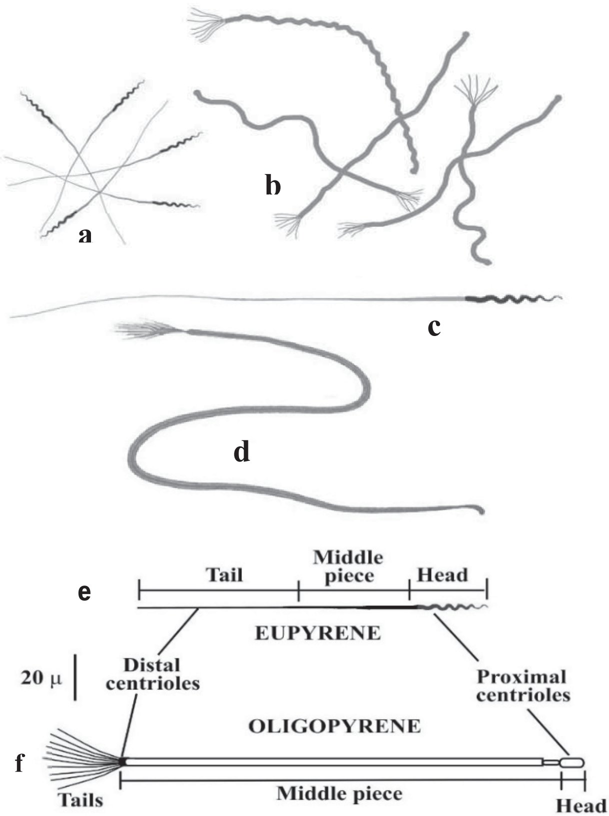


Figure 5-41. Two types of sperm produced by *Viviparus viviparus*. Both (a, b) are drawn from Plate X of Siebold (1836), no scales given: (a) hair-like type with screw-shaped heads (Figure X5); (b) worm-like type with terminal flagella brush (FigureX3). Both (c, d) are drawn from Figure 13q, Plate XXII in Auerbach (1896), both 1000X magnification: (c) flagellated type with screw head; and (d) vermiform type with terminal flagella. Both (e-f) are structures of (e) eupyrene and (f) oligopyrene spermatozoa, drawn from Figure 1 in Hanson, Randall, and Bayley (1952).

Hanson, Randall, and Bayley (1952) examined the microstructure of the apyrene and oligopyrene spermatozoa of *V. viviparus,* the former having nuclei containing the full haploid number of seven chromosomes (Figures 5.41e, f). They also stated that the oligopyrene spermatozoa, which they observed were as numerous as the eupyrene forms, possess only one chromosome and are infertile. As the middle-piece elongates, the spermatid shrinks, and the tails thicken and shorten to 40% of their original length. They found large, densely-packed masses of both types of spermatozoa in the primary oviduct (uterus) near the opening of the oviduct. Still, only the eupyrene spermatozoa were active, and the oligopyrene forms were usually non-motile, and the middle-piece sheath either disintegrates or disappears in the uterus. Hanson, Randall, and Bayley (1952) also observed oligopyrene spermatozoa in the female at copulation and suggested that the products of the broken-down sheaths may nourish the eupyrene spermatozoa.

Healy and Jamieson (1981) reviewed Reinke's (1914) terminology and proposed the terms euspermatozoa and paraspermatozoa to replace what they called unsatisfactory or inappropriate earlier terminology. Since then, others (e.g., Buckland-Nicks 1998) have used the terms eusperm for typical forms and parasperm for atypical forms.

The development of the three types of spermatozoa have also been well investigated but are not discussed here. Details of spermiogenesis for *V. Viviparus* are given by Duval (1880), Brunn (1884a, b), Auerbach (1898), Meves (1900, 1903), and others. Ottaviani, Rebecchi, and Fantin (2001) give an ultrastructural description of the euspermatozoa and paraspermatozoa for *Viviparus atar*, as Kuschakewitsch (1913, 1921) and Reinke (1914) do for prosobranchs.

ii. Vas Deferens and Pallial Vas Deferens

The vas deferens passes sperm from the testis to the seminal vesicle, and the pallial vas deferens transfers sperm to the prostate gland and then to the penis, located in the right tentacle (Figure 5-40 b, c). The fluid contents of the vas deferens create a whitish appearance, making the structure somewhat transparent; it is long with a large diameter, while the pallial vas deferens has a much smaller diameter (Figure 5-40b). The vas deferens has a dendritic arrangement of ducts within the testis, anastomosing to form the main collecting duct, which joins the seminal vesicle (Figure 5-40d) (Vail 1977b).

The white pallial vas deferens of *V. georgianus* is located ventral to the seminal vesicle on the floor of the mantle cavity and extends diagonally from the distal end of the seminal vesicle to the posterior proximal end of the prostate gland (Figure 5-40b).

iii. Seminal Vesicle

The seminal vesicle, which temporarily stores sperm before copulation, is short and straight and originates immediately behind the posterior end of the mantle cavity (Figures 5-40b –d). It is located along the posterior third of the mantle collar (Figure 5-40b). Internally, numerous villi of irregular shape and differing size project from the walls into a small, central lumen (Vail 1977b).

iv. Prostate Gland

The prostate gland of *V. georgianus* is located beneath the anterior end of the mantle and spans nearly the entire length of the mantle cavity (Figure 5-40b, e). It has a thick muscular coating, consisting of an external circular layer and an inner longitudinal layer around the entire organ. The gland varies in color from dark grey in the distal part, deep rose in the central part, and dull white in the anterior part. Beneath the muscle layers, the prostate has a smooth, non-convoluted duct, from whose walls numerous villi protrude toward a small central canal (Vail 1977b).

v. Right Copulatory Tentacle (Penis)

The right tentacle of viviparids contains the penis. In living specimens of *V. georgianus*, its surface contains flecks of bright reddish-orange pigment atop a solid, subepidermal concentration of melanin, also seen in all non-copulatory tentacles (Vail 1977). The penis has a hook at its tip on the anterior right side of the tentacle (Figure 5-40e) (Vail 1977b).

ii. Females

The female reproductive system of viviparids consists of the ovary, oviduct, albumen gland, pallial oviduct, often called the uterus, the seminal receptacle, and the vagina. A separate birth pore is present in some species through which the larvae are released. The female reproductive system in *V. georgianus* is situated almost entirely ventral to the posterior end of the pallial oviduct (Figure 5-42a–c) (Vail 1977b).

i. Ovary

In living *V. georgianus*, the ovary is long, thin, and translucent with a yellow to gold appearance owing to its contents comprising eggs, embryos, and fluids (Vail 1977b). Relative to the massive albumen gland, the ovary is relatively tiny and somewhat linear. As is typical in viviparids, the ovary is located along the columellar axis of the apical whorl and usually has one or more branches at variable locations along its length. The ovary connects with the albumen gland via a short duct and nearby to it the oviduct, which carries sperm from the seminal receptacle to the albumen gland (Figure 5-42b–d).

ii. Albumen Gland

In living *V. georgianus*, the albumen gland is a large, elongated structure, yellow to gold with concave sides and a ventral ridge, and it is tapered and flattened posteriorly (Figure 5-41d). Most of this gland is positioned beneath the posterior third of the pallial oviduct, behind the posterior end of the mantle cavity (Figure 5-42b–d). Only an anterior, right side lobe projects upward and toward the columellar axis in the region of the ovary-oviduct junction. Several small ducts within the gland anastomose form the wide, short albumen gland duct, which enters the oviduct within the albumen gland at the point of the junction of the ovary with the oviduct (Figure 5-42d) (Vail 1977b). The gland is lined by tall, epithelial secretory cells that secrete albuminous material that completely envelops fertilized eggs (Hyman 1967). Otto and Tönniges (1905) show in their Figures 39 and 40 of Plate XXIV for *V. viviparus* a short, narrow lumen lacking cilia that connects the ovary and oviduct and, like the oviduct and albumen gland, contains spermatozoa.

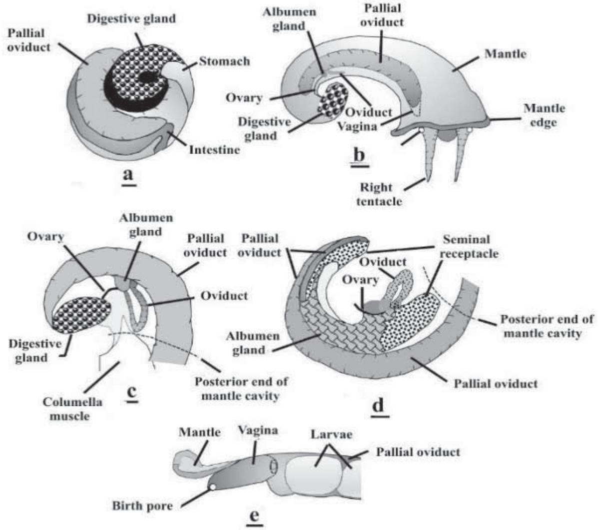


Figure 5-42. Reproductive anatomy of the female *Viviparus georgianus*. All scales below figure letters are 1 mm. (a) Dorsolateral view of intact apical and part of the body whorl to show natural topographical locations; (b) dorsal schematic view of reproductive system in a largely uncoiled animal; (c) dorsolateral view of posterior portion of body whorl; (d) ventrolateral view of relationships of proximal components of the female system; (e) sinistral view of distal end of pallial oviduct and vagina. All are drawn from Vail's (1977b) Figures 32, 33, 35, 36, and 38a.

iii. Oviduct and Pallial Oviduct

The entire oviduct in *V. georgianus* lies posterior to the mantle cavity (Figure 5-42a–e). It connects the albumen gland to the seminal receptacle. In contrast, the pallial oviduct connects to the albumen gland (Figure 5-42d) and carries the fertilized eggs with albuminous protein from the gland to the vagina. The pallial oviduct can be divided into three regions: the proximal part with developing eggs, a middle part with eggs of advanced development, and a distal part with developing to fully developed larvae ready for birth (Vail 1977b). The distal part is often referred to as a brood pouch. The literature is not consistent with the names uterus and pallial oviduct, but the latter is generally preferable (Hyman 1967).

iv. Seminal Receptacle

The elongated, whitish seminal receptacle of living *V. georgianus* is located between the ventral surface of the posterior third of the pallial oviduct and the dorsal surface of the albumen gland (Figure 5-42d). Its anterior and posterior ends are reversed from those of the albumen gland, its blunt posterior end being at the level of the posterior end of the mantle cavity (Vail 1977b); the tapered anterior end of the seminal receptacle curves slightly clockwise and opens ventral lateral side into the posterior end of the pallial oviduct (Figure 5-42c, d).

v. Vagina

The vagina, elliptical in shape, opens at the distal end of the pallial oviduct (Figure 5-42e). Curving slightly to the middle, it terminates nearly at the right edge of the mantle (Figure 5-42e). The elliptical birth pore is on its middle anterior edge. The vagina is dorsally attached to the right edge of the mantle roof for most of its length. The wall of the vagina is muscular, consisting mainly of circular muscle fibers. Vail (1977b) describes the vagina as dark grey due to melanin in its sub-epidermis. In contrast, the region around the birth pore contains numerous flecks of bright orange pigment above a speckled grey background of melanin.

b. *Cipangopaludina chinensis*

Lu, Du, Li, and Yang (2014) examined the reproductive systems of both male and female *C. chinensis* from several provinces in China, and much of the text and illustrations below are from their studies.

i. Males

Sexual dimorphism in shell size exists in some viviparids; *V. contectoides*, males have a smaller maximum height (25 mm) than females (40 mm) (Van Cleave and Lederer 1932); in *V. angularis*, females are generally longer, wider and heavier than males (Pagulayan and Cepillo 1991). No such shell dimorphism has been demonstrated for CMS, but the right tentacle of males is short and distinctly curved in males, both tentacles being slender with narrow tips in females. The male genital system of CMS is shown in Figure 5-43.

i. Testis

Lu, Du, Li, and Yang (2014) describe the testis as a compact, semi-lunar organ in the right mantle cavity (Figure 5-43). It extends to the upper end of the mantle cavity close to the pericardial cavity, housing the heart and the lower surface of the digestive gland. The testis is flattened laterally with its right surface abutting the columellar mussel, while the left surface abuts the right wall of the ureter (Figure 5-43).

ii. Sperm (Spermatozoa)

The dimorphic spermatozoa of *Cipangopaludina chinensis* have received considerable attention, mostly on its synonym, *Viviparus malleatus*, since the early work cited above on *V. viviparus*. The typical and atypical forms are present in CMS, although the morphologies within each form differ among studies. Gall (1961) followed the meiotic divisions of the spermatocytes of each form and found two kinds of spermatocytes present. These give rise to typical uniflagellate sperm (Figure 5-44a), which carry the haploid number of nine chromosomes, and atypical multiflagellate sperm (Figure 5-44b) with only one chromosome. After two aberrant meiotic divisions in the atypical form, centriole clusters give rise to basal bodies that form the posterior flagellar brush (Figure 5-44b). The spiral head of the uniflagellate sperm in *V. viviparus* described earlier is obvious in Figure 5-44a and has been described by others for CMS (e.g., Kaye 1958, Plate 3, Figures 7–9). The multiflagellate form, however, has a somewhat variable form.

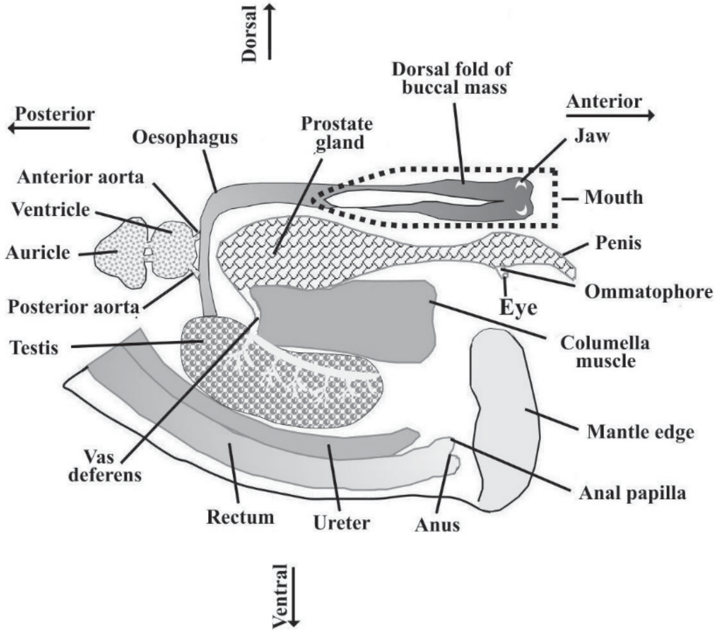


Figure 5-43. Schematic drawing of the male genital system of *Cipangopaludina chinensis* with shell removed to show internal features of animal. Drawn from Figure 2A of Lu, Du, Li, and Yang (2014).

Pollister and Pollister (1943) examined the development of atypical multiflagellate forms of CMS with a primary interest in the formation of the multiflagellate end piece. In most cases in CMS, one spermatid receives a large number of centrioles. The atypical spermatozoon is multiflagellate because each centriole functions as a basal body associated with a flagellated cell. The atypical form of an early adult is shown in Figure 5-44c.

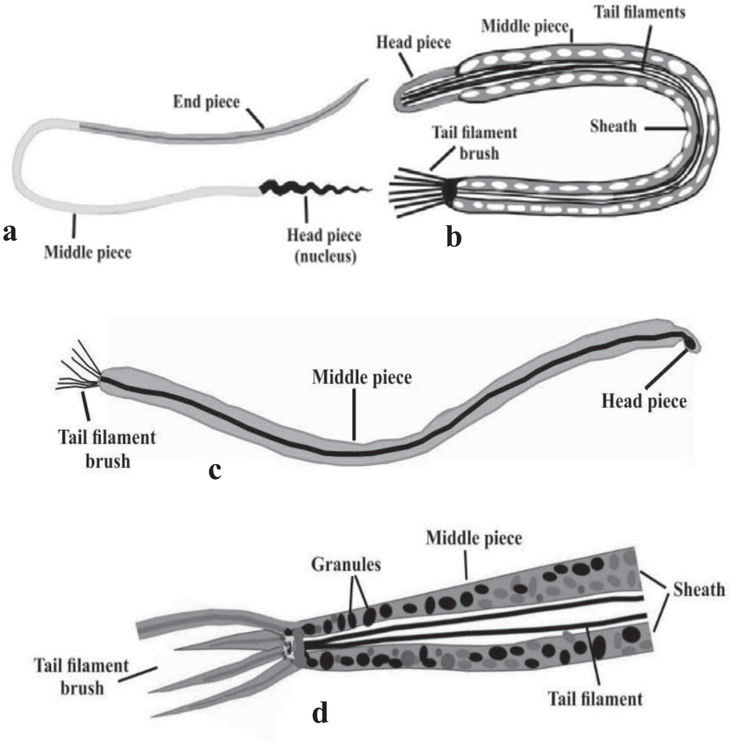


Figure 5-44. Schematic drawings of spermatozoa of *Cipangopaludina chinensis*. (a) An adult typical form and (b) atypical form (both redrawn from Figures 1.5 and 1.15 of Gall 1961); (c) an early adult atypical form (redrawn from Plate 5, Figure 79 in Pollister and Pollister 1943); (d) terminal end of an atypical form of a spermatid (drawn from Plate 306, Figure 20 in Yasuzumi and Tanaka 1958).

Yasazumi and Tanaka (1958) examined the development of typical and atypical spermatozoa of *Cipangopaludina malleata*, another synonym of *C. chinensis*. Their muse of ordinary light micrographs of smear preparations of spermatozoa showed that the typical spermatozoa have the characteristic helical-shaped head, a shrunken middle piece, and a more shrunken end piece. The heads of atypical spermatozoa appear in various forms, long oval, rhombic, or rod shape. The middle piece of atypical spermatozoa is wider than that of the typical ones (compare Figure 5-44a with b and c). The end piece appears brush-like (Figure 5-44d, at 1000x), has 7 to 17 terminal flagella, and operates in one plane on the principle of the pendulum (Yasazumi and Tanaka 1953).

The function of the atypical (oligopyrene) form has been of interest because they are eventually consumed or absorbed within the male or female reproductive system. Dembski (1968) showed that spermatocytes and spermatids, in addition to mature eupyrene and oligopyrene sperm, are deposited in the female's reproductive tract during copulation. He found that pieces of both types of sperm were ingested by the epithelial cells that line the vagina and the brood pouch. Dembski (1968) believes the ingestion of sperm parts by the epithelial cells of the female reproductive tract throughout the year provides the female with a continuous source of nutrition. The intact oligopyrene sperm were not ingested. The oligopyrene sperm disintegrated in the brood pouch and seminal receptacle.

So, what is the purpose of the oligopyrene forms before or after they succumb? Reinke (1914, 236) proposed the following hypotheses: "(a) they may serve as nurse-cells to the eupyrene spermatozoa after copulation and before the latter reaches the seminal receptacle; (b) they may, by the liberation of some substance, stimulate the eupyrene spermatozoa or the eggs or both during fertilization; (c) by the liberation of some substance to which the eupyrene spermatozoa are negatively chemotactic; and (d) they may act as an aid in the final disposition of the latter." Hanson, Randall, and Bayley (1952) and Anderson and Personne (1976) also suggested that the atypical sperm serve as nurse cells and that upon disintegration they provide an energy source for the eupyrenes.

Dembski (1968) found the sheath of the middle piece of the oligopyrene sperm contains glucose granules. After copulation, the disintegration of the oligopyrene sperm and some of the eupyrene sperm released glucose and polysaccharides into the brood pouch and seminal receptacle. He suggested these processes may provide nutrition for the eupyrene sperm as they move toward the seminal receptacle, oviduct, and albuminous gland, where they are stored and later fertilize the eggs. The nutrition is obtained from the disintegrated and ingested sperm found in the albuminous gland that are converted into yolk by the glandular cells of this gland.

Glycogen aids in metamorphosing mitochondria during spermiogenesis of *Viviparus ater* (Ottaviani, Rebecchi, and Fantin 2001). In typical mitochondria and the ovoid mitochondrial complex, cytochrome oxidase activity is restricted to the outer surface of the internal membranes. The glycogen stores are located in the helical heads of the spermatozoon and represent an endogenous substrate pool used to produce energy. Yasazumi, Tsubo, and Matsuzaki (1970) found the middle piece consists of glycoprotein, which seems to have originated from the DNA molecules. Glycoprotein was not found in the plasma membrane or the limiting membrane of any of the bodies constituting the middle piece or tail flagella.

Anderson and Personne (1976) described two types of sperm, Type I and Type II. *Viviparus viviparus, V. malleata,* and *V. japonica* all have Type II sperm with elongate membranous mitochondrial derivatives, a periaxonemal (surrounding an axoneme, the core of a cilium or flagellum) and axonemal structures in the tailpiece, in which the former covers the latter. They reasoned that the spermatozoa are specialized to survive under conditions of high sperm density and low oxygen tension while stored in both males and females. They proposed that glycogen located in the middle piece and flagellum of the spermatozoa may well be an essential endogenous energy source. The glycogen presumably serves as a source of energy for metabolism and motility.

iii. Vas deferens

Lu, Du, Li, and Yang (2014) describe the vas deferens as very narrow, running on the testis' columellar and inferior ventral margin. It has two main branches: an anterior branch with five to six parallel secondary branches and a shorter branch that connects the anterior branch to the prostate gland (Figure 5-43). The secondary branches send numerous anastomosing branches throughout different portions of the testis. The vas deferens opens in the distal third of the testis and runs to the prostate gland in the mantle cavity along the mantle cavity floor for about three-quarters of its length. There, the vas deferens abruptly narrows and is surrounded by very thick, muscular walls. It runs along the right cephalic tentacle, its inner surface relatively broad, with some inner, longitudinal folds (Lu, Du, Li, and Yang 2014). This format is similar to *V. angularis* (Pagulayan and Cepillo 1991), who found a smooth, thickly muscular appearance in contrast to the grainy appearance of the testis. The vas deferens spans most of the entire length of the mantle cavity, then narrows into a terminal vas deferens that passes through the right tentacle and opens at its tip.

iv. Seminal Vesicle

Lu, Du, Li, and Yang (2014) did not describe a seminal vesicle in CMS. Presumably, the vas deferens is modified to store sperm somewhere along its path through or along the prostate gland or receives a duct from the prostate gland. However, some prosobranchs lack a seminal vesicle; the sperm duct runs its course without showing any differentiation (Hyman 1967). In *V. angularis*, for example, the vas deferens passes through the posterior end of the food groove and then enters the prostate gland and passes forward beneath the groove toward the right tentacle; no seminal vesicle was reported (Pagulayan and Cepillo 1991).

v. Prostate Gland

Lu, Du, Li, and Yang. (2014) did not elaborate on the structure of the prostate gland. Figure 5-43 shows the prostate gland as a large organ situated just dorsal to the testis. In most prosobranchs, the prostate gland is lined by a tall epithelium of cuneiform ciliated cells and large gland cells filled with secretion spherules (Hyman 1967). Pagulayan and Cepillo (1991) found that the prostate gland in *V. angularis* has a thin muscular coating of an external circular muscle layer and an internal longitudinal muscle layer around the entire tissue, consisting of simple cuboidal cells.

vi. Copulatory Tentacle (Penis)

The vas deferens opens in the right tentacle tip as a broad papilla with a rounded tip and possesses a deep concavity located on the right of the genital papilla, which can retract into its concavity (Lu, Du, Li, and Yang 2014). The copulatory tentacle is often described as hooked, being distinctly curved.

b. Female

Figure 5-23a, illustrated earlier for digestive systems, shows the configuration of some female components of CMS with the shell removed.

i. Ovary

Lu, Du, Li, and Yang (2014) describe the ovary as grey in living animals, located in the same position as the testis and in close contact with the posterior wall of the cardiac region of the stomach and along the course of the hepatic artery.

ii Albumen Gland

The albumen gland is tongue-shaped and slightly curved, with the eggshell gland on the dorsal and posterior surface; the gland opens into the brood pouch (Figure 5-23a) (Lu, Du, Li, and Yang 2014).

iii. Oviduct

The oviduct is very narrow, running from the albumen gland to the posterior end of the columella, where it turns left, making a loop. Then, the oviduct increases in size.

iv. Seminal receptacle

Lu, Du, Li, and Yang (2014) did not report on aspects of the seminal receptacle of CMS. It is a key structure in all females because it temporarily stores sperm from males during and shortly after copulation. Ova must pass by the receptacle to be fertilized. The seminal receptacle is usually located between the posterior part of the pallial oviduct and dorsal to the surface of the albumen gland, as in *V. georgianus*.

v. Pallial Oviduct (Uterus, Brood Pouch)

The pallial oviduct is located dorsal of the intestine (Figure 5-23a). The walls of the pallial oviduct are thin, semitransparent, and smooth. The brood pouch may be filled with about 45 to 84 embryos in various stages of development (Lu, Du, Li, and Yang 2014).

c. *Cipangopaludina japonica*

Van Bocxlaer and Strong (2016) examined male and female *C. japonica* from rivers and lakes in Virginia and gave detailed descriptions with excellent illustrations of both males and females. Figures 5-46 and 5-47 are schematic drawings of their images and drawings. The following descriptions are also from their article.

a. Males

Male and female shells differ slightly, with females having slightly more inflated body whorls than males, as shown in Figure 3 of Van Bocxlaer and Strong (2016). The only prominent sexually dimorphic feature of JMS is the right copulatory tentacle is shorter, stouter, and more distinctly curved than that of the female. Figure 5-46 illustrates the male genital system of JMS.

i. Testis

The testis is situated at the right side of the pallial cavity, bordered ventrally and on the right by the columellar muscle and the ureter on the left (Figure 5-45). It is semilunar to bean-shaped with a more expansive, rounded dorsal side and a more pointed ventral side. The testis in Figure 5-45 is deflected to the left from the dorsal position to expose other parts of the genital system. The left side of the testis is more convex, whereas the right side is concave. The organ is compartmentalized, with the vas deferens branching into smaller canals and anastomosing into the seminiferous follicles. The smaller tubules drain the follicles, the sperm being conveyed to converging canals, which connect to the central drainage canal in the ventral region where the vas deferens emerges (Van Bocxlaer and Strong (2016)).

ii. Sperm

Details on sperm structure in JMS are desiring. However, in light of the descriptions of sperm given previously for *Viviparus* species and CMS, the sperm of JMS are likely dimorphic, the typical sperm being uniflagellate with a spiral or screw-like nuclear headpiece. The number of chromosomes appears to differ among species, with a haploid number of seven chromosomes in *V. viviparus* and nine chromosomes in CMS; the number of chromosomes in JMS appears unknown.

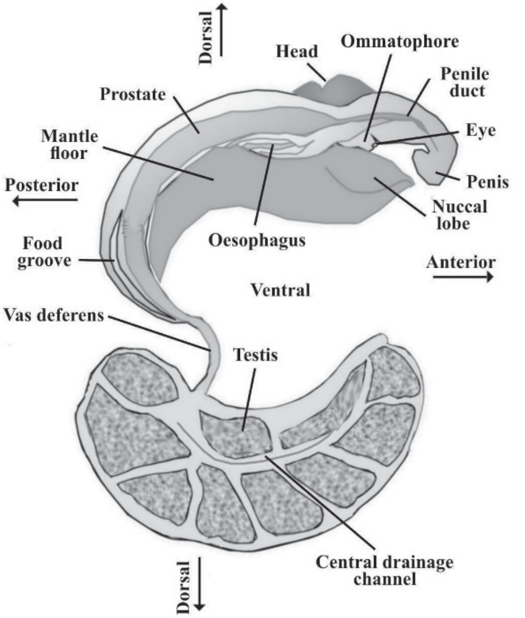


Figure 5-45. The male genital system of *Cipangopaludina japonica*. See text for details. The figure is drawn from Figure 11 of Van Bocxlaer and Strong (2016).

iii. Vas Deferens

The vas deferens in JMS crosses just below the mantle floor toward the elevated area underneath the food groove at the left of the mantle cavity (Figure 5-46). There, it opens to the prostate base, which continues anteriorly below the food groove for more than half the length of the mantle cavity (Van Bocxlaer and Strong 2016). After leaving the prostate, the vas deferens deflects into the penile duct.

iv. Seminal vesicle

Van Bocxlaer and Strong (2016) did not report a seminal vesicle in their study of the genital system of JMS. In Viviparidae, usually the sperm duct, shortly after leaving the testis, enlarges and is thrown into numerous convolutions that act as seminal vesicles for sperm storage (Hyman 1967). In *C. japonica* the vas deferens is enlarged in the food groove region before entering the prostate gland, perhaps acting as a seminal vesicle (Figure 5-45) Van Bocxlaer and Strong (2016).

v. Prostate Gland

Details of the prostate gland structure were not given by Van Bocxlaer and Strong (2016) in their study of the male reproductive system of JMS. The prostate gland of JMS is probably like many viviparids. In this case, it is likely comprised of gland cells, cuboidal ciliated cells (Hyman 1967), and many tubules radiating from a central seminal lumen, the tubules being lined with secretory cells containing spherules, as in described in *Siamopaludina martensi* and *Filopaludina sumatrensis* by Berry (1974). The prostate gland secretes seminal fluid for conveying sperm to the penis, the cilia of the ducts being the conveyance mechanism and not the flagella of the sperm (Hyman 1967).

vi. Copulatory Tentacle (Penis)

The penile duct conveys sperm into the right tentacle before reaching the head. In this copulatory tentacle, the glandular penile duct continues below the central blood vessel and the tentacle nerve, which are more conspicuous and better developed in the male than in the female JMS (Van Bocxlaer and Strong 2016). The male gonopore opens at the tip of the tentacle. The tentacle and the process of copulation are described later under d) Copulation.

b. Females

The reproductive organs of the female JMS encompass the pallial cavity and part of the visceral mass to the posterior end of the pericardium, and the junction of the intestine with the rectum (Figure 5-46a) (Van Bocxlaer and Strong (2016).

i. Ovary

The ovary is very small in *V. japonica*. It consists of an elongate, lobate mass ventral to the anterior lobe of the digestive gland and follows the columellar aspect of the pericardium (Figure 5-46a, b) (Van Bocxlaer and Strong 2016). It borders the posterior esophagus at the right and extends posteriorly to the anterior ducts of the digestive gland (Figure 5-46a). It constricts somewhat at its anterior end, connecting to the very short visceral oviduct (Figure 5-46b).

ii. Copulatory Bursa

The distal, ascending limb of the renal oviduct has a slightly wider diameter than the proximal limb in *C. japonica*. It opens to the bulbous tip of the copulatory bursa, roughly at the level of the connection between the proximal limb and the seminal receptacle (Figure 5-46b). The bursa is an elongated tube extending posteriorly and bordered by the albumen gland and the seminal receptacle their entire length (Figure 5-46b). Cross-sections through the bursa reveal a conspicuous outer layer of circular muscles embedded in connective tissue, as shown in Figure 13E of Van Bocxlaer and Strong (2016). Its lumen is lined by conspicuous longitudinal folds containing copious quantities of unoriented eusperm. The distal bursa opens largely to the posterior end of the albumen gland (Figure 5-46b).

iii. Visceral and Renal Oviducts

The visceral oviduct continues anteriorly as the renal oviduct, which forms a narrow, muscular, ciliated U-shaped tube at the ventral margin of the proximal brood pouch (Figure 5-46a, b). The narrower, proximal, descending limb of the renal oviduct is connected with a seminiferous duct to the seminal receptacle. A gonopericardial duct is lacking (Van Bocxlaer and Strong 2016).

iv. Albumen Gland

The voluminous albumen gland is lined interiorly by tall, drooping, glandular, longitudinal folds (see Figure 13C in Van Bocxlaer and Strong 2016). The gland has a longitudinal ventral channel lined with numerous goblet cells, extends forward along the left floor of the albumen gland, and enlarges anteriorly. Van Bocxlaer and Strong (2016) found unoriented eusperm and parasperm in the vicinity of the channel. They also observed large quantities of flocculent material within which small, unencapsulated developing embryos were embedded. The albumen gland opens widely at its anterior end into the voluminous, thin-walled brood pouch, which spans about five times the length of the albumen gland. A tall, longitudinal fold extends the length of the brood pouch along its ventral floor; it is bilobed in cross-section, with a tall, free-standing left arm and a smaller, thicker right arm under which passes the sperm groove, the anterior extension of the albumen gland ventral channel.

i. Seminal Receptacle

The seminal receptacle of *C. japonica* is complexly branched by the seminiferous duct (Figure 5-46c) (Van Bocxlaer and Strong (2016). The duct enters at the anterior ventral margin of the seminal receptacle and continues posteriorly along the right ventral aspect of the receptacle (Figure 5-46c). Acini of the seminal receptacle contain numerous eusperm with their heads oriented toward the lumen.

ii. Brood Pouch (Pallial Oviduct)

Embryos become encapsulated in the posterior brood pouch, which is homologous to the capsule gland. Strings of capsule gland material form at the angular intersections of the freshly encapsulated eggs but disappear anteriorly as the eggs mature. In smaller females, the eggs in the brood pouch usually maintain a tightly packed formation (with angular margins). Still, these angulations disappear as the eggs mature, and in large females, the eggs typically obtain a more chaotic arrangement. In large females, the brood pouch usually contains many eggs, embryos and juveniles in advancing stages of development toward the anterior end (Figure 5-46a). Developing juveniles usually rupture the egg membrane before birth (Van Bocxlaer and Strong (2016).

Anteriorly, the pallial oviduct narrows and bears a set of transverse epithelial folds (Figure 5-46a) before narrowing further and terminating near the mantle collar in the vagina. The vagina is a free-hanging muscular tube with a round terminal gonopore (Figure 5-46a).

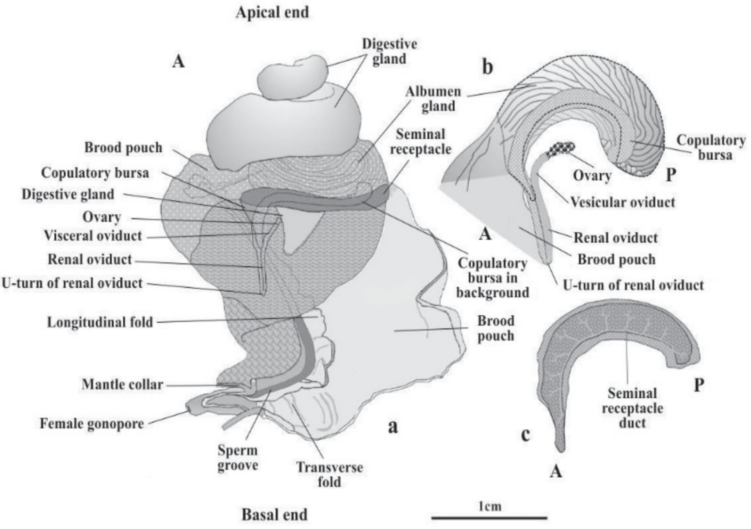


Figure 5-46. Reproductive system of female *Cipangopaludina japonica*. (a) Overview orientation with brood pouch cut and reflected back. (b) Oblique left-ventral view of albumen gland and copulatory bursa, position of seminal receptacle indicated by dashed line. (c) Seminal receptacle. A = Anterior, P = Posterior. Drawn from Figure 12A–C in Van Bocxlaer and Strong (2016).

c. Copulation

The penis structure of *V. viviparus* is described and illustrated in Fretter and Graham (1962). Mating rituals vary among species and seasons. The vas deferens runs through the right tentacle to a digitate process, which usually lies folded back in a pouch on the right, ventral side and opens at the apex of the bent tip (Figure 5-47). At copulation, the male inserts its penis into the copulatory bursa of the female and fills it with sperm. The male then withdraws from the female.

According to Moquin-Tandon (1855) the copulation act of *V. viviparus* is done without a prelude and the male crawls on the female's shell, arriving on the edge of the right side of the female. The male then unites with the female. She holds her tentacles tilted on the trunk of the male. The two molluscs then rub their heads against the surrounded bodies and withdraw from time to time.

Dembski (1968) described an odd copulation-like behavior between males during the spring and summer months, terming it pseudocopulation. He proposed this behavior resulted from an unknown sex-stimulating substance released by the female. In the vicinity of males, the substance stimulates the males to copulate with a female. His rationale was that a subsequent examination of the mantle cavity of the male, which played the role of the female during copulation between two males, revealed that no sperm transfer had taken place.

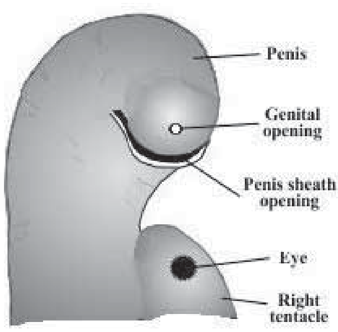


Figure 5-47. Details of the penis of *Viviparus viviparus*. Drawn from Figure 183B in Fretter and Graham (1962).

8. Circulatory System

All gastropods have an open circulatory system in which blood leaves vessels and fills spaces called hemocoels or sinuses that never open to the exterior. The heart is enclosed in a pericardial sac. The sac also serves as an essential structure in the excretory system as discussed in B. Internal Anatomy, Excretory System, b) Pericardium.

a. Blood (Hemolymph)

Two kinds of blood occur in molluscs: hemoglobin and hemocyanin. Of the aquatic gastropods, most pulmonates have hemoglobin, which has iron as its proteid pigment. Most prosobranchs have hemocyanin, which has copper as its proteid pigment.

Hemocyanins are giant molecules with about half a million molecular weights up to about 10 million (Brohult 1947). *Viviparus*' hemocyanin has a molecular weight of 8,700,000 (Ghiretti 1966).

Hemocyanin is a proteid containing carbon, hydrogen, nitrogen, sulfur, and two atoms of copper as its core (Kato, Matsui, Gatsogiannis, and Tanaka 2018). Hemoglobin is an albuminoid with the same elements as hemocyanin (C, H, N, S), but has iron (Fe) at its core. Hemocyanin functions in a similar but weaker fashion to hemoglobin by absorbing oxygen dissolved in the water and carrying it to the body's inner tissues. It has a bluish or violet color when rich in oxygen, but it gradually becomes colorless as oxygen is stripped from the pigment as it passes through the tissues (Kato, Matsui, Gatsogiannis, and Tanaka 2018). Hemoglobin has a greater affinity for oxygen than hemocyanin, especially at low DO levels. Invertebrates, like tubificid worms (e.g., *Tubifex* and *Limnodrilus*) and blood worms (insects of the genus *Chironomus*) can survive under aseptic conditions and are classified as pollution-tolerant or pollution-indicator organisms (Mackie 2004). Invertebrates with hemocyanin, especially viviparids, cannot survive under low DO tensions for long periods, as discussed later in the Ecology chapter.

b. Heart

Viviparids have a heart with one ventricle and one auricle, hence their classification as Monotocardia. In all Monotocardia, the ventricle gives off an aortic trunk, which immediately bifurcates into an anterior (cephalic) and posterior (visceral) aorta. In viviparids, the posterior end of the ventricle narrows and opens into an expansion, the aortic bulb, which is also known as the *truncus arteriosus* (Morton 1956) or bulbus aortae (Andrews 1979). The bulb forms a third chamber of the heart, giving rise at either end to the anterior or cephalic aorta and the posterior or visceral aorta. It bulges against the posterior side of the pericardium and is composed of non-contractile fibrous connective tissue (Morton 1956).

Andrews (1979) examined the heart of the Japanese Mystery Snail and provide a schematic drawing of its structure (drawn in Figure 5-48). The auricle is dividable into a central muscular portion and paired lateral compartments, the left end being expanded, the right end being contracted in Figure 5-48. Both lateral compartments are specialized for filtration of blood through the auricular walls, having pedicels with podocytes (see Excretory System for details). When the auricle is contracted, the pouches are dilated and filled with filtrate. Transverse bands of muscle form the innermost layer of the wall in the central part, and branches of these spread out laterally, where they attach radially to the basal lamina (Andrews 1979). They produce the superficial pouches of the wall on contraction, shown in Figure 5-48 in the contracted end. Another set of horizontal muscles runs in an anteroposterior direction (vertical in Figure 5-48), and their contraction isolates the lateral from the central regions of the auricle. Longitudinal muscles lie peripheral to the horizontal ones around the central part but are absent from the lateral compartments of the auricle. They extend into the walls of the ventral channel as circular fibers (three appear on each side in Figure 5-48). This arrangement of muscles results in systole separating the central part of the auricle, which refills the ventricle, from the lateral parts, which produce the primary urine by filtration (Andrews 1979).

The ventricle of JMS is pear-shaped. Its narrow base opens anteriorly to the ventral channel of the auricle and immediately posterior to this, to the bulbus aortae (Figure 5-49). Some stout bands of muscle in this region are continuous with longitudinal muscles in the wall of the ventral channel of the auricle. Still, the rest of the musculature forms a dense network of fibers of uniform thickness over the whole wall (Andrews 1979).

The bulbus aortae of JMS (Figure 5-49a, b) has a thin wall and a spacious lumen uninterrupted by muscles that are arranged in circular and longitudinal layers (Andrews 1979). No pumping pulsations in the bulbus aortae appear to provide room for blood forced out of the mantle skirt when the snail is retracted. There were no valves at the point where it bifurcates into anterior and posterior aortae in the ventral wall of the pericardial cavity (Andrews 1979).

c. The Arterial System

The anterior or cephalic aorta passes forward through the hemocoel of the body to supply the organs of the head, foot, anterior body, and mantle. Near its origin, it gives off a large branch to the style sac and the stomach. The remainder of the visceral mass draws its blood supply from the posterior aorta.

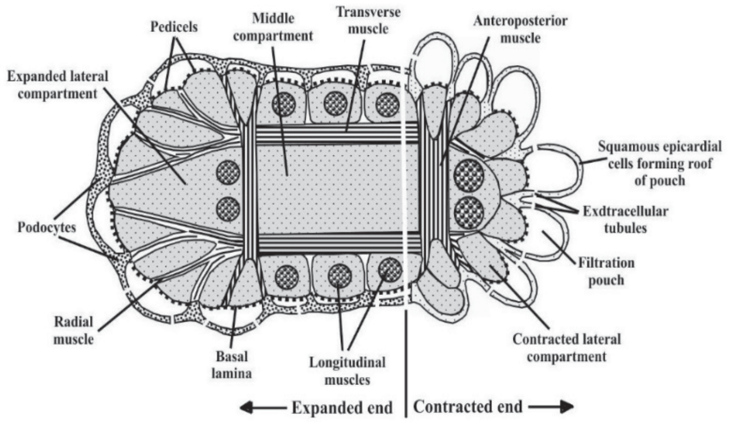


Figure 5-48. Diagrammatic representation of the transverse section of the whole auricle of *Cipangopaludina japonica*, showing partially contracted lateral compartment on the right. Not drawn to scale. Drawn from Figure 2b of Andrew (1979).

The cephalic aorta runs just beneath the pericardium, directly alongside the esophagus, to enter the cavity of the trunk on the left side (Figure 5-49). The cephalic aorta gives rise to several branches, including a gastric artery, that innervates the style sac and stomach, especially the sorting area. In the course of the passage of the cephalic artery, it gives rise to (1) a subcutaneous artery, (2) an artery to the outer integument, (3) esophageal arteries splitting regular intervals into the esophagus, (4) a sub-intestinal artery, (5) a pallial artery that divides into anterior and posterior branches of the mantle, and (6) a pedal artery that sends off branches to the anterior and lateral margins of the foot. When the foot is extended, the pedal sinus has little to no blood, but as the foot relaxes, blood is expelled into the cephalic sinus and the hemocoel of the body (Morton 1956).

Several longitudinal intestinal arteries, run beneath the intestinal epithelium and arise from the posterior aorta near its origin from the heart. The posterior or visceral aorta turns abruptly backward from the bulbus aortae and passes between the style sac and digestive gland. From here, two small arteries arise, one to the middle intestine and one that splits into the anterior parts of the rectum and gonad. Arteries also innervate the digestive gland, the albumen and prostate glands and the genital ducts (Figure 5-49).

d. The Venous System

Morton (1956) describes several sinuses in the prosobranchs. The cephalopedal sinus is a wide space lying upon the floor of the hemocoel. It is formed by two closely separated parallel sinuses, the right and left cephalopedal sinuses, the right being larger than the left. The cephalopedal sinus receives blood from closed veins off the tentacle, penis, subcutaneous layer, and mantle (Figure 5-50). The venous blood gathers in lacunae, which fuse into increasingly larger sinuses.

The two cephalopedal sinuses converge into a narrow canal that widens into a pedal sinus that forms a large cavity in the foot; it is flooded with blood when the foot expands (Figure 5-50). The left and right cephalopedal sinuses converge also into another narrow canal that empties into a triangular subrenal sinus that receives blood from the cephalopedal sinus and the visceral sinus (Figure 5-50). Thus, depending on the species, blood from the subrenal sinus reaches the auricle by one of four paths: (1) through the ctenidial systems alone, the blood being conveyed via the rectal sinus to the afferent lamella and then to the auricle via the efferent renal vein; (2) through the renal organ alone by the left renal portal vein, then to the auricle via the left efferent renal vein; (3) through both the renal organ and the ctenidia; (4) or through the mantle alone, directly to the efferent ctenidial vein into the auricle (Figure 5-50).

Venous blood from the subrenal sinus is distributed to either the renal portal or afferent renal sinus veins, which open directly into the rectal sinus (Morton 1956). The visceral sinus receives blood from numerous veins of the digestive gland and gonads as well as stout gastric veins from the stomach (Figure 5-50). A large efferent ctenidial vein passes along the left edge of the ctenidium and receives blood through a series of wide apertures from the basibranchial sinus. This vein passes through the posterior wall of the pallial cavity into the pericardium, opening through the anterior end of the auricle (Morton 1956).

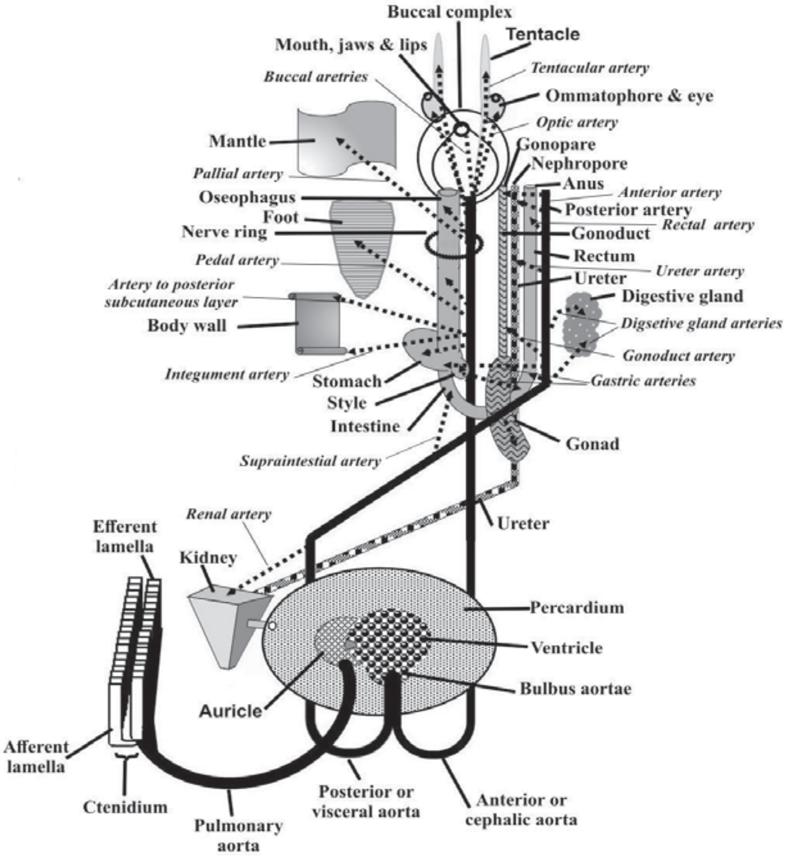


Figure 5-49. Schematic of the arterial system of Viviparidae showing the main organs and their arteries in heavy dashed lines with arrows.

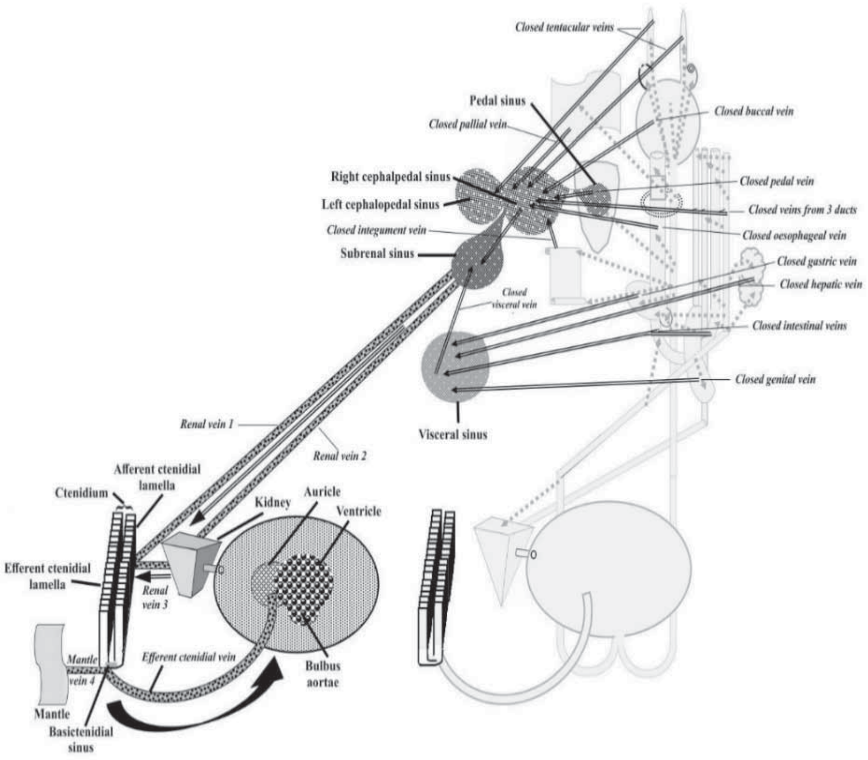


Figure 5-50. Schematic drawing of the venous system of Viviparidae. The arterial system is faded on the right to show the relationship of the two systems.

9. Muscular System

According to aficionados of escargot, the flesh consists of masses of muscles constituted by bundles of fibers together enveloped by a strong membrane. Each fiber element is surrounded by a thin sheath of connective tissue and arranged with its length parallel with the direction of pull of the muscle (Taylor 1900). Connections with nerve cells cause the filament to contract when stimulated and draw together the opposite ends of the muscle, which are affixed to the point of origin (e.g., bone) and insertion (e.g., tendon).

The muscles of all prosobranchs are either voluntary or involuntary, depending on whether they are or are not under the control of the animal. Some voluntary muscular movements may merely be reflex actions responding to external stimuli. Involuntary muscles are nonstriated and predominate in molluscs, especially in the abdominal muscle layers (e.g., intestine, stomach, hepatopancreas, kidney) and are usually composed of exceedingly elongated, smooth muscle fibers. They typically contract slowly and rhythmically, as exemplified in muscle contraction and relaxation (peristalsis) in the digestive tract. Smooth muscles usually work over greater length ranges than striated ones.

The voluntary muscles are pseudo-striated (i.e., faintly striated) in molluscs. They are primarily retractors but also include the buccal mass of many gastropods, the epidermal muscles, protractors (e.g., radula protractors), levators (e.g., gastropod neck muscles), and extensors (e.g., columellar muscles). Many muscles, especially protractors, are coordinated with concerted blood pressure, as in the protrusion of the foot of gastropods and bivalves. The striation is incomplete or absent in lethargic molluscs and most pronounced in the more active forms.

Molluscs have different types of muscles to perform a variety of functions. Circular muscles radially contract or constrict and force fluids forward of the constriction. Longitudinal muscles shorten the structure they envelop and, in the process, pull it toward the origin. Obliquely striated muscles contain bands of thick and thin filaments that are arranged helically. Obliquely striated muscles maintain tension over long periods without using too much energy, such as maintaining the operculum’s closure.

The literature abounds in the ultrastructure of the muscles of many gastropods (e.g., Hoyle 1964; Hunt 1972; Plesch 1977a, b), but unfortunately, viviparids are not among the taxa examined. However, many gastropods studied for musculature are streptoneurans, to which viviparids belong, and are incorporated into the following discussion.

In the brief initial introduction to the muscular system of gastropods, it should be evident that many other systems are involved. The following discussion examines the musculature in the different structures and systems of viviparids, following the order of their presentation, first for the external morphology: (a) shell (columella), (b) head (neck, buccal mass, and tentacles), (c) operculum, and (d) foot; this is followed by the internal anatomy: (e) torsion, (f) digestive system, g) respiratory system, (h) excretory system, (i) reproductive system, (j) circulatory system, and (k) nervous system.

a. Columellar Muscle (Spindle Muscle, Shell Muscle)

The columellar muscle is one of the largest muscles in prosobranchs, the foot being another. The general character of molluscs' musculature largely depends on the development of a protecting shell, which provides a firm attachment for the retractor muscles of the body to enable the animal to withdraw within its shell or to push the body out of the shell. The columellar retractor muscles function in the withdrawal of the head, buccal mass, sensory tentacles and eyes, and the operculum.

Brown and Trueman (1982) examined the columella muscles of five prosobranchs, one freshwater pulmonate, and one land snail. Most fibers in this muscle lie parallel to its winding axis, and their contraction draws the animal into the shell. Also present are fibers running at right angles to the longitudinal fibers, the fibers forming a three-dimensional network. When any one of the dimensions is held constant, the muscles in the other two planes may antagonize each other directly (Brown and Trueman 1982). Shortening of the muscle results in its thickening, or by tension of the dorsoventral and or transverse fibers. The tension in the dorsoventral and or transverse fibers causes elongation of the longitudinal fibers. The columellar muscle as a whole exerts a force that pushes the foot out of the shell (Brown and Trueman 1982).

The columellar muscle is affixed at its distal end to the columella near the commencement of the penultimate whorl. In CMS, the columellar muscle is thick and flat (Figure 5-23a); in JMS, it is moderately long, extending 0.5–1.0 whorl posteriorly (Van Bocxlaer and Strong 2016). Brown and Trueman (1982) and Thompson, Lowe, and Kier (1998) described the columellar muscle of three prosobranch snails as a flat, sheet-like muscle that originates on the lower part of the columella and inserts on the operculum. They found the muscle comprised a three-dimensional array of muscular and connective tissue fibers. The fiber arrangement includes three regions that grade into one another: (1) nearest its origin, the muscle consists primarily of longitudinal muscle fibers with a few dorsoventral or transverse fibers and no oblique fibers; (2) the middle portion of the columellar muscle consists of longitudinal, dorsoventral, and transverse fibers enveloped by two opposed layers of oblique fibers; and (3) the third region extends through the foot and includes longitudinal, transverse, and dorsoventral fibers with a layer of oblique fibers on the dorsal surface. Compared to a muscle that is circular in cross-section, the elliptical cross-sectional shape may increase the muscular force necessary to twist the foot relative to the shell and may decrease the resistance to buckling (Thompson, Lowe, and Kier 1998). Frescura and Hodgson (1992) describe two types of muscle in five prosobranch species. Type I cells are present in all prosobranchs and contain randomly thick and thin filaments, the diameters of which varies among species; Type II cells contain bundles of thin filaments that are striated in appearance and are associated with collagenous connective tissue but are present in only some species. The types of cells in viviparids are unknown.

Price (2003, 352) describes three functions to columellar folds: “1. guidance”, whereby the folds guide the columellar muscle as the animal moves in and out of the shells, like “a railroad track guiding a train,” to prevent the animal from slipping in its shell; “2. maneuverability, whereby the folds enhance a snail’s ability to, “maneuver its shell”; and “3. predator avoidance”, by withdrawing “more deeply into their shells, increasing their ability to escape from predators”.

b. Head (Cerebral) Muscles

The cerebral retractors of prosobranchs form an essential part of the body’s musculature, the principal components being the pharyngeal (neck and buccal mass) and tentacular retractors. The pharyngeal and buccal musculature is discussed later in this section, under (g) Buccal Apparatus.

In prosobranchs, the tentacular retractors are paired, matching muscles for the body’s right and left sides. They are united posteriorly with the columellar muscle. The right copulatory tentacle of the male in the Viviparidae is stouter than the left and has a thicker musculature of smooth muscle. The penial retractor is unpaired and attached to the distal end of the penis sheath and the floor of the mantle cavity.

Retractors also innervate the right and left ommatophores, the paths differing between males and females (Taylor 1900). The tentacles of viviparids are not invaginable and lack retractors for their withdrawal. Instead, each of the tentacular retractors, before entering the tentacles and before re-bifurcating, gives off a broad tripartite muscle to the anterior part of the foot; the retractor of the dorsal tentacle expands noticeably before reaching the apex, while that to the lower tentacle again divides, sending a strong branch to the lip (Taylor 1900).

c. Operculum

Due to a concentric operculum on the dorsal surface of the foot, the columellar retractor in the viviparids exhibits a special modification. According to Checa and Jiménez-Jiménez (1998), the concentric turns seal together, and the rotation of the operculum is allowed to approximate the aperture size. Migration of the operculum into the aperture is permitted by its connection to the adoral end of the columellar muscle, which constitutes an efficient means of retraction, sealing, and resistance against extraction by predators. When an increase in size occurs on the whole surface of the foot lobe and more or less equally around the sub-central nucleus, the opercula do not alter their position upon the retractor muscle to which they are attached. Instead, as Checa and Templado (1998) reported, they adjust by growing in the aperture-closed position and fit snugly into the whorl. The retractors pass beneath the mantle cavity, along the inner or right side of the spiral, dividing to the right and left into numerous fibers that interlace with the foot's tissues.

Chiu, Chen, Lee, and Chen (2002) analyzed the variation in operculum characters in five populations of CMS and found less variation in most characters than in shell dimensions, mainly because the operculum characters were highly variable among individual snails. This variation suggests that the growth dynamics of the columellar muscle attached to the operculum is equally varying.

d. Foot

Earlier (see External Morphology, 6. Foot), the prosobranch foot is described as highly glandular with ciliated epithelial cells alternating with mucocytes, with the sides and dorsal surface of the foot mostly covered with non-ciliated, cylindrical epidermal cells often interspersed with mucocytes. Voltzow (1990) describes the prosobranch foot as primarily solid muscle consisting of two distinct regions, the columellar muscle region and the tarsos region. The columellar muscle region consists of thick bundles of muscle fibers bounded in connective tissue sheaths and arranged in a perpendicular lattice network. The tarsos also consists of bundles of muscle fibers wrapped in connective tissue sheaths. Still, large bundles from the dorsal portion of the foot divide into finer and finer branches as they contact the sole and sides of the foot, thus forming a network of small groups of muscle fibers embedded in a dense connective tissue matrix (Voltzow 1990). The muscle fibers of the columnar muscle region perform gross shell-foot movements, like protrusion, retraction, shell elevation (levator), and twisting. The tarsos muscle system furnishes more delicate movements of the foot, including propagation of locomotion waves. In both regions, one set of muscle fibers can directly antagonize another.

For burrowing gastropods, Trueman and Brown (1976) propose both muscular and hydraulic processes. First, the propodium is extended while the snail is anchored by the metapodium, which acts as a penetration anchor;

when the foot is buried, the shell follows. Second, the shell is drawn forwards and downwards toward the anchored propodium, the terminal anchor. Thus, snails that contain a greatly enlarged pedal sinus containing blood can function as a hydraulic organ. During each burrowing cycle, there are two pressure pulses. One affects propodium extension; the second draws the shell forwards. During this part of the locomotory cycle, the pedal hemocoel is separated from the remainder of the circulatory system, thus enabling the foot to function as a fluid muscle system at constant volume. In this burrowing mechanism, pedal extension involves both blood flow, the foot functioning as a hydraulic system, and direct muscular antagonism between the fibers of a three-dimensional muscle network in the opercular muscle.

e. Torsion

As described earlier, the muscles involved in torsion consist of a right-sided cephalic retractor with posterior attachment and a left-sided pedal retractor with an attachment in front of the other, the two crossing one another more or less at right angles. Eales (1950) showed that the velar retractor muscle initiates torsion. During larval development, contraction of the velar retractor muscle results in its straightening in a counter-clockwise direction, then a twisting of the neck through 90°, whereby the foot and operculum are placed at right angles to the mantle and pallial cavity, instead of being enclosed by them, and the displacement of the visceral mass toward the left.

f. Digestive System

Smooth muscles abound in the digestive system of prosobranchs, beginning from the mouth to the anus.

g. Buccal Apparatus

The buccal apparatus includes the mouth and pharynx. The mouth bears the buccal bulb; the buccal cavity with its odontophore and radula, and their musculatures; the jaw; the salivary gland. Amaudrut (1898) examined the buccal apparatus and its musculature of prosobranchs (Figure 5-51a). He considered the buccal cavity a dihedron, a polygon with two faces (the bulb and esophagus) that share the same set of edges, with the esophagus in the upper invagination set at a dihedral angle with the posterior region of the bulb demarked by a prolongation of the upper radular sac wall (Figure 5-

51a). Intrinsic and extrinsic muscles protract the odontophore, while superior and lower retractor muscles return the odontophore (Figure 5-51a).

The pharyngeal or buccal retractors are always median. They consist of paired and slightly divergent muscular slips or a more powerful single muscle. Still, they always pass through the nerve ring to become fixed to the buccal bulb by divided or by expanded extremities (Taylor 1900). The two pharyngeal retractors are separated muscular strands emanating from the columellar muscle attached to the buccal bulb. The pharyngeal or buccal retractor originates adjoining to and immediately in advance of the paired tentacular muscles, forming a sturdy ribbon-like muscle that divides before attaching to the buccal bulb ventrally and laterally by the broadened ends.

The buccal bulb also has extrinsic muscles that originate in another part than its insertion. The extrinsic muscles of the buccal bulb consist of the pharyngeal retractor and several slender, muscular bands that pass from its exterior to the walls of the anterior region of the body (Figure 5-51a). They function as a retractor, levator, or protractor muscle. The bulb also has intrinsic muscles, a group of muscles located within or situated deeper in its structure, in contrast to superficial extrinsic muscles (Figure 5-51a). The intrinsic muscles of the buccal apparatus are formed chiefly by the protractor and retractor fibers. They are attached to the radular cartilage anteriorly and posteriorly, respectively, conveying the motion to the radular membrane.

The muscles of the radula and odontophore were discussed earlier (2. Digestive System, a) Radula, and b) Odontophore) and illustrated in Figures 5-19 and 5-1. The following describes muscles of the bolster or radular bolster and the cartilage or odontophoral cartilage. The definitions of the terms used here are from Katsuno and Sasaki (2008): the bolster or radular bolster is any radula-supporting structure that possesses odontophoral cartilages but lacks true cartilaginous tissue. The odontophoral cartilage is any rigid structure in the odontophore composed exclusively of similar-sized inflated cells partitioned by an extracellular matrix.

Approximator muscles control the cartilages or radular bolsters and insert them on their ventral, medial, or outer lateral areas. These include a ventral approximator muscle, a ventral approximator muscle dorsal layer, and a ventral approximator muscle ventral layer. For example, in CMS, the cartilages are connected ventrally by a single-layered ventral approximator muscle (Figure 5-21b) (Katsuno and Sasaki 2008).

Hyman (1967) groups the buccal musculature under three headings: muscles between the odontophore, muscles from the odontophore to the radula, and muscles to and from the body wall. All three groups are shown in Figure 5-19. The more recent terminology of Katsuno and Sasaki (2008) is used instead of the older terminology used by Hyman (1967).

Both the radula and odontophore have retractor and protractor muscles. The muscle holding the odontophore cartilages together is the ventral approximator, or protractor muscle, which extends the cartilages forward into the buccal cavity; protractor retractor muscles return the cartilages. The protractor muscles must originate anterior to their insertion and the retractor muscles posterior to their insertions (see Figure 5-19).

The two odontophore muscles are somewhat coordinated with the two radular muscles, which create a to-and-fro rasping action, scraping algae and organic material off solid substrates. The retractor radular muscles are dorsal to the odontophore, a prerequisite to the radula residing upon the odontophore. Likewise, the radular protractor muscles are ventral to the odontophore protractor muscles (Figure 5-19 and 5.51b).

Graham (1973) describes the muscular anatomy of the buccal mass of *Viviparus* as composed of buccal constrictors and dilators, protractors and retractors of the odontophore, protractors and retractors of the sub-radular membrane, and an approximator muscle of the supporting cartilages. His studies revealed that several small muscles in the body wall contribute to the coordinated action of the odontophore and the lips. Contraction of longitudinal muscles of the body wall pulls the lips backwards. Contraction of some fibers of the lateral and ventral protractors of the odontophore moves the odontophore forwards, but the lips are pulled apart simultaneously. Closing the mouth is brought about by a ring of circular muscles lying around the oral tube in the most anterior part of the buccal cavity (Graham 1973).

Viviparus also has lateral protractors of the sub-radular membrane. They insert on the membrane alongside median muscles, but more laterally, and run back beside the median protractors. Their origin is on the posterior end of the odontophore cartilages. Throughout their course, they lay ventral to the ventral approximator muscle of the cartilages. They are strap-shaped and more powerful than the median protractors (Graham 1973).

A jaw is also part of the buccal apparatus and also has muscles. It is opposite the radula (Figure 5-51a) and helps hold food steady while the radula works. Graham (1973) describes the following actions of muscles that operate the jaw: some branches of the lateral protractor muscles end anteriorly in the inner lips, while others attach to the lateral parts of the jaw and the dorsal wall of the buccal cavity at about the same level (Figure 5-51a). Contraction of the lateral protractors presses the jaws and buccal roof against the tip of the odontophore as it moves forward. This action keeps the groove on the odontophore within which the radula lies, thus avoiding premature spreading and erection of the teeth. It also helps rotate the odontophore ventrally toward the mouth.

h. Alimentary Tract

Included here are the muscles of the esophagus, intestine, rectum, anus, and digestive gland. The stomach of viviparids, including CMS and JMS, has thin walls and is non-musculature, the food being churned and moved primarily by cilia in the sorting area. The musculature of the remaining parts of the intestinal tract consists primarily of smooth muscle but is very meager in extent.

Once the radula has captured the food, it is passed to the esophagus, mainly by way of the dorsal folds and a food channel on the roof of the buccal/pharyngeal cavity. The folds bear cilia beating toward the esophagus, but suction and peristalsis created by muscles in the folds also help to pass food into the esophagus (Graham 1973).

Graham (1939) divides the esophagus into three regions. First is the anterior esophagus, which begins immediately behind the point where the radula sac separates from the gut, its roof with a pair of folds enclosing a groove, the ciliated dorsal food channel. Second, the mid-esophagus begins behind the anterior esophagus and continues as the dorsal food channel on its roof. Food and mucus from the anterior esophagus are mixed with the secretion of the pouches, and the mixture is carried back. This region is involved in the torsion of the visceral mass. Third, the posterior esophagus lays behind the mid-esophagus, its wall bearing numerous longitudinal folds and carries the mixture from the food channel to the stomach.

The esophagus of viviparids is composed primarily of ciliated and gland cells. The anterior esophagus appears at the dorsal posterior side of the buccal apparatus and has the dorsal folds and dorsal ciliated food groove, described by Graham (1939). The dorsal folds and dorsal ciliated food groove continue through the mid-esophageal region of both CMS (Lu, Du, Li, and Yang 2014) and JMS (Van Bocxlaer and Strong (216). While the esophagus is commonly lined with short to tall ciliated columnar epithelium containing mucocytes, thin layers of circular and longitudinal muscles are present in many prosobranchs (Hyman 1967).

The intestine of viviparids is lined with two ridges, the major and minor typhlosoles. The major typhlosole is present for half the length of the intestine in JMS (Van Bocxlaer and Strong 2016). The epithelium of the typhlosoles is delimited by connective tissue often containing some muscle fibers, or less often, with a discrete muscle layer present (Hyman 1967).

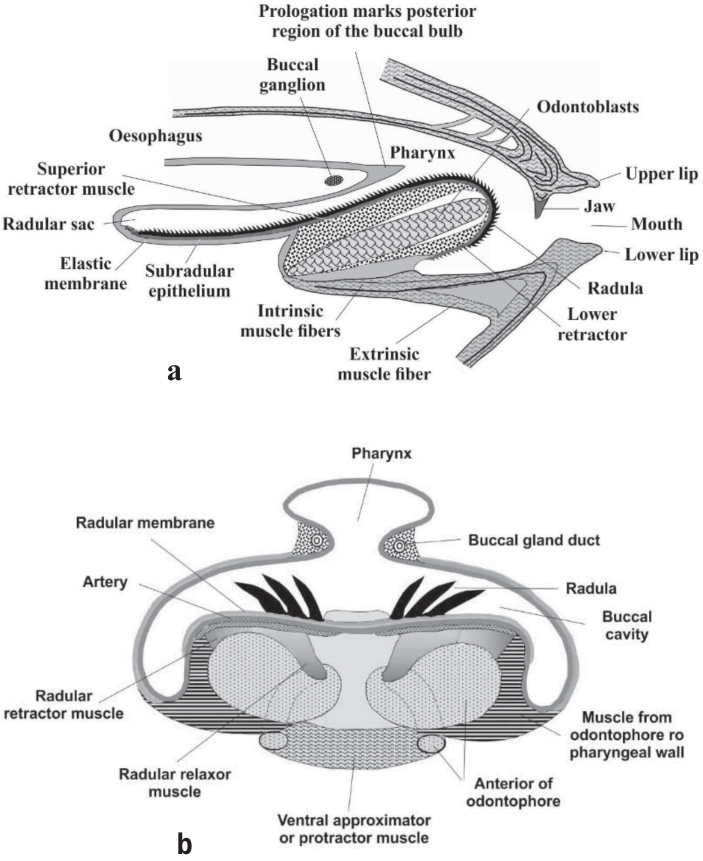


Figure 5-51. Schematic drawings of the buccal apparatus: (a) a longitudinal view of prosobranchs, drawn from Figure 15 in Amaudrut (1898); (b) a cross-sectional view of the *Viviparus* buccal complex. Drawn from Figure 108C in Hyman (1967). The buccal apparatus shows the relative positions of mussels in an extended radula.

In CMS, the feces are whitisg335h and vary from short strings to pellets. Hyman (1967) states the forms vary according to the species and according to color with the nature of the food. Inserted in the epidermal layer of the rectum of prosobranchs is a band of longitudinal muscular fibers that retract the anal collar, resulting in a shortening of the rectum and ejecting the contents. The anus is closed by a sphincter with circular muscle. Hyman (1967) found that its position varies the position ctenidial orifice, but its termination usually lies in the path of the excurrent stream.

The rectum of JMS is thin-walled and semi-transparent; Van Bocxlaer and Strong (2016) found the contents to be easily visible externally. The rectum is surrounded by a layer of connective tissue with little musculature and terminates in a free anal papilla with circular muscle.

The digestive gland has tall digestive cells with bulging free ends and a cytoplasm filled with granules and vacuoles. Other cell types (e.g., calciferous cells with calciferous spherules) may be present but have not been reported in the viviparids. The gland is largely devoid of musculature. The digestive system of viviparids is either poorly described or wanting in their musculature.

i. Respiratory System

The respiratory system is represented mainly by the ctenidium, but the mantle may also contribute to the exchange of respiratory gases. As discussed earlier, the ctenidium, which plays a dual role in respiration and feeding, contains no musculature. The mantle has mainly glandular and sensory activities, largely for shell formation, and is covered on both sides with epidermis. The epidermal layers have circular muscle, especially in the mantle edge (see Figure 5-2).

j. Excretory System

The principal components of the excretory system are the kidney, pericardium, renopericardial canal, kidney reservoir or sac, and ureter. Much of the movement of fluids in the excretory system is due to the contraction of circular and longitudinal muscles of the body wall. The heart also plays a significant role in urine formation, and its musculature was discussed earlier.

Excretory structures with muscles include some vessels and papilla. The distal end of the canal that connects the kidney to the kidney bladder has a papilla, which has a slit-like opening into the ureter, the opening being controlled by a sphincter (see Figure 5-32). The papilla muscle closes the kidney pore.

The renopericardial canal is surrounded by a rather heavy musculature (Perrier 1889), but it is covered with ciliated epithelium internally. When the pericardium fills with fluid, the increase in pressure forces the liquid into the kidney, the kidney expands and with the help of tension exerted by the inflated kidney on surrounding organs, forces fluids into kidney spaces, and thence into the bladder. When the kidney muscles relax, the renopericardial canal opens. Some kidney vessels are lined interiorly by muscles (see Figure 5-33a, b). The ureter consists of large circular and oblique bundles of muscles, longitudinal muscles being absent; any musculature in the ureter may contribute to the stirring of fluid retained in it (Perrier 1889).

k. Reproductive System

The prostate gland usually has a thick muscular epidermal layer, consisting of an external circular layer and an inner longitudinal layer around the entire organ. However, its extent appears to vary with species in viviparids. Pagulayan and Cepillo (1991) found the gland to have a thin muscular coating with an external circular muscle layer and an internal longitudinal muscle layer around the entire tissue, consisting of simple cuboidal cells. Beneath the muscle layers, the prostate has a smooth, non-convoluted duct.

The wall of the vagina is also muscular, consisting mainly of circular muscle fibers. Cross-sections through the bursa reveal an outer layer of circular muscles embedded in connective tissue (Van Bocxlaer and Strong 2016).

l. Circulatory System

The most obvious muscular structure in the circulatory system is the heart. The muscles of the auricle have already been described (see 6. Circulatory System, b). In summary, the auricle has a central muscular portion and paired lateral compartments. The lateral compartments are where ultrafiltration of the blood occurs. Transverse bands of muscle form the innermost layer of the wall in the central part, and branches of these spread out laterally, where they attach radially to the basal lamina. Another set of horizontal muscles runs in an anteroposterior direction. Longitudinal muscles lie peripheral to the horizontal ones around the central part but are absent from the lateral compartments of the auricle. The arrangement of muscles results in systole in the central part of the auricle, which refills the ventricle. The ventricle is pear-shaped. Some stout bands of muscle in the ventricle are continuous with longitudinal muscles in the wall of the ventral channel of the auricle, but the rest of the musculature forms a dense network of fibers of uniform thickness over the whole wall of JMS. The bulbus aortae have a thin wall and a spacious lumen uninterrupted by muscles that are arranged in circular and longitudinal layers.

10. Nervous System

The nervous system is the last system to discuss because it innervates virtually every organ in the snail's body, and all these organs have now been described. Recall that viviparids belong to the subclass Streptoneura, based upon the modification caused in the arrangement of the visceral nerve-loop by its being twisted into a figure-eight after torsion (see B. Internal Anatomy, 1. Torsion).

The nervous system and/or the nerves of viviparids have received much attention, beginning in the 19th century with Moquin-Tandon (1855), Speyer (1955), Lankester (1873–74, 1875, 1883), Simroth (1881), Spengel (1881), Lacaze-Duthiers (1872), Bouvier (1887, 1889), and Simroth (1896–1907). Most of their research was performed on *Viviparus* species, especially *V. viviparus*, or its aliases, *Paludina* and *Vivipara* species. Since then, Taylor (1900), Rohrbach (1937), Wölper (1950); Morton (1956), and Plesch (1977) in the 20th century and Lu, Du, Li, and Yang (2014) and Van Bocxlaer and Strong (2016) in the 21st century have examined nervous systems of *Bellamya* and *Cipangopaludina* species as well as *Viviparus*. The following discussion extracts information from all these authorities.

The structures that are the hubs of nerve generations are ganglia, which distribute impulses to connectives, conveying large lateral or peripheral nerves. The large peripheral nerves radiate into increasingly smaller nerves that anastomose and innervate all the muscles and sensory organs in the snail's body.

The nerve ring (Figure 5-52) connects several ganglia or sends connectives to other ganglia remote from the nerve ring. The ganglia are discussed in this order: (a) cerebral ganglia, (b) pedal ganglia, (c) pleural ganglia, (d) visceral ganglion, and (e) ganglia branching somewhat remotely off these. The primary sense organs discussed here are as follows: (a) tentacles; (b) eyes; (c) osphradium; (d) hypobranchial gland; and (e) statocysts. The foot receives special attention because of the complexity of the nervous system.

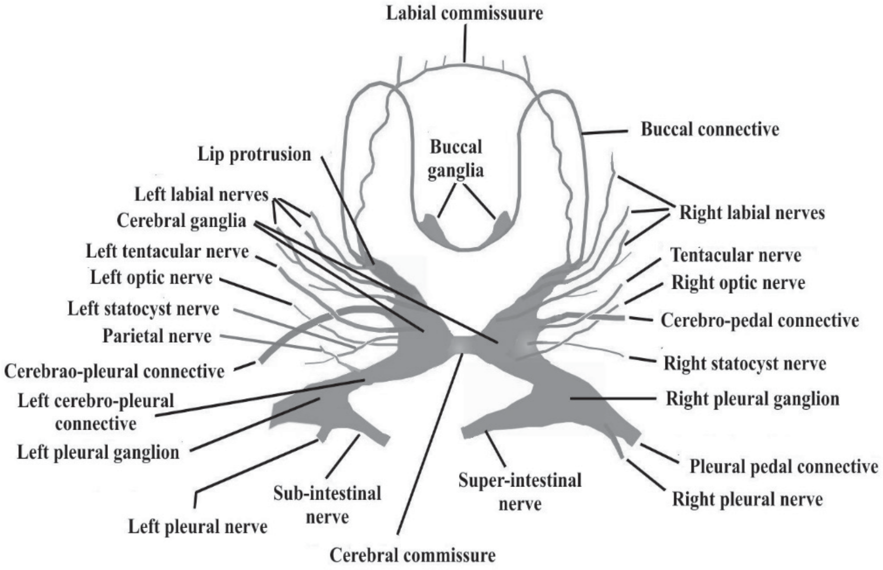


Figure 5-52. Schematic of the ganglia and nerves emanating from the nerve ring complex of *Viviparus viviparus*. Drawn from Plate 4, Figure 16 of Bouvier (1887).

a. Ganglia and Commissures

i. Cerebral Ganglia

The somewhat flattened cerebral ganglia are attached to the sides of the posterior part of the buccal mass and are united by a broad, short commissure (Figure 5-52). They extend anteriorly and below in a long protrusion. From this protrusion, the buccal connective arises and penetrates the buccal mass to end in the related buccal ganglion. The two cerebral ganglia are somewhat elongated through the labial region due to their connectives, including a pedal connective from the more ventral pedal ganglion, better shown in Figure 5-53. The labial protrusion also gives rise to a labial commissure, which passes under the buccal mass anteriorly and establishes a new connection with the cerebral ganglion.

Below and behind, the two cerebral ganglia send two connectives; the one from the left cerebral ganglion is larger but shorter and more anterior cerebro-pleural connective; the one from the right ganglion is a longer and more diminutive cerebro-pedal connective.

The nerves of the snout and the lips are four in number, including the two nerves that anastomosis to form the labial commissure (Figure 5-53). They all emerge from the inner edge of the cerebral ganglia; the first from the ganglia themselves, the next two from the labial protrusion, the last from the very tip of the protrusion (Figure 5-53). These nerves innervate by anastomosing branches, the lateral and upper walls of the snout and the lips.

ii. Pleural Ganglia

The pleural ganglia each send a connective to the pedal ganglion connectives. A pleural-pedal connective merges with the cerebro-pedal connective a short distance anteriorly (Figure 5-53). On each side, in addition to the cerebro-pedal connective is a large nerve extending between the cerebral ganglion and the very long pedal ganglia (Figure 5-53). This nerve is the pleural ganglion, located at a short distance from the cerebral ganglion (Figure 5-53). Each nerve is ganglionic over its entire length, with the pleural ganglia appearing as rather weak swellings.

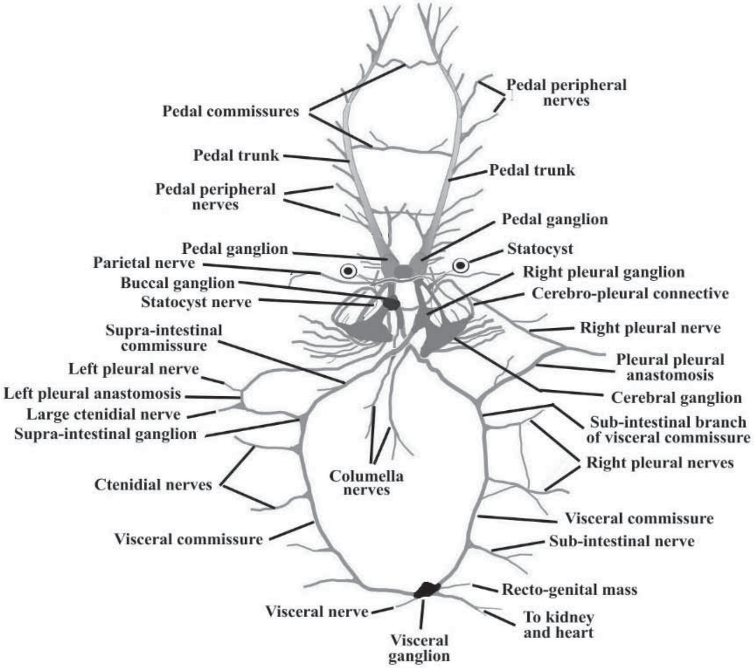


Figure 5-53. Schematic of the nervous system of *Viviparus viviparus*. Drawn from Plate 4, Figure 15 of Bouvier (1887).

The nerves originating from the pleural ganglia are relatively slender and arise on the left off the cerebral-pleural connective, and on the right, off the pleural ganglion. This parietal nerve innervates the walls of the body behind the cephalic parietal nerves. The right pleural ganglion gives rise below its base to the right pleural nerve (Figure 5-53). Further on, this nerve unites with a much smaller pleural nerve and arises from the sub-intestinal branch of the visceral commissure. It then goes to the right in the edge of the mantle, where it sends many branches (Bouvier 1887). The right pleural nerve has its correspondence on the left in the left pleural nerve from the left pleural ganglion. The right pleural nerve sends a branch to the pleural viscera, the edge of the mantle, and into the mantle, where it sends numerous branches. One branch is lost in the walls of the body; another branch emerges in the external edge of the epipodium.

The visceral commissure has its origin in the two pleural ganglia (Figure 5-53). Its sub-intestinal branch runs transversely from left to right, below the esophagus, at first a bit behind, then much more (Bouvier 1887). When it has reached the right walls of the body, it emits a relatively weak but sharp branch that goes toward the mantle. The branch from the mantle branch merges with the large right pleural nerve, originating from the base of the right pleural ganglion. The branch under the intestinal nerve of the visceral commissure ends behind in the visceral ganglion located near the heart, behind the dorsal rim of the animal (Bouvier 1887).

The supra-intestinal branch of the visceral commissure runs from right to left transversely over the esophagus. It then slants a little behind and, arriving in the walls of the body at the level of the ctenidium, forms a supra-intestinal ganglion, after which it runs backwards, tapering off a little, and ends in the visceral ganglion above the digestive tract (Bouvier 1887). The supra-intestinal ganglion sends a large nerve to the ctenidium. This nerve anastomoses with the left pleural nerve from the left pleural ganglion through one of its weaker branches.

iii. Pedal Ganglia

The pedal ganglia are also weakly represented, each forming a long cord, which originates on the floor of the mouth behind the angle of the snout. The two ganglia are a little swollen at their origin and unite by a broad and short commissure (Figure 5-53). Next, they extend into the metapodium, diverging first, then converging to form an elongated ellipse (Bouvier 1887). Three transverse commissures unite them in this course. In addition, a quasi-transverse anastomosis unites the two large pedal nerves of the propodium, as described later for the foot nerves.

iv. Visceral Ganglion

The visceral ganglion is located at the posterior end and to the right in the roof of the animal. It is somewhat triangular and gives rise to at least three nerves: one goes forward on the recto-genital mass, the second is larger and very branched and innervates the kidney and probably the heart, and the third sinks into the viscera (Figure 5-53).

On the sub-intestinal branch of the visceral commissure, near the pleural ganglion, two to three columellar nerves detach to innervate the columellar muscle. Usually, the visceral commissure sends one or two small branches into the wall of the body or the mantle. Between this nerve and the visceral ganglion, the sub-intestinal branch of the commissure sends three (and rarely, four) nerves to the right, the first two anastomosing at a small distance from their origin (Figure 5-53). These send several anterior branches to the anal end of the rectum and the tip of the female genital duct, anastomosing posteriorly over the visceral mass and the mantle above.

b. Sensory Organs

i. Tentacles

The cerebral ganglia innervate the tentacles, the eyes, the snout, and the head's lips. The cerebral ganglia are the tentacular nerves (above the labial protrusion and the cerebro-pedal connective) and the optic nerve above the cerebral-pleural connective. The tentacular nerve is large and branches out at the thick base of the tentacle. In the male right tentacle, which acts as a penis, it is disproportionately enlarged; the right tentacular nerve is slightly smaller and becomes the pelvic nerve. Taylor (1900, Figure 494, p. 244) cites Simroth (no date or reference) in his illustration of the kinds of epithelial, ciliated sensory cells in the tips of the tentacles of *Viviparus viviparus* (Figure 5-54a, b). The cells are directly continuous with nerve fibrils. The hairs and cilia protrude through the tentacles, and the fusiform bodies are internal. The length of tentacles of CMS is about 1.3 times longer than the snout length, which is cylindrical with a flat anterior margin (Lu, Du, Li, and Yang 2014).

ii. Eyes

A pair of eyes is present in viviparids, each embedded in a short peduncle, the ommatophore, fused to the outer base of each cephalic tentacle. In CMS, the ommatophore is short and located between the basal and middle third of the outer surface of each cephalic tentacle (Lu, Du, Li, and Yang 2014). The optic nerve is small, and it terminates without branching at the eye, located on a projection at the base of the tentacle (Bouvier 1887) (Figure 5-53). The optic nerve anastomoses over the eye outside the retinal epithelium as a nervous layer of fibrils and ganglion cells (Hyman 1967).

According to Taylor (1900), all land and freshwater molluscs are myopic; they do not perceive ultraviolet rays but are specially adapted for vision in dim crepuscular light. Exposure to bright sunlight has a dazzling or blinding effect on them, and most shun bright light and seldom voluntarily leave their retreats except during twilight or total darkness. The aquatic pulmonates have feeble ocular powers and cannot discriminate the form of objects even in immediate proximity to their eyes. *Vivipara contecta* is comparatively long-sighted, perceiving objects at a distance of 30 cm from the eye. If the mollusc is crawling in the dimness, sudden exposure to bright light at a greater distance will cause it to withdraw into its shell at once (Taylor 1900).

iii. Osphradium

The osphradium of *Viviparus* is located beneath the ctenidium, lying in the inhalant current of the mantle cavity. It is characterized by a series of pits at each side, lined by ciliated cells only, and is innervated by the osphradial nerve emanating from the parietal ganglion. The microanatomy and histology of the osphradium of *Viviparus* species have been described by Bernard (1890) and Wölper (1950). See 3. Respiratory System, b) Osphradium in this chapter for details of its structure.

iv. Hypobranchial Gland

The hypobranchial gland of *Viviparus viviparus* has also been described in detail previously (see 3. Respiratory System, c) Hypobranchial Gland). The gland is innervated by nerves emanating from the ctenidial nerves that branch off the sura-intestinal commissure. The hypobranchial glands of the Chinese and Japanese mystery snails have received little attention to date.

v. Statocysts

The statocyst nerve is thin and descends between the two connectives that go to the pedal ganglia, passes over them, and diverges outward and forward to reach the statocysts (Bouvier 1887). The nerves are embedded in the tissues at the dorsal origin of the foot, on each side of the pedal ganglia. They innervate the cerebral ganglia, not the pedal ganglia, which was clearly shown in the examination of *Paludina* (*Viviparus*) *viviparus* by Lacaze-Duthiers (1887a, b) and the innervation of its otocysts, an obsolete term for statocyst (Figure 5-55a, b). The statocysts lay adjacent to the pedal ganglia, but the statocyst nerve bypasses these ganglia. Lacaze-Duthiers (1887) also found a muscle connecting the two statocysts (Figure 5-55b).

The statocyst is a spherical sac containing a lumen filled with liquid and contains a statolith that functions to convey balance and orientation to the snail when it changes position. The statolith’s inertia pushes it against sensory hairs lining the vesicular walls. The wall consists of cuboidal epithelium delimited by connective tissue and muscle fibers to anchor the statocyst.

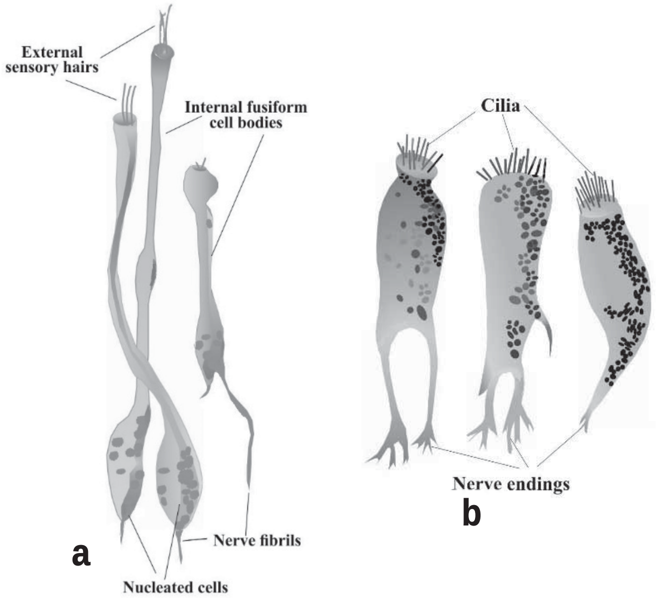


Figure 5-54. Terminal nerve cells (a) and epithelial ciliated cells (b) from the tentacle of *Viviparus viviparus*. Drawn from Figures 493 and 494 in Taylor (1900).

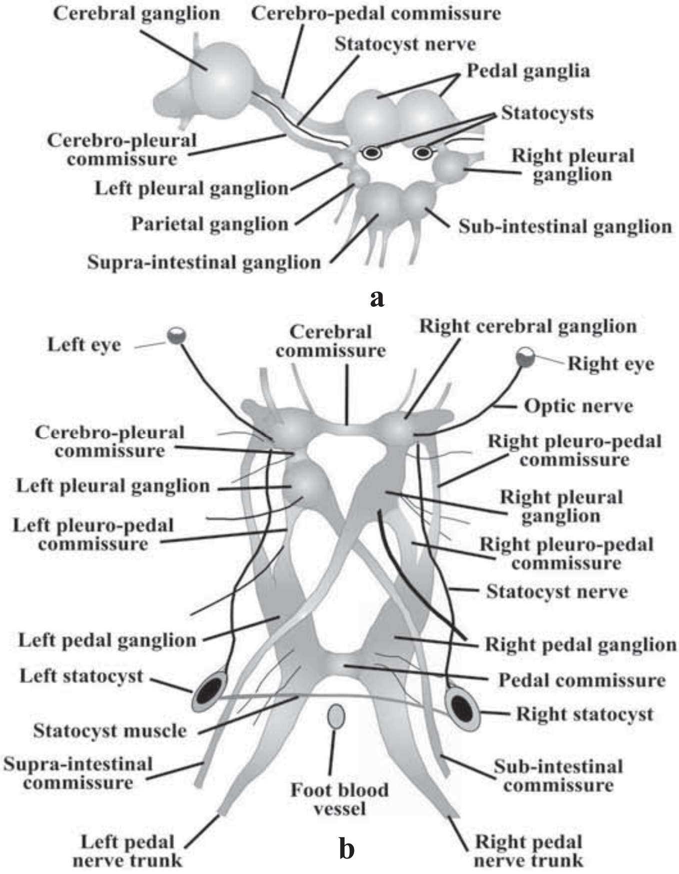


Figure 5-55. Nerve innervation of the statocysts of *Viviparus viviparus*. (a) Configuration of the associated ganglia and locations of the statocysts when the foot is relaxed. (b) Configuration of the nerves and ganglia showing the statocyst nerves clearly arising from the cerebral ganglia. Illustrations are drawn from Figures 4 and 11 in Lacaze-Duthiers (1887).

c. Foot Nerves

The sole of the snail! Figure 5-56 is a redrawing of the network of nerves in the foot of *Viviparus viviparus* described by Simroth (1881). The median pedal sinus is also shown. Simroth (1881) reported two lateral sinuses, which diverge from front to back, but these were not included in his Figure.

The foot has an anterior and a median commissure that is curved to the front, the two posteriorly toward the metapodium (Figure 5-56). The peripheral nerves that radiate from the pedal trunks into the sole run at fairly regular intervals. The inner branches, however, are very irregular (Figure 5-56). The outer peripheral nerves emerge symmetrically around the outside and change their length according to the distance between the nerve trunk and the sole edge (Figure 5-56). The nerves branch out repeatedly, each time with some thickening at the bifurcation.

The first inner pair of nerves first branch distally and then loop abruptly anteriorly to the propodium. The nerve divides into two branches, a stronger lateral one, which trends in a direct line to the lateral corner of the propodium, and a weaker medial one, which inclines slightly toward the center and runs almost straight ahead. On its way, the lateral branch gives off a few units to the front, and of these, the first connect by an anastomosis with an extension of the medial branch. Anastomosing pairs also occur in the neighboring units (Figure 5-56). They branch out profusely in the propodium, in which they innervate almost to the edge.

11. Summary of the Internal Anatomy

The main objective in the analyses of the internal anatomy of Viviparidae in this subchapter is to provide differences in structures that help distinguish the Chinese Mystery Snail from the Japanese Mystery Snail. In this analysis, the description of the anatomy of Viviparidae relies heavily on those for *Viviparus viviparus*, predominately from the 19th-century literature due to a lack of more recent descriptions for CMS and JMS.

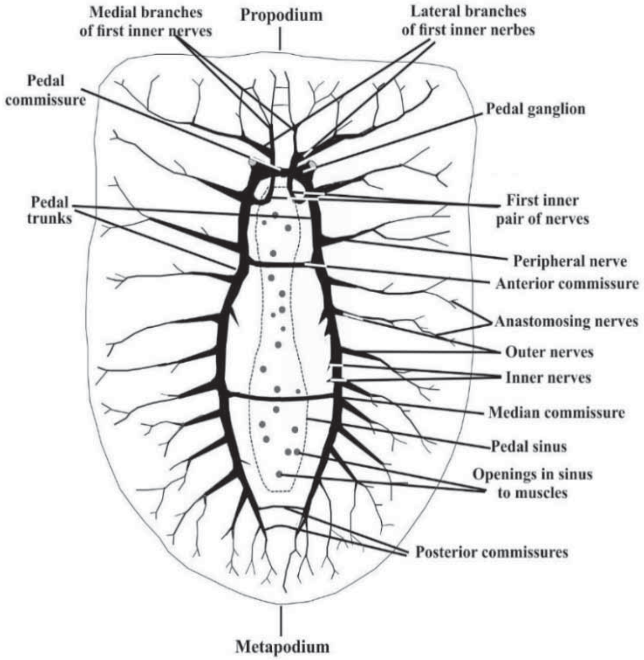


Figure 5-56. Nerves of the foot of *Viviparus viviparus*. Drawn from Figure 5-1 in Simroth (1881).

Eight internal anatomical systems are examined. Within each, several structures and or their processes are described. The systems, organs, and or their processes examined within each is:

- Torsion, which is typical for all prosobranchs
- Digestion, beginning with the radula and odontophore in the buccal complex, the esophagus and stomach with its crystalline style, the hepatopancreas, and finally the rectum
- Respiration, and its pallial complex, including the ctenidium, osphradium, and hypobranchial gland
- With modern technology, excretion has revealed an ultrafiltration process referred to herein as “auricular urination”
- Reproduction in three species, *Viviparus georgianus*, *Cipangopaludina chinensis*, and *C. japonica*, with details of male

  and female structures and the unique “screw-type” nuclear heads of sperm
- Circulation of both venous and arterial systems, with illustrations of ultrafiltration through the auricle
- The musculature of all systems, with emphasis on the larger muscles, the columella, and foot
- The nervous system, with emphasis on the ganglia and their commissures, sensory organs (e.g., tentacle, eyes, and statocysts), and the foot

Few differences exist among species for most systems because differences in the evolution of systems are more pronounced at the family level than at the species level. Those characters found useful to distinguish species include the structure of the radula, stomach (especially the crystalline style), kidney and urine formation, and the testis and ovary structures.

D. Chapter V Summary

The external morphology and internal anatomy of mystery snails have been well described, particularly for *Viviparus viviparus*. However, much of the descriptions provided are for *Viviparus* species from the 19th century, the 20th- and 21st-century literature providing descriptions for the Chinese and Japanese mystery snails.

For the external morphology, the main objective was to provide diagnostic characters to help distinguish between the Chinese and Japanese mystery snails. The morphological features examined include shell and mantle, periostracum, spire and body whorl, neck, head, foot, and operculum. Table 5-1 lists the characteristics that, used in combination, may help separate the two species. The table is based on information provided by authorities between 1965 and 2016. The most valuable characters to separate the two species appear to be adult shell shape; their shell H: W ratio; and the angle of the spire, number of whorls, and periostracal hairs on spire vs. body whorls.

Similarly, the main objective of the internal anatomy was to provide diagnostic features that distinguish the Chinese Mystery Snail from the Japanese Mystery Snail. This objective was more daunting than defining the two species based on their external morphology. Descriptions of the anatomy of Viviparidae relied heavily on those for *Viviparus viviparus*, predominately from 19th-century literature. The internal anatomical systems and the numbers of organs examined within each (in parentheses) are torsion; digestion (7); respiration (3); excretion (6, plus two processes); reproduction in *Viviparus georgianus*, *Cipangopaludina chinensis*, and *C.*

japonica (details on 5 to 6 structures in each of males and females of each species); circulation (4); musculature (10 headings, including systems and structures); and the nervous system (3). Not surprisingly, few differences exist among species for most systems because differences in the evolution of systems are more pronounced at the family level than at the species levels. However, some characters are useful to distinguish species. These include structures of the radula; stomach, especially the crystalline style; urine formation in a process referred to here as “auricular urination”; and testis and ovary structures.

CHAPTER VI

ECOLOGY

A. Introduction

A wide variety of topics on Viviparidae is covered in this chapter, including their life history from embryos to adults, biogeology (i.e., interactions of freshwater snails concerning aquatic and terrestrial contributions from geology), population dynamics, parasitism, predation, biogeography, and requirements and tolerances for survival and establishment. There are some significant differences in the ecology between the Chinese and Japanese mystery snails in their population dynamics, requirements, and tolerances, but their life histories are typical of all viviparids.

B. Life History

Jablonski (1985) asserts that only free-swimming stages should be termed larvae; for brooding species, the term embryo is preferred, which is adopted here. Planktonic, or planktotrophic forms, have rows or tufts of cilia on a velum to serve as swimming organs, and they have larvae that develop in the water. The cilia also serve as food-collecting organs, selecting food from the suspended or floating plankton. Development in planktotrophic forms usually proceeds from an egg to a trochophore, several veliger stages as plankton, and finally into settlement stages as the swimming ciliary velum is absorbed, such as in the zebra mussel, *Dreissena polymorpha* (Mackie and Claudi 2010).

Non-planktotrophic development, or direct development, proceeds without an external food source but profits from the yolk of the egg or some other nutrient provided by the female (Jablonski 1985). This nonfeeding category includes species (e.g., *Melania*) in which larvae are free-swimming, often termed lecithotrophic (Jablonski 1978), as well as species in which embryos undergo development entirely within an egg capsule or brood chamber and emerge after metamorphosis as juveniles (e.g., Viviparidae).

Within the lecithotrophic group, Muley (1978) traced the origin of different organs and organ systems through the trochophore stages. Figure

6-1a is the front view of the trochophore stage of *Melania scabra*, a marine pleurocerid. The endodermal mass forms a mass of nutritive cells filling the interior of the embryo with scattered nuclei. The mesoderm cells are loosely arranged as a narrow band appearing like mesenchyme. The foot and mouth are only slightly differentiated, as are the rudiments of two statocysts, even before the foot's appearance (Figure 6-1b). Lying close to each of them is a proliferation of the ectodermal cells constituting the visceral and cerebral ganglia (Figure 6-1c). As typical gastropod development, the rudiments of most organ systems are evident after torsion has been completed (Figure 6-1d).

1. Embryology and Development in the Viviparidae

Viviparidae belong to the direct development group. The egg undergoes typical spiral determinate cleavage. The first two cleavages result in the formation of four blastomeres of equal size. The third cleavage splits off four small micromeres at the animal pole. In the fourth and fifth cleavages, two more tiers of micromeres are separated from the macromeres. A cleavage cavity is absent in all stages of development to this point.

a. Early Embryonic Development

The cleavage cavity appears in the formation of the gastrula stage after micromeres envelop the macromeres (Figure 6-2). The gastrula is followed by a slight invagination of the macromeres resulting in a small depression representing a rudimentary archenteric cavity and blastopore (Figure 6-2a). The endodermal cells originate from the micromeres and fill the whole interior of the embryo (Figure 6-2b). The cell margins disappear in the endodermal mass, and many yolk spherules with a few scattered nuclei appear (Figure 6-2c). Immediately after gastrulation, the blastopore elongates in the anterior direction. Lastly, the anterior end of the slit closes, giving rise to the stomodaeum or mouth near the point of its closure.

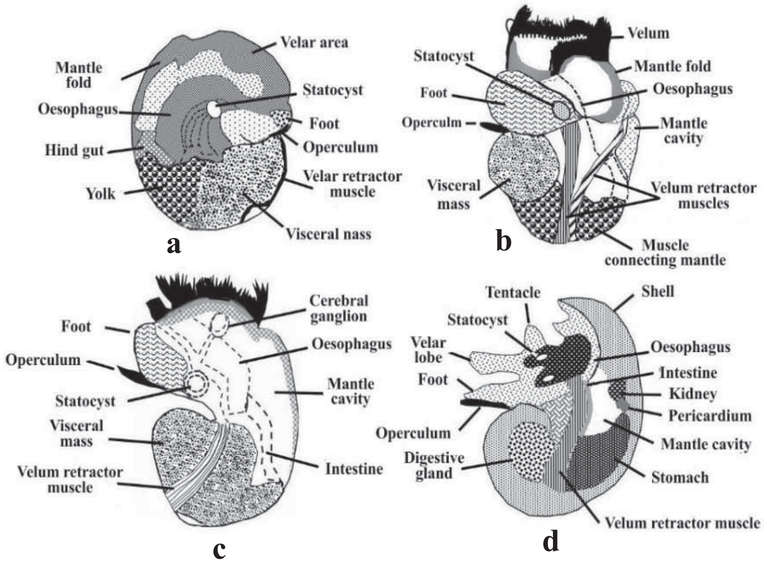


Figure 6-1. The post-trochophoral stages in the development of *Melania scabra*. (a) Right view of the preveliger stage. (b) Left view of veliger showing commencement of torsion. (c) Left side view of veliger during torsion. (d) Left side view of veliger in which torsion has been completed. Drawn from Plate 2, Figures 5–8 in Mulvey (1978).

b. Final Embryonic Development

Erlanger (1891a, b) thoroughly examined the embryology of *Viviparus* (as *Paludina*) *viviparus*. The early embryonic stages are shown in Figure 6-3. Rather than describing all the successive stages of development, only the stages recognizable as snails, from the first appearance of the tentacles to the mature embryo, are examined here and shown in the semi-schematic drawings in Figure 6-3.

At the stage shown in Figure 6-3a, the heart is divided into an auricle and a chamber, which was initiated by the central constriction of the heart.

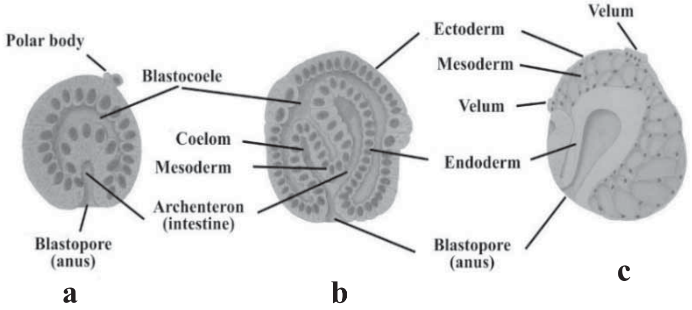


Figure 6-2. Stages in gastrulation to form the blastula in *Viviparus viviparus*. (a) Stage when micromeres envelope the embryo. (b) Innervation of the mesoderm into the archenteron. (c) Blastula with intestine developing within the endoderm. Drawn from Plate XX, Figures 1, 3, and 9 in Erlanger (1891a).

The foot is flattened with a posterior metapodium and the abutment of the operculum. Erlanger (1891a) states the operculum is secreted in the same way as the shell by opening the ectoderm corresponding to the shell gland. The esophagus is long and narrow. Immediately behind the mouth opening, which has a chitinous thickening, lies the radula sac, which appears as an extension of the septum. The velum can still be seen, but its field becomes small because it only takes up the dorsal surface of the head region and bends close behind the tentacles. As the embryo is viewed from the left, only a tiny part of the gill cavity can be seen, in which a large number of gill filaments are already visible. The pericardium on the posterior border of the gill cavity carries the heart on its dorsal wall. The anterior half corresponds to the atrium and the posterior half to the ventricle.

Figure 6-3b is the following stage from the left side showing the kidney duct (renopericardial canal). The rectum gradually grows elongated, separates from the upper part of the gill cavity, and empties into the mantle cavity on the right and at the bottom through a narrow opening. To the left of the ctenidial bulge, a protrusion of the ectoderm forms the osphradium, which Erlanger (1891a, b) and others often refer to as a false gill or olfactory organ.

In the next stage (Figure 6-3c), which Leydig (1850) describes as a mature embryo, the kidney begins to enlarge significantly, intensifying its relationship to the heart in the pericardium by an opening in the kidney from the renopericardial canal that originates at the pericardium. The kidney also opens into the ureter. A reconstruction of the kidney at this stage from a sagittal series of sections by Erlanger (1891a) shows the cells of the kidney wall decreases in height as the kidney enlarges and forms a cubic epithelium, which gradually takes on the shape of a tetrahedron. The cells are arranged very regularly and show a distinct nucleus and a single honeycomb protoplasm in which no excreta granules are noticeable. Erlanger (1891a) found that when the kidney joins the heart, the kidney cells become lower and simply pass into the flat cells of the pericardial wall.

Leydig (1850) describes this stage as a mature embryo. It is characterized by the blunt processes that develop on the right edge of the mantle. It has developed four blunt processes, and the shell has long stiff hairs or bristles. However, Erlanger (1891a) found the mature embryo stage (Figure 6-3d) has essentially the same structure as the full-grown embryo only after it has reached three to four times the size of this stage (Figure 6-3c).

In Figure 6-3c, a semi-schematic drawing of a whole embryo, the digestive gland has already formed, but this is not shown so as not to complicate the figure. The intestine forms a loop just behind the stomach, continues to the rear outline of the shell, arches upward, and penetrates the stomach on the right side and the right wall of the mantle cavity.

In Figure 6-3d, the mantle cavity descends in an arch on the left side to meet the left side of the heart, where it ends near the auricle, which is attached to the inner end of the ctenidium by the afferent ctenidial vein. The ctenidium has already developed a large number of gill filaments. The osphradium appears as a broad bulge on the ceiling of the mantle cavity on the left and ventral side of the gill and extends gradually flatter toward the posterior. From the posterior wall of the mantle cavity arises the attachment of the genitalia, which adjoins a genital duct, which ends at the digestive gland. The kidney lies on the posterior shell wall dorsally above the liver and opens out through the long ureter into the urinary bladder just below the rectum.

Erlanger (1891b) described the origin of the visceral commissure in the pleural ganglion. The visceral cord starts from the right pleural ganglion, then turns to the left and up over the long esophagus, and shows a minor swelling of the statocyst approximately midway to the visceral ganglion, which Erlanger (1892b) states is the supra-intestinal ganglion, from which a large nerve branches off to the left half of the mantle. From there, the right cord continues to the visceral ganglion, which is slightly dorsal to the heart at the foremost ventral end of the septum, which separates the pericardium from the mantle cavity (Figure 5-60d).

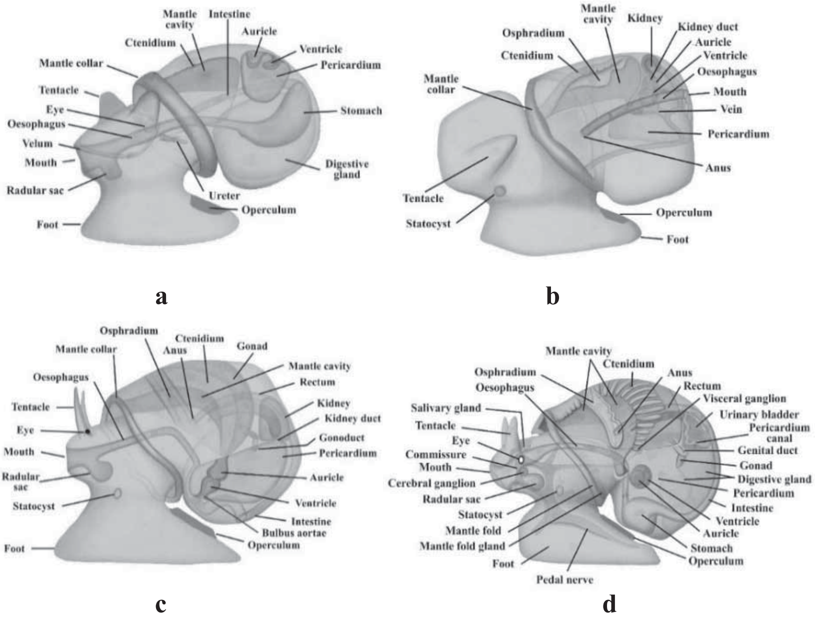


Figure 6-3. Embryo development in *Viviparus viviparus*. (a) View of left side of an embryo with a uniform pericardium, length 0.52 mm. (b) View of left side of an embryo in which the pericardium is divided into two sections by a septum, length 0.64 mm. (c) View of left side of a nearly mature embryo in which the heart and kidney duct are evident, length 0.7 mm. (d) View from left side of a mature embryo with most organ systems evident, length 1.6 mm. (a–c) are modified from Plate XXII, Figures 1,2,5 drawn from Erlanger (1891a); (d) is modified from Plate XXXII, Figure 9 of Erlanger (1891b).

C. Population Dynamics

Invasive species have different traits and strategies for successful establishment than native species; these are summarized as r- and K-selection traits by Pianka (1970) and Stearn (1976) and apply to nuisance invasive species, such as the zebra mussel (Mackie 2004; Mackie and Claudi 2010). Mackie (2002) lists several traits of reproductive potential that needed to be considered to predict its population dynamics and, hence, the rarity or invasiveness of a species: (a) the species' sexual state (e.g., monoecious or dioecious); (b) its egg-laying habit (e.g., oviparous, ovoviviparous, viviparous); (c) its fecundity (number of eggs produced); (d) its natality (number of eggs surviving); (e) its annual frequency of egg-laying habits (e.g., univoltine, bivoltine, multivoltine); and (f) its lifetime frequency of egg-laying habits (e.g., semelparity, iteroparity). The challenge here is to apply these traits to CMS and JMS to determine their invasiveness and nuisance to ecosystems. This is discussed in Chapter VII. Dispersion.

David, Thebault, Anneville, Duyck, *et al.* (2017) distinguish between native species (present in the community since prehuman times) and resident species (includes ex-invasive species that have become established locally relative to a particular time and the invader). When contrasting *invasive* and *resident*, the residents are all species that were established before the arrival of a particular invasive. Invasive species have been intentionally or accidentally introduced and can maintain, spread, and reproduce in the new habitat (David, Thebault, Anneville, Duyck, *et al.* 2017). Logically, the Chinese Mystery Snail, which has been in North America since 1892 (i.e., more than 130 years), can be considered an ex-invasive species relative to zebra and quagga mussels, which have been here since 1986.

Nuisance is defined here as a potential threat to native species through the economy, predation, grazing, competition, parasitism, disease, hybridization, or habitat alteration (Núñez, Bailey, and Schweitzer 2010; Pimentel, McNair, Janecka, Whitman, *et al.* 2001; Skandrani, Lepetz, and Prévot-Julliard 2014). An economic nuisance refers to control and damage costs from invasive species; for example, in the US, the zebra mussel, Asian Clam, and shipworm are estimated at costs of US$1.305–3.21 billion per year (Pimentel, Lach, Zuniga, and Morrison 1999; Pimentel, McNair, Whitman, Simmonds, *et al.* 2001; Pimentel, Zuniga, and Morrison 2005; Pimentel 2011).

Several interesting aspects of populations of mystery snails emerge from the literature, particularly the Chinese Mystery Snail under the synonym *Viviparus malleatus* and the River Snail, *Viviparus viviparus*. The topics covered here include methodologies for studying population dynamics, such as density, fecundity and natality, mortality, growth in shell dimensions and biomass, life span, and intraspecific and interspecific competition. Economic costs are not discussed because of the apparent lack of published data for mystery snails.

There are several studies on the population dynamics of CMS, but fewer for JMS. The following discussions provide several growth relationships, or regressions, mainly for CMS, to allow researchers to formulate hypotheses of population consequences or compare postulates essential for understanding introduction success and dynamics of invasive species, such as survival probabilities.

1. Methodologies for the Study of Population Dynamics

Some of the difficulties in comparing population data arise from different methodologies, especially for estimating population density, survival, mortality, and life span. However, each method has its shortcomings. The methods can be divided into metrics for a portion of a population or individuals within a population. All individuals within an area, such as 1-m^2 quadrats, are collected and measured for parts of the population. For individuals, specimens are randomly collected to represent all size classes and then marked or tagged.

a. Quadrat Method

The densities of mystery snails are often determined with 1-m^2 quadrats, made from dense material such as copper tubing, as long as it sinks and rests on the bottom. A sieve is also required. The mesh size depends on the size of the animal for which one is interested. The mesh size for capturing mystery snails should be smaller than 5 mm to include all sizes from 5 mm of juveniles to 65 mm or greater for adults. Sediment from within the quadrat is scooped into the sieve; the contents are washed by swirling the sieve in the surface water, then collecting all living snails from the residue. The depth of sediment taken depends on the species being investigated, but usually the top 5–10 cm will yield all size classes. The process is continued until all the sediments within the quadrat are sampled. The resulting number of snails is expressed as individuals m^{-2}. The quadrat method is commonly used in the capture-mark-recapture method, discussed later.

b. Marking or Etching

Only species with large, thick shells should be marked by etching with a tool (e.g., an awl or a bit in an electric engraver). Ideally, only the periostracum is scratched away, exposing the nacre. One disadvantage of this method is small shells or juveniles are difficult to mark. The codes used must be short and usually consist of a letter and one or more numbers (e.g., A1, B123). Due to marking, it is essential to use controls (unmarked) of similar sizes to account for mortality, stress, etc. Specimens are released into the population and then recaptured at regular intervals and dimensions (e.g., height, width, aperture length, wet weight, etc.).

c. Tagging

Various methods of marking and tagging freshwater gastropods have been tested and used. Tags are often considered to be better than marks because they are less likely to harm the snail. I have used Hallprint tags, which are 9 mm x 5 mm, and are available in several colors, have a unique four-digit code number (e.g., A001), and come in rolls of 1,000 tags. The tags are attached to the shell using water-insoluble glue, like Krazy glue, containing cyanoacrylate, a strong, fast-acting adhesive, and it has many industrial, medical, and household uses. Krazy glue works best on damp surfaces, but the surface must be clean. The snail dimensions (height, width, etc.) are recorded, and the snails are released into the area of their capture or within enclosures. The different colors help find the snails during recapturing, but this method comes with some criticism.

Lemarié, Smith, Villella, and Weller (2000) evaluated three varieties of tags—Northwest Marine Technology (NMT) Visual Implant Tag, Floy Fingerling Tag, and Hallprint Shellfish Tag—as well as types of adhesives, such as 3M two-part epoxy and Krazy Glue cyanoacrylate. The NMT tag was eliminated from further testing because the printing dissolved in the cyanoacrylate. While both Floy and Hallprint tags performed equally well under laboratory and field tests, they chose the polyethylene Hallprint tag because it was more flexible and thinner and available with a larger number of individual codes than the fingerling tags. Tags bonded to the shells of live mussels with cyanoacrylate could be immersed in water in as little as two minutes after application without affecting retention. Other tags, such as plastic honeybee tags and plastic bird bands, are likely good alternatives to Hallprint tags. Again, the smallest size of the shell that can be tagged depends on the size of the tag.

The effect of tags on the survival of the snails was found to be minimal by Bourns (1968); the presence of a colored plastic bird band affixed to the apex of *Lymnaea stagnalis* did not influence the animal's survival. Similarly, Henry and Jarne (2007) found no effect of bee tags on the thin-shelled *Physa acuta* or *L. stagnalis*, both of which have much thinner shells than those of mystery snails.

d. Painting

One method for marking young, small snails was recommended by Gosselin (1993), who used nail polish in three colors on a marine prosobranch, *Nucella emarginata*. Once the shell was dry, he applied a color (up to six colors) code of up to three dots to each newborn under a dissecting microscope. The nail polish was applied using a small brush trimmed down to three to five strands of stiff hairs. The newborn was returned to the water as soon as the nail polish was dry. Gosselin (1993) used blue, red, yellow, green, orange, and purple paint that generated 186 different combinations when applying up to three nail polish dots; combinations with two consecutive dots of the same color were not used.

To determine whether this method affected the growth or survival of juveniles, Gosselin (1993) placed each of nine marked and premeasured newborns into separate cages in a tank with flowing seawater. Each cage also received one unmarked newborn from the same sample of newborns. Small mussels and rock with barnacles were added as competitors. The snails were measured regularly over a period of 365 days; an additional drop of nail polish was applied to the new shell growth of all marked hatchlings on day 71. These new marks persisted for the remainder of the experiment. Throughout the experiment, the average size of marked and unmarked snails remained closely matched. Growth in shell length of marked and unmarked individuals was not significantly different over the 365 days, and all snails were alive after one year.

Chaine, Allen, Fricke, Haak, *et al.* (2012) used two types of paint, a general hardware-store grade multipurpose red enamel and a white porcelain appliance touch-up paint to estimate the population size of CMS in a Nebraska reservoir. All snails received two marks, one of each color, on the tip of the shell, or nuclear whorl, with one color and a round spot of the other color painted onto the penultimate whorl. The paint lasted several months but missed younger age groups and based their population estimate on adult recaptures.

Wong, Allen, Hart, Haak, *et al.* (2013, 231) tested enamel car paint, plastic bee tags, nail polish paint, and gouache paint as marks on the penultimate whorls of three *C. chinensis* over 181 days. They found "enamel paint was superior to a nail polish mark, which lasted a median of 100 days. Enamel paint marks also had a lower rate of loss (0.00 month^{-1}, 181 days) than plastic bee tags (0.01 month^{-1}, 57 days), gouache paint (0.07 month^{-1}, 18.5 days), or car body paint from studies found in scientific literature. The legibility of enamel paint marks had a median lifetime of 102 days." The authors concluded the use of enamel paint on the shells of gastropods is a viable option for studies lasting up to 6 months.

e. PIT Technology

One method commonly used on fish and other vertebrates is the use of PIT tags, which are passive (do not require batteries) integrated (microchip with unique identification) transponders (emit an identifying signal). They are used to track tags without power but have an internal (or external) microchip activated when it passes close to a special antenna. The tags are usually implanted into the flesh of vertebrates (fish, turtles, snakes, birds, etc.). They allow the assessment of growth rates, movement patterns, and survivorship for many species. Still, they currently have limitations, including high purchase cost, low detection distance, and potential tag loss in some circumstances. PIT tags offer many opportunities to unravel animal mysteries that heretofore could not be addressed effectively (Gibbons and Andrews 2004).

PIT tags have become popular for tracking freshwater mussels, less so with freshwater gastropods. Cooke, Midwood, Thiem, Klimley, *et al.* (2013) recommended criteria (e.g., strengths, weaknesses) to select the best systems (tags, readers, antennas) for different freshwater animals. Perhaps the reason for the lack of PIT use in freshwater gastropods is their size. Most are small (< 10 mm shell height), but viviparids are much larger (3- to > 6-cm shell height), making PIT technology a viable alternative to other marking techniques discussed previously. PIT tags can be used externally, glued to shells, or implanted into the flesh. The tags are easy-to-deploy devices used widely to increase recapture rates and long-term identification of individuals. They range in size from 1.4 mm x 8.5 mm (10 mg). Kurth, Loftin, Zydlewski, and Rhymer (2007) found PIT tags offer improved recapture rates (72–80%) of translocated mussels (vs. 30–47% for visual searches) and increased accuracy of post translocation monitoring.

Young and Isely (2008) tested two adhesives for externally mounted PIT tags on freshwater mussels, cyanoacrylate and underwater epoxy. Tag retention and survival were 100% after a 30-day laboratory period for each adhesive; during 18 months of field observation, underwater epoxy and cyanoacrylate proved to be good adhesives for attaching PIT tags and transmitters. Epoxy performed best with 100% PIT tag retention. Cyanoacrylate also provided high retention rates of PIT tags and transmitters at more than 90%. Mortality was minimal at 4.7% for all relocated mussels over 18 months. All mortalities were those tagged with cyanoacrylate. Transmitters are small with an electromagnetic coil encapsulated in glass. Implantation appears to have adverse effects on the behavior of juvenile bivalves. Wilson, Arnott, Reid, and Roberts (2011) marked immature *Margaritifera margaritifera* individuals with externally mounted PIT tags and found decreased juvenile mussel burrowing rate and, therefore, increased time taken to burrow into the substrate. They attributed the decrease in burial rate to the detrimental effects of handling during tag attachment, which affected activity, burrowing ability, and the time taken for each individual to emerge and begin probing the substrate.

f. Capture-Mark-Recapture (CMR)

The CMR method comprehensively determines population statistics (density, size classes, growth, natality, mortality, age structure, etc. It is more comprehensive because quadrats cannot document size-specific survival or mortality factors essential for understanding introduction success and dynamics (McCann 2014). Small to large snails are collected, ideally from quadrats for initial density estimates, and tagged or marked.

Henry and Jarne (2007) believed the lack of standard, validated marking techniques contributes to the limited use of CMR, so they evaluated two fundamental requirements for a marking technique to be suitable, i.e., tag loss and impact on life history traits (survival, growth, and fecundity). They tested five marking techniques on a freshwater pulmonate snail: (1) numbered, colored plastic marks for queen honeybees; (2) dots of gouache paint using a pen with a soft point; (3) dots of paint for car body using a felt tip pen; (4) dots of nail varnish using a pencil; and (5) dots of corrective fluid from a pencil. The tag-loss rate per month was lower for glued plastic marks (0.01) than for paint marks (0.03–0.07), and the tag-loss rate varied among colors (gouache paint). Under laboratory conditions, the life history traits were not significantly affected by any markings. The minimum recommended shells size was 4 mm for plastic tags and nail varnish and 3 mm for the rest. Ease of use was considered inferior for plastic tags and nail varnish, and good for the other three.

Henry and Jarne (2007) found the average time lag between marking and recapture for gouache paint was 18.5 days. In this time lag, the loss of gouache paint dot under natural conditions was 0.041, but the proportion depended on color ranging from 0.003 for red to 0.217 for dark blue. The average time lag between marking and recapture using tags was 57 days. The proportion of tag loss was 0.015 for plastic marks and 0.066 for car body paint. For car body paint, the proportion was independent of color and time. They recommended using glued plastic marks for long-term studies, paint marks for mass marking, and double marking to account for tag-loss rate.

The CMR method also comes with other shortcomings. Henry and Jarne (2007) believed the color of the tags might have increased the visibility to potential predators, like largemouth bass and pumpkinseed sunfish, which are visual hunters. Hence, estimates of survival probability may be underestimated compared to unmarked snails. Also, one cannot assume that the failure to find marked snails is due to mortality by senescence, predation, parasitism, etc. because some or all snails emigrate from the transplanted area in the fall into deeper water. Mortality can be calculated from tagged dead snails during recapture. There are models to estimate the survival probability of snails throughout a sampling season, such as the Cormack-Jolly-Seber open-population model (McCann 2014), which estimates both survival probability and capture probability. Population estimates can also be made for closed populations (which assumes no births, deaths, immigration, or emigration) (McCann 2014).

2. Density

One can expect seasonal variations in density depending on when and how many snails reproduce. For example, the proportion of copulating individuals of *Viviparus ater* ranged from 1% to 6% (average 3%) of the active population at any one time in Lake Zurich, Switzerland (Staub and Ribi 1995). Staub and Ribi (1995) reported snail copulation 60 times on average from April until November. Snails were abundant and copulated in shallow water close to shore in spring, then moved toward deeper areas in autumn. The snails copulated on all substrates at any depth (1–9 m). The spatial distribution of copulations throughout the summer reflected the pattern of snail abundance.

Densities of CMS range from < 1 m^{-2} to > 40 m^{-2} (Johnson, Olden, Solomon, and Vander Zanden 2009), or larger, according to some “eyeballed” estimates. The densities vary seasonally and are usually the highest in the spring and summer. In most but not all cases, population densities increase after the first few years of introduction, but several factors affect the rate and size of the increase. In some cases, populations could even disappear. Stañczykowska, Magnin, and Dumouchel (1971), in their studies of three populations of CMS, found 18 specimens in the Soulanges Canal near Montreal during July 1969, but the species had disappeared by 1970.

Stañczykowska, Magnin, and Dumouchel (1971) examined the growth in shell dimensions and biomass of three populations of CMS (as *Viviparus malleatus*): Madora Bay, Soulanges Canal, and Beaver Lake, all in the

Montreal region. They reported large, highly localized assemblages of CMS in the three populations; the Ottawa River population had densities ranging from 0.1 m^{-2} to 10-15 m^{-2} between 1969 and 1970, discussed further below. The Beaver Lake population was estimated at 25 m^{-2}, but no density estimate was made for the Soulanges Canal population.

The average densities of CMS are generally in the range of 1–8 m^{-2}. Therriault and Kott (2002-2003) reported the highest densities observed in the littoral zones of their 11 populations examined ranged from 0.1 to 5.6 m^{-2} on rocky substrates, 3 to 6.1 m^{-2} on sand substrates, and a mean of 0.8 to 4.5 m^{-2} on rocky and sandy substrates over the same periods from June 29 to September 2, 1992. Chaine, Allen, Fricke, Haak, *et al* (2012) sampled 127 m^2 of littoral zone substrate for CMS in Wild Plumb Lake in southeastern Nebraska, and estimated densities of 5.2 m^{-2}.

Wolfert and Hiltunen (1968) report density variations in Sandusky Bay of Lake Erie due to strong southerly winds, where the bycatch of snails by fishermen along the north shore was high. This shift in the distribution was probably a direct result of water movements caused by the prevailing winds. Depth, bottom type and character, turbidity, and water temperature seemingly have little effect on the snail distribution, for these characteristics are nearly uniform throughout the bay. This shift in the distribution is probably a direct result of water movements caused by the prevailing winds. Depth, bottom type and character, turbidity, and water temperature seemingly had little effect on the snail distribution, for these characteristics are nearly uniform throughout the bay.

Therriault and Kott (2002-2003) observed an increase in density at a reservoir that was likely due to a migration of individuals from deep water, as an overwintering habitat, to shallower, littoral zone habitat. Jokinen (1982) previously noted *C. c. malleata* migrations to deeper waters in October, with females migrating first. Therriault and Kott (2002-2003) suggested the time needed to complete the migration in deep and large lakes is probably much longer than for shallower and smaller lakes. An increase observed in July may have been a result of the littoral zone migration.

These are some factors affecting population density:

- The quantity of food available (Stañczykowska, Pliñski, and Magnin 1972)
- The quality of food available, especially in carbon and nitrogen content (Jokinen 1982)
- Seasonal variations in immigration and emigration of snails affecting densities of males and females, females moving before

the males; see discussion below based on Stañczykowska, Magnin, and Dumouchel (1971)

- Size-dependent mortality between years, with snails smaller than 30 mm shell length disappearing first (McCann 2014)
- Differences in water body size; densities affected by seasonal migrations between deeper water overwintering locations and shallower littoral zones, toward deeper in fall and winter and toward littoral zone in spring and summer (Therriault and Kott 2002-2003)
- The concentration of calcium, whereby CMS require > 5 mg^{-1} to establish themselves
- Mortality due to senescence, predation, and parasitism
- Interpopulation differences due to water chemistry, especially in buffering variables (pH, calcium content, total alkalinity, total hardness)
- Strong water currents created by winds, especially on the fetch (the longest distance that wind blows uninterrupted by land) of large lakes (e.g., Sandusky Bay on Lake Erie)

3. Growth

Table 6-1 gives the chemical and physical characteristics of the three study stations studied by Stañczykowska, Magnin, and Dumouchel (1971). Madora Bay receives water from the Ottawa River; Soulanges Canal from the St. Lawrence River; and Beaver Lake is an isolated pond, about 100 m in diameter, located within Mount Royal Park, Montreal. The Ottawa River had the lowest buffer variables (pH, Ca, Mg) values, while the Soulanges Canal had the highest. The substrates were very different, especially the canal with its concrete walls.

Table 6-1. Chemical and physical characteristics of three study station for growth and biomass of *Cipangopaludina chinensis*. Data are from Stañczykowska, Magnin, and Dumouchel (1971).

Water Body	**pH**	**[Ca] mgL^{-1}**	**[Mg] mgL^{-1}**	**DO mgL^{-1}**	**Depth m**	**Substrate**
Madora Bay, Ottawa River	7	24	13	7	0.2–2.5	Water brownish; bottom a mix of soft mud and detritus; diversity of plants
Soulanges Canal	8.4	97	31	10	2–3	Concrete walls; silt bottom
Beaver Lake	7.75	75	25	11	3	A small pond, spring-fed; concrete banks; mud bottom

a. Shell dimensions

Jokinen (1982) examined shell growth in both *C. chinensis* and *C. japonicus*, but called the latter, *C. chinensis* morph *japonicus*, because, at the time, there was no resolution of CMS and JMS being separate species. Figure 6-4 shows both species' shell width (W) vs. height (H) relationship. The regression equations, both with significant r^2 values, are:

$$C.\ chinensis\text{: Log W} = 0.17 + 0.84 \text{ Log H}$$
$$C.\ japonica\text{: Log W} = 0.23 + 0.78 \text{ Log H}$$

The lower slope value of 0.78 for *C. japonica* indicates the shell width increases less rapidly than the shell width of *C. chinensis*. Juvenile CMS had a different shell shape than older snails and revealed marked periostracal spiral hirsuteness arranged into three rows of stiff hairs. The same hirsuteness on CMS was discussed earlier, but Jokinen (1982) described the hairs as hook-shaped, hooks facing outward, and 0.35 mm long. As Figure 5-16 illustrates, the hairs disappear.

Stañczykowska, Magnin, and Dumouchel (1971) collected 352 specimens of CMS from July to October 1969 and from May to July 1970 in the Ottawa River, Quebec. The Castors (Beaver) Lake and Soulanges Canal stations were only visited once, the former in June 1970 when 58 specimens were collected, the latter in 1969 when 18 specimens were collected. The monthly percentages of males, females, and juveniles and densities in the Ottawa River population are shown in Table 6-2.

Stañczykowska, Magnin, and Dumouchel (1971) examined changes in shell shape during its life to determine whether the shell shape of males is different from that of females. They measured the height and width of shells of both sexes and juveniles from the Ottawa River population; the numbers are given in Table 6-2. They calculated the allometric regression lines (Log width = log a + b x Log height) for the two dimensions and the three groups. They analyzed covariance to check for significant differences in the slope and intercepts of the lines. There was no significant difference in the height–width relationships of the shell between males and females. Therefore, a regression equation was developed for both sexes; it did not differ significantly from juveniles. Hence, Stañczykowska, Magnin, and Dumouchel (1971) used a single equation to predict width using height for males, females, and immature snails:

$$\text{Width} = 0.376 + 0.700 * \text{Height}$$

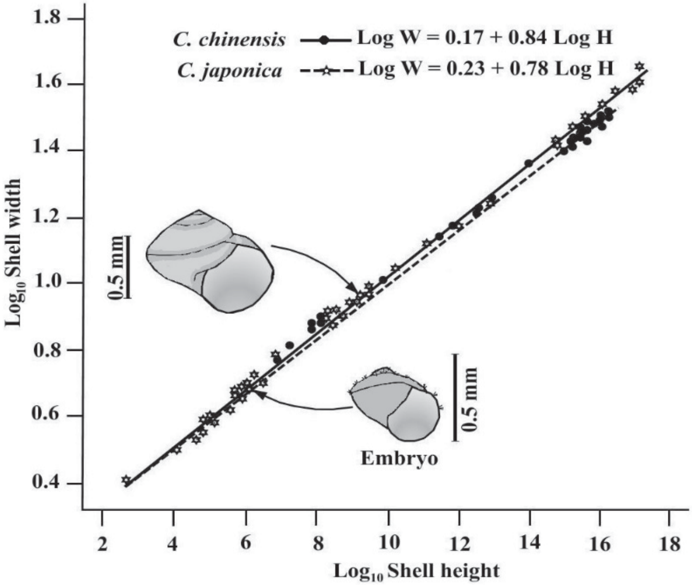


Figure 6-4. Allometric shell growth of *Cipangopaludina chinensis* and *C. japonica*, with sketches to illustrate the shape of the shells on the regressions. Modified from Figure 2 in Jokinen (1982).

Table 6-2. Female to male ratio of *Cipangopaludina chinensis* in the Ottawa River population using data from Stañczykowska, Magnin, and Dumouchel (1971).

Date	N	% Female	% Male	% Juvenile	♀/♂ ratio	Density m^{-2}
1969						
July	69	62	23.9	14	2.6	10–15
August	75	66	9.1	25	7.3	10–15
September	79	30	35.9	34	0.8	5–10
October	13	33	0	67	0	0.1
1970						
May	30	43	56.7	0	0.8	5
June	86	55	45.0	3	1.2	20

The Beaver Lake population had 53% females, 47% males, and 10% juveniles, the sex ratio being essentially 1. Stañczykowska, Magnin, and Dumouchel (1971) plotted the width vs. height data, but they did not calculate a regression line, merely stating that the relationship is more or less the same as the Ottawa River population (Figure 6-5). They did compare the growth in the height of the three populations through the five age groups and found it was slower in Beaver Lake than in the Ottawa River but similar to the Canal de Soulanges snails (Figure 6-6). Five age groups were found for the Beaver Lake population, with only one female of 58 specimens in the fifth age group. The Canal de Soulanges population had four age groups, with only one of 18 females in the fourth age group. The same results were obtained for biomass growth.

McCann (2014) used CMR to determine the growth of CMS. He started in April 2010 with snails of shell lengths ranging from 5.81 to 64.50 mm (average 46.63 ± 0.50 S.E.). Then, 89 of the 447 individuals were recaptured in October 2010, and 10 of the 447 from 2010 were recaptured in 2012. In April 2012, he captured 158 individuals over two capture occasions. Ten snails were still alive from 2010 and were recaptured in 2012. Six snails originally tagged in 2012 were recaptured on the second capture occasion. Shell lengths of all 2012 captures ranged from 8.66 to 62.18 mm (average 49.74 ± 0.55 S.E.); only a single juvenile snail (8.66 mm in shell length) was captured in 2012.

Lu, Du, Li, and Yang (2014) measured 23 specimens of CMS and reported a range in height from 37.3–63.5 mm, mean of 52.6 ± 7.56 SE, and 28.5 to 47.9 mm of 40.2 ± 5.68 SE.

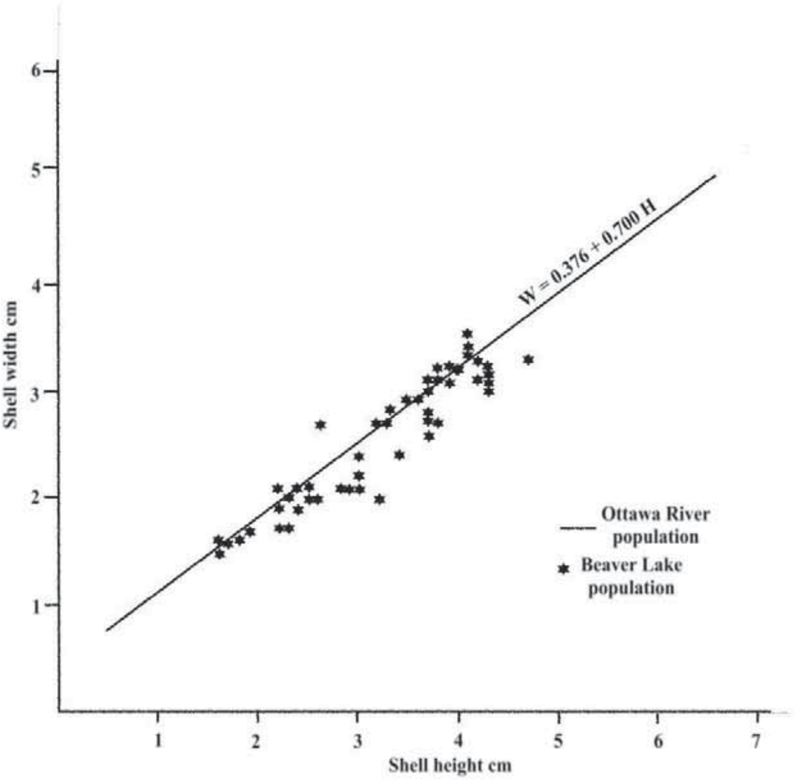


Figure 6-5. Relationship between shell width (cm) and height (cm) of *Cipangopaludina chinensis* in Beaver Lake relative to the Ottawa River population. Redrawing of Figure 8 in Stañczykowska, Magnin, and Dumouchel (1971).

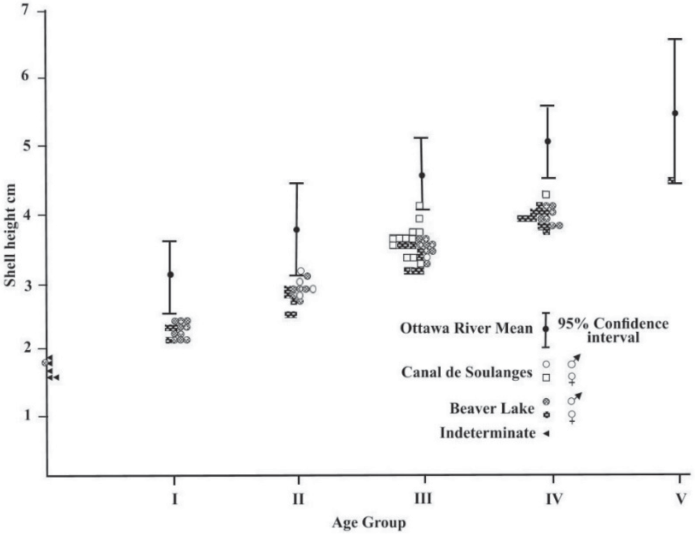


Figure 6-6. Growth in shell height of the Chinese Mystery Snail in three populations examined by Stañczykowska, Magnin, and Dumouchel (1971). Figure is modified from Figure 6 in Stañczykowska, Magnin, and Dumouchel (1971).

b. Biomass

Stañczykowska, Magnin, and Dumouchel (1971) expressed the relations between the weight (W) and the height (H) of the shell of CMS in the allometric form, W = aHb, in which a and b are constants. The logarithmic form, log W = Log a + b*Log H, is linear and was compared to other equations of the same kind by simple statistical methods. For the Ottawa River population, they established three equations, expressing log W as a function of log H for [1] adult males, [2] adult females, and [3] juveniles, respectively:

[1] $\text{Log } W = -3.3392 + 2.4484 \text{ Log } H$
[2] $\text{Log } W = -5.2491 + 2.4245 \text{ Log } H$
[3] $\text{Log } W = -3.2858 + 2.4264 \text{ Log } H$.

They found no significant differences between the male and female regressions and combined the data to describe the relationship for both groups:

$$[4]\ \text{Log } W = -3.3977 + 2.2455 \text{ Log } H$$

The relationship between biomass and shell height for [4] the combined male and male regression and [3] juveniles was also found to not be significantly different, resulting in a regression [5] for all three groups:

$$[5]\ \text{Log } W = -3.3740 + 2.4664 \text{ Log } H$$

For the Beaver Lake population, Stañczykowska, Magnin, and Dumouchel (1971) performed similar analyses, and because of the lack of significant differences between [6] male and [7] female biomass vs. height regressions, they developed a regression [8] combining the two sexes:

$$[6]\ \text{Log } W = -3.7655 + 2.6170 \text{ Log } H$$
$$[7]\ \text{Log } W = -2.4723 + 2.0988 \text{ Log } H$$
$$[8]\ \text{Log } W = -3.1362 + 2.3611 \text{ Log } H$$

They next compared equations [5] and [8] and found no significant difference and proposed the following regression [9] for all individuals in the Ottawa River and Beaver Lake:

$$[9]\ \text{Log } W = -3.3829 + 2.4863 \text{ Log } H$$

They found no relationship between body weight and shell height and the environmental parameters (pH, calcium, magnesium, and DO concentrations in the ranges found in 1969 and 1970.

c. Life Span

Estimating the longevity of snails requires knowledge of age groups through time. The age of operculate snails can be calculated in four ways: (1) annual rings (annuli) on the shell, (2) annual rings on the operculum, (3) following the growth of individually marked snails held within cages in their native habitat, and (4) length-frequency analyses. The aging of operculate snails using annual rings on the operculum and shell is dealt with together here and is similar to the aging techniques of fish scales.

Stañczykowska, Magnin, and Dumouchel (1971) used the rest marks on the shell and operculum in their age group studies.

The annual rings indicate cessation of growth, usually due to winter hibernation. But other environmental phenomena, such as desiccation due to lowered water levels and extended periods of anoxia, can cause growth rest rings. As a result, rings may occur more than once annually (see Figure 5-10). Counting annual rings on the operculum and shell, therefore, can be very subjective. For this reason, it is best to count rest marks and decide later which ones are annual rings for determining their age. Figure 6-7 illustrates opercular rest marks with the shell rest marks on the same living specimen. If only dead representatives are available (e.g., determining age at mortality), only the shell is used to guestimate age. It is best to have two or three people determine a snail's age to reduce some subjectiveness.

Uvayeva and Utevsky (2021) used both shell and opercular rest bands to age *V. viviparus* and *V. contectus* in water bodies in Ukraine; the maximum age of *V. viviparus* was five years and of *V. contectus* was six years. However, populations with maximum ages were lower: three to four years in *V. viviparus* and four to five years in *V. contectus*. Their Figure 8 nicely illustrates aging in the opercula of *V. contectus* at 0+ through 6+ aged snails.

Jakubik and Lewandowski (2007) used field and laboratory experiments to establish the relationship between the growth rate and age of *V. viviparus*. Age was determined using shell growth rings, but the rest rings were not overtly apparent in laboratory-raised snails. Juveniles appeared in the lab experiments when females were 18 months old and had achieved three years of growth. The shell growth lines of the females were uniformly distributed, without visible dark winter rings or rings of summer growth inhibition. Winter and summer rings appeared in the second year of the field culture; the second winter ring appeared in the third year of field culture.

Wolfert and Hiltunen (1968) used life history analysis to age Japanese Mystery Snails (as *Viviparus japonicus*) in Sandusky Bay of Lake Erie, where local fishermen sometimes reported two tons bycatch in a seine haul in the spring. The frequency distributions of shell height and diameter suggested two age groups of adults in the population.

Jokinen, Guerette, and Kortmann (1982) used both size-frequency analysis and opercular rings to age *Viviparus georgianus*. Most snails could be aged by shell size alone because cohorts tended to separate along a size axis. Upon occasion, the smallest individuals of an older cohort overlapped with the largest individuals of a younger cohort. The number of opercular rings was consistent for each known age cohort and was also used to age the snail. The widths of the rings varied greatly in different opercula and depended on the growth rate. In addition to the usual annual rings, most individuals have a mid-summer cessation of growth during their second and third summers, producing a scar on the shell and an additional narrow band on the operculum.

The shell in Figure 6-7 shows the aging of three shells from the same population, based on the opercular rings and the rest marks on shells, the center shells showing a sunken nucleus. Three rest marks are labeled in each shell, each representing one year of growth. The nucleus represents the embryonic growth of the operculum. Year one begins at the outer margin of this embryonic growth period. The outer limit beyond the third year represents the summer growth in its third year (3rd+ year). Other less apparent ridges represent short-term rest marks due to periods of stress, such as desiccation, anoxia, etc.

Another method for aging operculates uses labeled (tagged, etched, marked, painted, etc.) specimens held in maintenance cages in their native habitat. Ideally, juveniles are used at time = 0, but snails with known age at time = 0 can also be used. Juveniles are often too small to label. However, cage effects have to be considered. The method can be long term (defined by the snail's longevity), risk loss of cages, tampering by curious people, extreme weather (e.g., drop in water level, lethal temperatures), etc.

Figure 6-8 shows CMS grows throughout its life in the Ottawa River, as is the case for most viviparids, such as *V. georgianus* by Van Cleave and Lederer (1932) and Browne (1978) as well as *V. viviparus* by Young (1975). However, Stańczykowska, Magnin, and Dumouchel (1971) found the growth rate decreased with age; for example, there was an increase of 1.5 cm between the I and II age groups and only about 0.5 cm between IV and V age groups. They also found the growth of males occurs at the same rate as that of females (i.e., snails of the same age occur at the same rate as females). Females are much larger than males not because of a faster growth rate but because of a longer life. Figure 6-6 shows that for age group IV, there is only about half the number of males than females, and in group V, there is only one male out of 27 snails. This result is different than for *V. georgianus* in which females attain larger sizes not only because of longer length of life but also because of faster growth (Browne 1978).

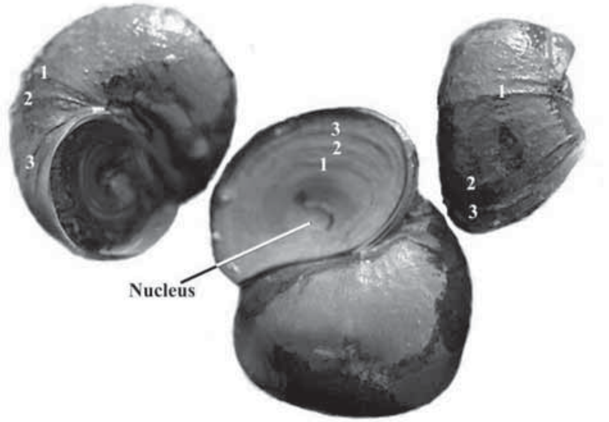


Figure 6-7. Determining the age of an operculate snail (Chinese Mystery Snail shown) from its operculum and growth rests on its shell. 1, 2, and 3 refer to its age. All three are from the same population. Images are modified from photo 2734482, by Hyun-tae Kim. Shell dimensions were not provided. Note the deep depression of the nucleus.

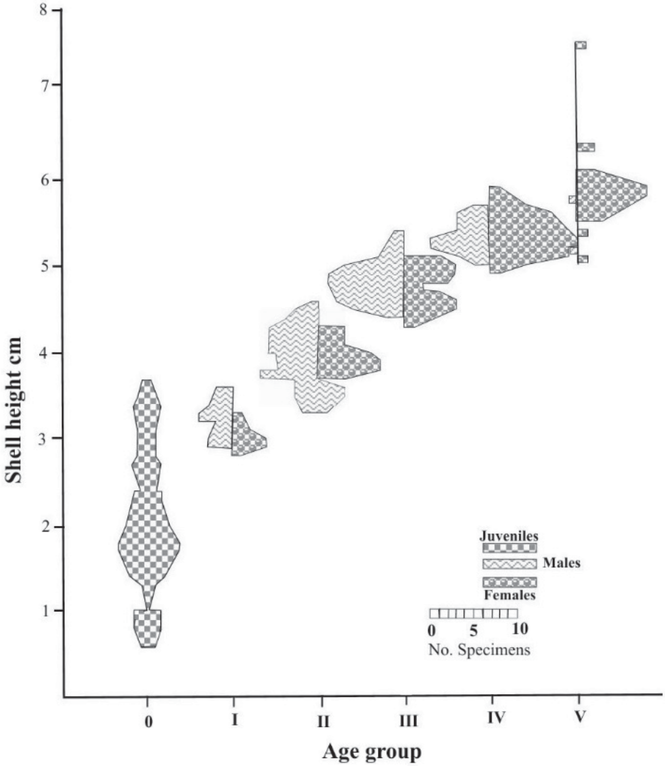


Figure 6-8. Growth in height (cm) of *Cipangopaludina chinensis* through five age groups in the Ottawa River. Graph modified from Figure 3 in Stañczykowska, Magnin, and Dumouchel (1971).

4. Fecundity, Brood Size, Natality

Some preamble on these three metrics is required. Fecundity is the number of eggs produced. Of this number, many will develop into embryos as they proceed down the oviduct to the brood sac, each egg encapsulated in a gel-like mass. Yolk in eggs is the main source of nutrition for embryos in many gastropods, but the oocytes contain moderate or small amounts of yolk; perivitelline fluid of the albumen gland is added as the primary source of nutrition. In young *V. viviparus*, oocytes degenerate in all stages of development, and mature oocytes are extruded into the acinar lumen where they degenerate (De Jong-Brink and Geraerts 1982). Hence, some embryos perish along their path to the brood sac and are unrecognizable as embryos. Their remains will contribute to the nutrient pool for viable embryos. The number of embryos that survive on the way to the brood sac represents the brood size. While in the brood sac, more embryos will perish for various reasons (e.g., some are more developed and stronger than others). The difference between the number of eggs and the number of embryos is brood mortality. The net result is brood size. The brood still consists of weaker and stronger individuals, most of which will be released as viable juveniles, the numbers representing natality, the difference contributing to more brood mortality. Once released into the wild, many will succumb to parasitism, predation, competition, etc., the loss of which represents mortality in the wild.

After having gone through the literature, there is rarely a distinction between the three metrics, and interpretations of a brood size number could represent fecundity, brood size, or natality because no definitions were provided. There is a need to standardize the three metrics, which for viviparids is more complicated than for oviparous and ovoviviparous species, which have brood sacs.

- For example, oviparous species like *Bithynia tentaculata*, lay eggs on macrophytes. Fecundity is the number of eggs in the clutch. The number of eggs that hatch into viable young represents natality, which can easily be determined by clipping the macrophytes with the clutch of eggs and hatching the eggs in an aquarium with the lake water in which eggs were laid.
- Ovoviviparous species like *Sphaerium* and *Musculium* species (Sphaeriidae), produce three kinds of brood sacs (primary, secondary, tertiary), each being a sequential stage. Primary sacs contain eggs (i.e., numbers = fecundity). Some eggs perish while primary sacs grow to secondary and tertiary sacs. Most embryos within the tertiary sac break free, releasing extra-marsupial larvae into the marsupium and thence into the wild as newborn (Mackie 2007). The brood size is the numbers of embryos surviving to the tertiary sac stage; natality is the number of extra-marsupial larvae (newborn).

There have been no methodologies for calculating the three metrics for viviparids, and these are needed before expressing results as fecundity, brood size, or natality. Perhaps the primary issue is the numbers for these metrics are often estimated from specimens preserved in ethanol or formalin, after which it is difficult to determine which embryos were alive and viable before preservation. One solution is to evaluate the three metrics on living specimens by either rearing them in their native water, which could take a long time, or immediately dissect the females, release the embryos into their native water, using the total numbers in the brood sac as an estimate of brood size and the number alive (e.g., crawling) as an estimate of natality. Fecundity is more challenging to estimate in viviparids and may be the number of uterine eggs, or it requires more innovation than dissection.

Freshwater snails usually attain sexual maturity before they finish their growth (Fretter and Graham 1962; Buckley 1986; Jakubik and Lewandowski 2007). Viviparids generally become fecund in their first year and continue producing young until they attain their final age group, females living longer than males. Augustyniak and Jakubik (2002) examined the reproduction of *V. viviparus* in the Narew River, Poland. They found females comprised 53–90% of the population, mainly size classes (III and IV), while most males were class II. Most miniature snails (class I) were found only among the males (up to 50%). Gravid females predominated in most sites (size class IV, 80–100%), producing an average of 18 embryos per female (range 1–59).

Embryo development in viviparids was first described by Crabb (1929, 126), with a dramatic narrative of four embryos of *V. contectoides* (= *V. georgianus*) escaping from their membranes as "kicking and biting" the membrane within the uterus: "After about an hour of more-or-less constant kicking and biting, the membrane parted across the anterior region," then the newborn snail filled its branchial chamber with water. They remained motionless for several minutes before crawling away with the membrane still clinging to its shell. In the uterus, eggs that were ready to be laid were transparent, while those higher up in the tract were successively opaquer. Crabb assumed the albumen had been consumed in the transparent embryos. Uterine eggs ready to be laid created currents by fluid contents of the embryos released into the water; Crabb believed the eggs still contained an appreciable amount of albuminous material at the time of their emergence.

Of two large females that Crabb (1929) collected from a pond in March, one produced 16 young four days later and two more on the fifth day; at this point, 81 eggs were counted, 79 of which appeared ready for laying. The other individual was opened two days after being brought into the laboratory, and 129 eggs were removed. Of these, 122 were ready for laying, 5 contained no vitelli (yolk), and 2 were opaque. Of the 122 eggs, 89 were put in a Petri dish with water; 90 minutes later, more than half had hatched and were clinging to the side of the dish. Including an individual collected in November 1927, which carried 130 eggs, the proportion of transparent to opaque eggs collected in the spring was 201:4. In those collected in the fall, the ratio was 76:50, suggesting that oviposition was probably discontinued during the cold months and that developmental processes were perhaps retarded but not entirely discontinued.

Crabb (1929) saw similar results for seven specimens of the Chinese Mystery Snail collected on September 22, 1928. His data are given in Table 6-3, with opaque being the newest eggs, translucent the developing eggs, and transparent eggs ready for birth. Including embryos from a November sample, he estimated approximately 89% were opaque and contained very young embryos. One snail was collected on May 29, 1927, with embryos in all three stages of development. All 11 of its eggs were transparent. In CMS, the egg membrane is ruptured either by the young snail before extruding or during extrusion. Rapid imbibition of water by the eggs apparently caused the membranes of the embryos to rupture within a few minutes after they were placed in water. An individual collected November 2, 1927, contained 130 eggs, 4 of which were without vitelli (dead?), 76 were transparent or nearly so, and 50 were opaque.

Table 6-3 shows *C. chinensis* collected in September by Crabb had the majority (356) of their embryos still in the opaque stage, very few in the translucent stage (8), and some in transparent stage (26), or ratios of 356:8:26, suggesting development was continuing. As stated above, for snails collected in November, Crabb estimated a ratio of 76:50 for the proportion of opaque to transparent embryos, and oviposition had probably discontinued or was retarded. These data suggest that embryo development was continuing through September (i.e., from April through September).

The presence of embryos in several stages of development within the female's uterus of viviparids, as reported by Crabb (1929), is commonly recounted in recent studies. Young (1975) collected small specimens (3–6 mm) of *V. viviparus* from April to August and found fully developed young in the brood sacs of the adults throughout the same period; there was a continual release of young during the summer. Their release and the presence of many adults gave rise to a peak in numbers in August 1971 and April 1972.

Therriault and Kott (2002-2003) found a significant difference in population densities of CMS between a smaller, shallower lake and a larger, deeper reservoir. They attributed the difference not due to the level of eutrophication but rather because the young of CMS were not released simultaneously but instead displayed a continuum of release. The young reached shell heights of 10.6 mm within the uterus and were released as free-living individuals starting at shell heights of 6.5 mm. A positive relationship between fecundity and female shell height was observed for one of two populations studied.

Table 6-3. Different stages of embryos in seven Chinese Mystery Snails examined by Crabb (1929).

Number of Embryos of the Chinese Mystery Snail in Different Stages of Development			
Snail #	Opaque	Translucent	Transparent
1	9	0	3
2	83	0	6
3	58	3	0
4	51	5	3
5	9	0	0
6	102	0	14
7	44	0	0

Therriault and Kott (2002-2003) found fecundity was related to female shell height for one of the two Chinese Mystery Snail populations studied. A significant positive relationship between the number of young and female shell height was observed for a Lakeside Park population. The average number of young was 34, and the median value was 33 for this population. Conversely, the fecundity relation for the Deer Creek Reservoir population indicated no significant relationship between the number of young and female shell. The average number of young was 25, and the median value was 28 for the Deer Lake population.

In addition, the variance in the number of young accounted for by mother's shell height was 62% for the Lakeside Park Lake population, but only 3% for the Deer Creek population. Therriault and Kott (2002-2003) rationalized the relatively strong relation at one location and none at the other as there being more females (10 of 20 were 45 mm high) at Lakeside Park Lake than at Deer Creek Reservoir, with only 2 of 24 females greater than 45 mm in height. They believed that younger females do not produce as many young, and females at Deer Creek had not yet reached full sexual maturity. An analysis of covariance of female shell heights suggested larger individuals had a significant impact on the relationship between the number of young and female shell height.

Therriault and Kott (2002-2003) found that the snails were continually giving birth, with more females collected from Deer Creek giving birth before being collected. The data collected on the size of the young within the uterus were similar for Deer Creek Reservoir and Lakeside Park Lake; smaller individuals in the uterus were 0.1 mm, and the largest was 0.6 mm. In addition, snails maintained in an aquarium for observation gave birth to young ranging from 6.5 mm to 9.0 mm in shell height. They believed the size of young when released may be governed by environmental factors, such as time of year, water chemistry, food abundance, and locality. Vast differences in sizes of individuals in the uterus, from unfertilized eggs to 10.6 mm, indicates not all of the young are released at once. Still, instead, there is a continuum of young growth in the uterus before being released. The young that were released in the aquarium were not all released at once but over some time. A female may give birth to more than one individual at a time, but she is unlikely to release her young at once.

Buckley (1986) reported spat sizes of *V. georgianus* positively correlated with female age irrespective of female size, though brood output increased with maternal size and growth rates. His caged experiments showed spat born early to older females grow fastest, and the younger of the older females have greater expected lifetime fecundity and fitness. In the *V. georgianus* population studied, third-year females produced approximately 50.0% of each new cohort, with second-year and fourth-year females having 21.0% and 26.0%, respectively.

Jakubik and Lewandowski (2007) used field and laboratory experiments to establish the relationship between growth rate, age, mortality and fecundity of *V. viviparus*. They found fecundity to depend on the female's size. Shell size did not affect the size of newborn snails; females of different size classes produced offspring of the same shell height (4.0 mm) and width (4.5 mm). Ribi and Gebhardt (1986) found age-specific fecundity was common in *V. ater*, with fecundity and offspring size positively correlated with the size of females. Still, fecundity was higher, and offspring were larger in some lakes than others.

Jakubik (2007) found embryos of *V. viviparus* in 2nd-year females (8.1:12.0 mm shell width: height of the shell), third-year and fourth-year size classes and the mean number of embryos per female, ranged from 0.9–6.7, 1.1–9.6, and 2.0–9.1 for second, third, and fourth-year size classes, respectively. His analysis of embryonic development revealed the presence of three growth stages in oviducts of females: oval, transparent egg capsules (youngest embryos); egg capsules with the visible contour of a shell (medium embryos); and snails with a shell (oldest embryos)—the youngest and oldest embryos dominated in particular size classes in his analyzed sites.

There was a significant positive relationship between the mean sum of embryos, shell height and width, and dry weight of a female's body and shell weight. The most significant correlation was between dry body weight and the mean number of embryos. The number of oldest embryos increased with the increase of shell height and width. A female's dry body weight, on the other hand, was best correlated with the youngest embryos. Jakubik (2007) concluded that the relationships indicate the importance of the size of *V. viviparus* females for reproductive success and survival and the condition of young snails. Augustyniak and Jakubik (2002) also found a reproduction of *V. viviparus* in the middle and lower sections of the Narew River increasing with the shell height and body mass.

Stephen, Allen, Chaine, Fricke, *et al.* (2013) found 41 males out of 70 adult Chinese Mystery Snails in a Nebraska reservoir. The sex ratio did not differ from 1:1 (chi-square = 2.057, p = 0.15). Ripe females comprised 21 of the 29 females found in the sample. Ripe females contained 525 embryos, an average of 25 (standard error = 6.8) per female. Embryos were found at different stages of development and size: 377 were yolk capsules, and 148 were shelled. The size of yolk capsules, taken at the widest diameter, ranged from 1 to 5.5 mm with an average of 2.6 mm. Shelled embryos ranged from 2 to 7 mm in length with an average of 3.9 mm. Five female snails were found with embryos at both developmental categories (yolk capsules and complete shells).

Stephen, Allen, Chaine, Fricke, *et al.* (2013) described a positive relationship between female shell height and the number of developing embryos ($p = 0.0009$; $r^2 = 0.44$; Figure 6-9). A single 54 mm-long female contained 133 developing embryos. The largest female was 57 mm long and had 44 embryos. The smallest female was 31 mm in length and had 4 embryos. The average size of embryos was also positively related to female adult length, but the strength of the relationship was weak ($p = 0.07$; $r^2 = 0.15$; Figure 6-9).

The period of brooding for CMS is scantily reported. Stephen, Allen, Chaine, Fricke, *et al.* (2013) estimated annual fecundity for CMS at 9, 10, and 11 months of brooding. The average number of embryos per female and the expected brood time indicates each female should produce 27.2 to 33.3 young per year. There are data for other viviparids: the Banded Mystery Snail, *Viviparus georgianus*, has a brooding period of about 10–12 months found by Vail (1978), 10 months by Jokinen, Guerette, and Kortmann (1982), and 9 months by Browne (1978); for *V. contectoides*, Vail (1978) estimated an incubation period of 8–10 months. During a 10-month gestation period for *V. georgianus*, Rivest and Vanderpool (1986) found 80 µm zygotes take up the albumen and grow into a spat that emerges at around 3.5–5.0 mm in *V. contectoides.*

Annual production estimates are rare for CMS. Chaine, Allen, Fricke, Haak, *et al.* (2012) estimated the adult female population of CMS in Wild Plum Lake, a reservoir in Nebraska, at 84,500–112,500 based on a CMR study. They multiplied this estimate by the average production for each female and translated it into a yearly current output of 2.2 to 3.7 million young.

According to Vail (1977a, 1978), *V. georgianus* from a creek in Florida produced single broods per year, with both fertilizations and births occurring over the 10- to 12-month period. Small young were produced from the first fertilization, but continued fertilizations in the same adult produced broods of young in a size series. As the older young from the first brood was born, broods of large young from the more recent fertilizations occurred. Simultaneous incubation of two different broods also occurred. There was a seasonal variation in the young per brood, with maximum brood size occurring during late summer with the young in a size series. There was no correlation between the number of young per brood and parental size. Vail (1978) found the number of young per brood and the diameter of the young at birth was highly variable, even when parental sizes were nearly identical.

5. Survival

The survival of embryos is fundamental to the survival of a population. The production of embryos has energy costs. Smith and Fretwell (1974) recapped two intuitive relationships: (1) as the energy expended on individual offspring is increased, the number of offspring that parents can produce is decreased, and (2) as the energy expended on individual offspring increases, the fitness of individual offspring increases. A proportional increase of the reproductive effort with age decreases the probability of survival (Smith and Fretwell 1974; Pianka and Parker 1975; Caswell 1982; Jakubik 2007).

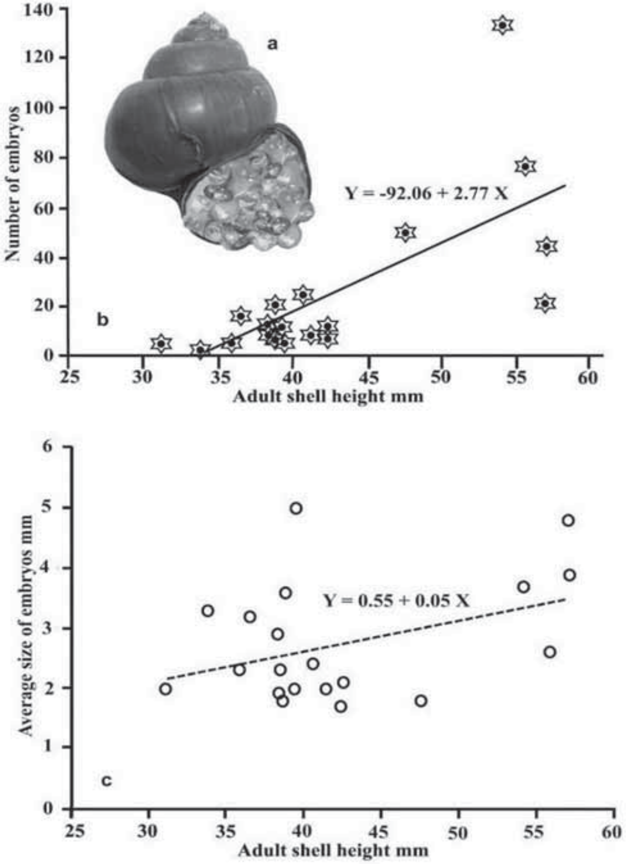


Figure 6-9. Number and size of brooded embryos as a function of shell height in the Chinese Mystery Snail. (a) Female with brood sac exposed showing several encapsulated embryos, modified from photo 87226688 by Oceanicadventures, see Appendix C for source. (b) Number of brooded embryos. (c) Size of brooded embryos. (a) GLM image. (b) and (c) redrawn from Figures 1 and 2 in Stephen, Allen, Chaine, Fricke, *et al.* (2013).

Caswell (1982) proposed that survival costs increased markedly with age, while fecundity costs should be nearly age-invariant for many organisms. Buckley (1986) found female survivorship of *V. georgianus* positively size-related, as is incremental growth within any year. In addition, the reproductive effort was age-related, increasing from 5.3% for two-year females to 79.7% for four-year females. Reproduction was size limited in two-year females; no females below 16 mm shell length were found containing broods. Reproductive females have greater biomass and hence greater survivorship.

There are meager data that show survival rates of CMS embryos within its uterus (pallial cavity). Crabb (1929), as stated earlier, observed an individual collected in March had 129 embryos of which 122 were ready for birth, 5 contained no yolk, and only 2 were opaque; assuming the yolkless eggs were dead, the survival rate would be 94.6%. Similarly, for a snail collected in November contained 130 eggs, 4 were without yolk, implying a survival rate of 96.9%. Crabb (1929) estimated the proportion of transparent to opaque eggs collected in the spring to be 201:4, suggesting a survival rate of 98.0%; for those collected in the fall, the ratio was 76:50, offering a survival rate of 60%, assuming the opaque eggs did not continue development the following spring.

By intuition, snails with the longest life span should have the highest survival rate. Browne (1978) supported this with *V. georgianus*, in four mesotrophic lakes in New York, three natural lakes (TUL, SON, CAZ), and one reservoir (JAM). He reported that the highest cohort survival rate was reached in different but older age groups for the four populations. Females outlived the males and had higher survival rates. He recorded cohort survival by setting the density at birth equal to 1,000 for the combined sexes (500 each) in each of the four populations. Subsequent densities were used to compute survivors per thousand, which he documents in his Table 2, shown here in Figure 6-10. Browne (1978) documented recaptures as cohort survival of *V. georgianus*, based on the snail transplants at his four sites over 36 months, but he did not account for emigration and immigration of snails in his study. Of the 1,000 snails transplanted, the highest recapture rate of males was 11.8% after 18 months, the lowest being 7.4%; no males were recaptured after 24 months. Females survived up to 30 months, with no recaptures at two sites and 4.1% and 4.3% at the other two sites. After 18 months, when 7.4% to 11.8% of males were recaptured, 10.6% to 23.4% of females were recaptured; after 24 months, 2.0% to 13.0% of females were recaptured.

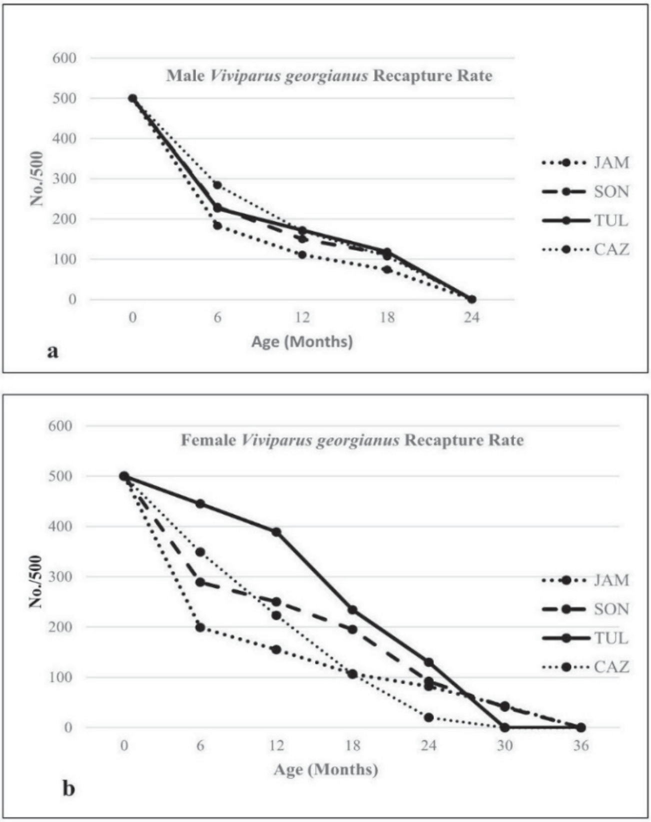


Figure 6-10. Recapture rates of male and female *Viviparus georgianus*. Data from Browne (1978), Table 2.

Emigration and immigration appear to be major factors in Browne's (1978) study estimating cohort survivorship. For example, at all four sites, of the 500 male and female snails he started with, none were recaptured after 24 and 36 months; the declines to zero can be attributed to one or more of four explanations: mortality, but dead shells were not counted; emigration, suggesting that more males emigrated than females after 24 months; more females immigrated after 24 months (no males survived at four months); or, indeed, the numbers represent cohort survival.

Young (1975) examined the migration of *V. viviparus* to explain variations in their abundance on a concrete wall of the Worcester-Birmingham Canal in Britain; abundance was affected by the migrations of the snails and the release of young. The numbers collected in the autumn declined rapidly due to migration to the under-sampled canal bottom. This movement is shown in Figure 6-11 by the changing patterns in vertical distributions. The wall zones were favored in the summer and the angle zone, including the canal sediments, in the winter. The arrows indicate the direction of migration, stable being little or no net movement. Young specimens reached at least 8 mm by October of their first year. They then apparently continued to grow and develop, returning to the wall zones the following spring carrying well-developed young. Some specimens died during their first breeding season, but many survived to breed in their second year, reaching 38 mm in length. Each adult specimen carried between five and eight developing young at any one time, but due to their migration, it is not possible to deduce either the overall fecundity of the specimens or the rates of survival or mortality. In common with the other species, lower reproductive success occurred in 1972 than in 1971, although the numbers of adults present at the beginning of each season were similar.

The survival rate is dependent on its environment or changes in its environment, especially in periods of drought. Alyakrinsaya (2004), in their review of the literature concerning drought survival, stated that all living beings follow the principle of a constant respiratory environment; gas exchange is possible only through a wet respiratory surface; therefore, the respiratory epithelium should be constantly wet. The operculates demonstrate this principle; under drying conditions, a period of active movement is soon followed by deep body withdrawal into the shell with water retained by sealing its aperture with the operculum. This reaction happens after substrate drying and inevitable dehydration of the soft tissue due to evaporation and mucus formation required for locomotion. Forced immobility of the molluscs and tight closing of the shell aperture provides for minimum water loss by soft tissues, and most importantly, prevents drying of the respiratory surfaces (Alyakrinsaya 2004). At present, the extent of ctenidial involvement, if at all, in this process is unknown. Alyakrinsaya (2004) believed such molluscs had developed cutaneous respiration by the entire free surface of the body facilitated by the capillary network of the mantle. He cited survival times of several viviparids: *C. chinensis*, 3 months; *V. complanata*, > 14 days; *V. fasciata*, 8–10 months; *V. viviparus*, 30–40 days.

Havel (2011) found the resistance of CMS to air exposure very robust with the ranges of temperature (T) and relative humidity (RH). He used both field and laboratory studies; in the field studies, with temperatures ranging from 8–30ºC and RH from 37–100%, the LT50 for medium-sized shells was > 28 days; for the lab studies, he used small shells with temperatures ranging from 19–22ºC and RH from 33–42%, the LT50 was > 3 days.

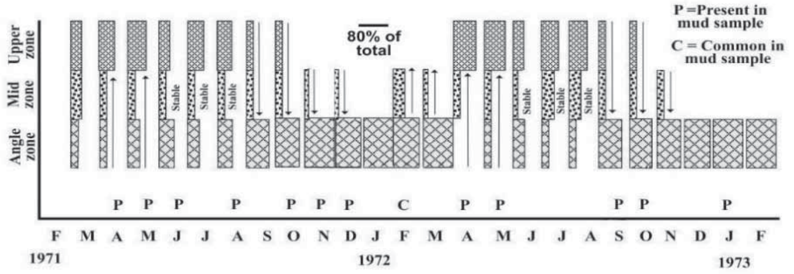


Figure 6-11. Frequency of occurrence of *Viviparus viviparus* in different vertical zones on a canal concrete wall from February 1971 to February 1973. Redrawn and modified from Figure 12 in Young (1975).

6. Mortality

Browne (1978) found a population of *V. georgianus* with the highest fecundity rate also had the highest juvenile mortality rate. He estimated mortality as the cumulative biomass of dead snails. Contributing to the declines in Figure 6-10, JAM and SON had a relatively high juvenile mortality and low adult mortality rate with three breeding seasons, while TUL and CAZ, which had lower juvenile and higher adult mortality, only had lower juvenile and higher adult mortality during two breeding seasons. Figure 6-12 shows the cumulative mortality of *V. georgianus* increasing in biomass relative to life span (months after birth) in the same four sites in central New York that Brown (1978) used for recapture rates in Figure 6-10. Cumulative biomasses of the snail were much greater in the JAM and SON sites than in the TUL and CAZ sites but increased over the 24- to 30-month life span.

Haak, Chaine, Stephen, Wong, *et al.* (2013) analyzed a die-off event of CMS in Wild Plum Lake in Nebraska to determine a mortality estimate for the population. They used a quadrat approach and assumed uniform distribution throughout the newly-exposed lake bed. It was estimated that 42,845 individuals had died during this event, which amounts to about 17%

of the previously estimated population size of 253,570. By assuming a uniform distribution throughout all previously reported available habitat (48,525 m^2), they estimate 99,476 individuals died, comprising 39% of the previously-reported adult population. The die-off occurred during an extreme drought event, which was coincident with abnormally hot weather.

During a preliminary survey of an area in Sandusky Bay, Ohio, in March 1963, Wolfert and Hiltunen (1968) found many decomposing Japanese Mystery Snail shells floating in the Bay. The observed mortality likely resulted from winter kill, old age, or both. Considerable mortality was also noticed in the marshes bordering the bay during the summer when the marshland was drying up, and many snails were stranded on hard, sunbaked mud and clay (Wolfert and Hiltunen 1968).

Mortality of viviparids due to hypoxia was reported to be the main factor in reduced frequency of occurrence and in the number and biomass of populations of *V. viviparus* and *V. contectus* in a Ukrainian lake (Uvayeva and Utevsky 2021). Flow rate, temperature, pH, and organic matter content were also limiting factors in the distribution of two Viviparidae species in varying biotopes. The most proximate reason was the declining environmental conditions induced by climatic changes and anthropogenic pressures. In waters of Ukraine, the maximum age is five years for *V. viviparus* molluscs and six years for *V. contectus*. High anthropogenic pressure disturbed the age structure of viviparid species in the water bodies. Higher ratios of middle-age (two to four years old) snails occurred, and younger (up to one year old) and older (five to six years old) molluscs decreased or were absent. The high level of saprobity of water bodies was accompanied by the formation of hypoxic zones and caused significant death rates in the youngest and oldest molluscs, which Uvayeva and Utevsky (2021) found to be the most vulnerable age classes in mollusc populations.

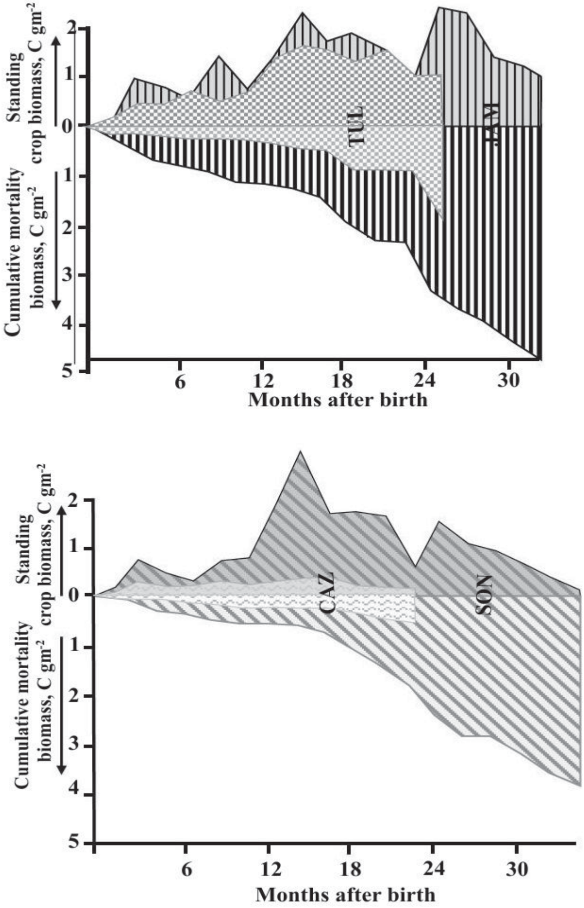


Figure 6-12. Standing crop biomass shown above the 0 line and cumulative mortality biomass between successive samples below the 0 line in grams of carbon m^{-2} for four populations of *Viviparus georgianus*. Modified from Figure 5 in Brown (1978). See text for explanation.

D. Food and Nutrition

Stañczykowska, Pliñski, and Magnin (1972) examined the qualitative and quantitative variations in food habits relative to size, sex, and degree of maturity of individuals and habitat and seasons of the year in *Viviparus* (*Cipangopaludina*) *malleatus*. The quantity of food available appeared to affect the population density, while food quality affected growth, fecundity, and production. They did not notice any differences in the quality and quantity of food in different summer and fall months; however, the amount of food was lower in the spring, and the variety of algae used was greater. There was no significant difference in the amount and quality of food between males and females except during the May breeding season when females ate less than males. Juveniles ate less than adults, but the ratio of the volume of the digestive tract to the volume of the body did not vary with shell height or sexual maturity. The composition of the food was also the same regardless of the size of individuals. The amount of food available to CMS influenced density, while the food quality likely played a primary role in their growth, fertility, and production. The gut contents of CMS were composed of algae, organic elements and inorganic elements. Among the algae, benthic and epiphytic forms dominated over planktonic forms.

Jokinen (1982) reported that epiphytic and benthic algae were detected in gut contents of *C. chinensis* collected from river, canal, and lake ecosystems. Fujibayashi, Ogino, and Nishimura (2016) noted that *Bellamya* (*Cipangopaludina*) *chinensis* in paddy fields of Japan was often densely fouled by shell-attached algae, which mainly consisted of filamentous algal species. Myriad factors potentially limit the diets of molluscs. Steneck and Watling (1982) suggested that the body size (relative to the size of algae) and body plan (e.g., shape of shell, location of mouth relative to foot) are most important in the overall pattern of functional feeding groups. As noted earlier, CMS has taenioglossid radulae as their feeding apparatus, which function as rakes for ingesting microalgae and filamentous algae (Fretter and Graham 1962; Steneck and Watling 1982). The most commonly grazed algae of taenioglossid radulae were microalgae (e.g., diatoms, blue-greens) and filamentous algae (e.g., *Cladophora*). Noting the high density of filamentous algae on the shells of CMS, Fujibayashi, Ogino, and Nishimura (2016) examined the use of algae attached to the shell of CMS as a food source and whether the assimilation of shell-attached algae enhanced host snail growth. They found that CMS assimilated substantial amounts of omega-6 fatty acids, abundant in shell-attached algae. The growth of CMS was enhanced by algal fouling on shells of neighboring individuals, which provided them with a nutritious food source.

Field experiments by Osenberg (1989) showed that grazing by three prosobranch species and five pulmonate species could limit the biomass of epiphytic algae. Using a gradient of snail densities, he showed that removing snails increased epiphyte biomass by approximately three-fold relative to that observed at natural snail densities. He also enriched the environment with phosphorus fertilizer and found a 20-fold increase in epiphyte biomass as a test of food limitation in the snail community. All snail taxa exhibited positive numerical or growth responses to enrichment. That snail's depleted resources and limited snail production demonstrated that snails competed exploitatively for epiphytes.

In soft-bottomed freshwater habitats with abundant snails, shells of living snails provide nutrient-augmented substrata that may indirectly boost overall snail production (Abbott and Bergey 2007). CMS is a deposit feeder and feeds on organic detritus, likely composed of moribund algae, suggesting that the shells of living snails can increase algal food and overall production in ponds. This effect would be larger in ponds with high snail densities and limited hard substrata.

Chaves-Campos, Coghill, Garcıa de Leon, and Johnson (2012) found evidence that snail shell hardness, and therefore resistance to predation, can be influenced by the abundance of organic compounds in the water. They tested whether snail shell thickness/strength is constitutive (i.e., does not require environmental stimuli, such as calcium content, for activation) or induced (i.e., requires environmental stimuli, such as fish predation). They found shell thickness was a better product of active calcification than a byproduct of reduced feeding and somatic growth. Still, the availability of organic matter contributed to shell crushing resistance. Hence, the local amount of vital organic compounds, essential for shell biomineralization, can determine organic material content in shells in a population, and thus the mechanical properties of shells, including their hardness.

Deposit feeding or the ingestion of organic detritus and micro-organisms in the top few centimeters (5–15 cm) of sedimentary deposits appears to be the main feeding strategy of mystery snails. Van Bocxlaer and Strong (2016) examined the pallial cavity of *C. japonica* and found a conspicuous food groove similar to that in filter-feeding viviparids. Oddly, they found many relatively large wood pellets in some specimens, the most abundant substrate at one of their collecting sites. The wood pellets were mainly in the rectum, suggesting long retention times needed to digest the wood pellets. The large size of the pellets indicates an unselective deposit-feeding strategy and the functional importance of the jaws in viviparids. Van Bocxlaer and Strong (2016) noted the versatility between ctenidial filter feeding, radular scraping, and non-selective deposit-feeding using the jaw and radula. They proposed the versatility in functional feeding explains the success of some *Cipangopaludina* and *Sinotaia* species upon long-distance transport in comparison to other viviparids. Additional research is needed to determine whether *C. japonica* populations undergo seasonal diet shifts and how food quantity and quality affect population density, growth, and fecundity (Van Bocxlaer and Strong 2016). Suspension feeding or ingestion of particles in suspension above the sediment water interface has not been reported for viviparids.

Fujibayashi, Ogino, and Nishimura (2016) examined the fractionation of stable carbon isotopes in essential fatty acids. They found that the isotopic composition of C20 and C22 essential fatty acids was strongly influenced by the fatty acid composition the diets of *C. chinensis*. They also observed shell-attached algae including two blue-green species, *Homoeothrix varians*, and *Lyngbya* sp.; both are filamentous and require the hard substrate to persist. The shell of *C. chinensis* provides the necessary substrate for such attached algae. Furthermore, they observed *C. chinensis* leaving pedal mucus on their trails, which stimulates algal growth. When *C. chinensis* grazes on shell-attached algae, they crawl on other individuals' shells and likely leave their pedal mucus on the shell surface, facilitating algal growth, and increase a high-quality food source for themselves. This activity implies a potential, positive feedback between shell-attached algae and *C. chinensis,* which benefit each other (Fujibayashi, Ogino, and Nishimura 2016).

It is clear from the studies reported above that CMS and JMS are benthic feeders, grazing on attached algae on other snails and deposit feeding on algal and organic elements, living or dying, in the sediments. The preference of epiphytic algae over planktonic algae suggests that CMS relies more on grazing and deposit feeding than on food filtration. Neither CMS nor JMS have been reported to feed on fish eggs. Eckblad and Shealy (1972) determined that, for the Banded Mystery Snail, *V. georgianus*, found in the laboratory and ponds, significant reductions and survival of largemouth bass eggs in guarded nests likely contributed to high incubation mortality seen in natural field settings.

E. Competition

Despite the long invasion history of *C. chinensis*, its broad distribution within North America, and often high biomass within invaded environments, few experimental studies have examined its ecological impacts. Early accounts are not experimental, only conjectures. Perhaps the source of characterizing impacts of CMS in the Great Lakes was Cook and Johnson (1974). They stated, "man has characteristically complicated historic patterns by introducing foreign species into the Great Lakes (e.g., *Viviparus malleatus*, a Japanese gastropod; and *Bithynia tentaculata*, a north European snail)" (Cook and Johnson 1974, 768). Little did they know the extent of impact the zebra mussel would have when it was introduced in 1986 (Claudi and Mackie 1994; Mackie and Claudi 2010). The Cook and Johnson study was reported in 1974, and the earliest record of CMS in the Great Lakes was 1942 in the Niagara River (Schmeck, 1942), which flows from Lake Erie into Lake Ontario. Clench and Fuller (1965) reported CMS in Lake Ontario along the shoreline. The earliest reports in iNaturalist (2020) of CMS in the Great Lakes are Lake Erie in 2016 at Long Point; Lake Huron, 2019; and Lake Michigan, 2020. None have been reported from Lake Superior as of December 26, 2020. The meagre reported occurrences of mystery snails in the Great Lakes between 1942 and 1974 raises the question of why *V. malleatus* was used by Cook and Johnson (1974) as an example of complicity of the "historic patterns" in the Great Lakes.

There are other examples of impact conjectures. Hebert, Muncaster, and Mackie (1989) noted some displacements of molluscs in sections of the Great Lakes colonized by *Bithynia* and *C. c. malleatus.* They categorized it as some interference as a competitor of native gastropod fauna. Therriault and Kott (2002-2003) reported no evidence of ecosystem impacts by *C. chinensis.* They suggested that due to its low vagility, the species will not become more than a local pest.

While not equivalent to ecosystem-level manipulations, mesocosm studies can provide important insights about mechanistic interactions in aquatic food webs, including snail–predator and snail–snail interactions (e.g., Nyström, Bronmark, and Graneli 1999; Turner and Chislock 2007). Johnson, Olden, Solomon, and Vander Zanden (2009) conducted an eight-week experiment in 24 outdoor, 1,200-L mesocosms (tanks), randomly assigned to one of the following treatments: (1) 45 of each of three native species of *Physa gyrina, Lymnaea stagnalis,* and *Helisoma anceps* only; (2) 45 native snails of each species with 45 CMS; (3) 45 native snails of each species with 45 invasive crayfish, *Orconectes rusticus*; and (4) 45 native snails with both invaders (six replicates per condition). They examined the effects of each invader on periphyton chlorophyll-*a* level on sediment and mesocosm walls, the Nitrogen-Phosphorus (N:P) ratio in the water column, and on one another (size and/or abundance of the co-occurring invader). After all, experiments were completed, they drew the following conclusions:

- "Within experimental mesocosms, realistic densities of CMS and crayfish each have significant effects on native snail communities and ecosystem properties. Relative to control treatments, rusty crayfish reduced the biomass of native *Lymnaea* and *Physa* snails by > 90%, consistent with previous field studies illustrating the predatory effects of invasive crayfish" (Johnson, Olden, Solomon, and Vander Zanden 2009, 167).

- "Competition by herbivorous Chinese Mystery Snails also caused substantial declines in the growth and abundance of native snails" (Johnson, Olden, Solomon, and Vander Zanden 2009, 168).
- There was "evidence that the dual effects of both invaders on native snails were as severe as or worse than were their individual effects. Importantly, *Bellamya* and *Orconectes* had only weakly negative effects upon each other. With its large size and thick shell, *Bellamya* was substantially less vulnerable to crayfish predation than were *Physa* and *Lymnaea*" (Johnson, Olden, Solomon, and Vander Zanden 2009, 168).
- "The presence of both invaders led to risk enhancement for *Lymnaea*, such that *Lymnaea* was completely extirpated from all replicates in which *Orconectes* and CMS co-occurred but persisted (albeit at lower densities) when faced with either invader in isolation. Similarly, the biomass of *Physa* declined by > 98% when confronted with both invaders. In contrast, *Bellamya* abundance declined by less than 15% in the presence of *Orconectes*, and biomass showed little change (< 3%). Concerning *Lymnaea* and *Physa* biomasses, however, the combined presence of *C. chinensis* and *Orconectes* led to risk reduction" (Johnson, Olden, Solomon, and Vander Zanden 2009, 168).
- CMS "reduced periphyton biomass, likely causing a reduction in growth by native lymnaeid snails" (Johnson, Olden, Solomon, and Vander Zanden 2009, 159).
- CMS also "increased the water column N:P ratio, possibly because of a low P-excretion rate relative to native snail species" (Johnson, Olden, Solomon, and Vander Zanden 2009, 159).

The inverse relationship between low P-excretion rate and reduced periphyton biomass suggests CMS either did not affect algae biomass production or an inverse effect relative to the N:P ratio. These results are supported by Zhu, Lu, and Liu (2013), who found *Bellamya aeruginosa* affected the phytoplankton community and water quality in mesocosm studies. The snail reduced phytoplankton biomass, the loss in weight being mostly by toxic cyanobacteria and flagellates, whereas those with positive weight were mostly colonial green algae. The taxa that increased most strongly were *Cryptomonas ovata*, *Euglena acus*, *Trachelomonas armata*, and *Microcystis flos-aquae*. The most seriously negative affected taxa were the Cyanophyta, *Merismopedia tenuissima* and *Microcystis viridis*, and the unicellular Chlorophyta *Selenastrum minutum*, *Ankistrodesmus angustus*, and *Actinastrum hantzschii*, and the floating *Scenedesmus acuminatus*. *Merismopedia tenuissima* produces sheets or mats. *Microcystis viridis* is a harmful, bloom-forming alga that can produce neurotoxins and hepatotoxins, such as microcystin, and forms large surface blooms through rapid division and buoyancy in the production of gas-filled vesicles. *Scenedesmus* is a colonial, green alga that forms small chains of four cells and is often found floating on the water and not attached to bottom rocks.

Prezant, Chapman, and McDougall (2006) performed lab mesocosm studies to examine the impact of a crayfish predator, *Orconectes limosus*, on brood production and rate of development in CMS. They used mesocosms as controls (with only CMS), tests using both crayfish with CMS, and CMS within perforated containers inside a larger container with crayfish emitting chemical cues (effluent) in the water circulating through CMS container. They found (1) juvenile CMS born in the presence of crayfish effluent were smaller; (2) more juveniles were released when brooding adults were exposed to predator effluent; (3) variability in the size of released juveniles was more pronounced in the presence of the predator; (4) predators induced a faster rate of release of juveniles, possibly reflected in their smaller size at release; (5) juveniles released from adults in the presence of predator effluent had a significantly higher ratio of shell organic to shell mineral content than controls; and (6) all juvenile specimens of CMS (control and experimental) had a considerably higher ratio of shell organic to shell mineral content than adults. In addition, adults released almost twice as many juveniles during the experimental period. Still, they retained nearly the same number of juveniles in utero at the end of the eight-week experiment, indicating that the experimental adults were producing and moving juveniles through the uterine system at a more rapid rate. They suggested the predator-induced response promotes a faster release of fertilized eggs into the uterus, and these eggs move more quickly through the uterus; as a result, released experimental juveniles were, on average, smaller than controls.

The smaller size of many of the juveniles released in the presence of predators was interpreted as more juveniles finding refuge in smaller retreats. They suggest that increasing the number of juveniles in the presence of predators is adaptive because, as the number of potential prey available to a predator increases, the number of juveniles that escape predation also increases. This proposal presumes an r-selected strategy, whereby increased numbers and greater variability are inextricably linked.

Solomon, Olden, Johnson, Dillon, *et al.* (2010) surveyed snail assemblages in 44 lakes in the Northern Highlands Lake District of

Wisconsin to be invaded by CMS. Their mission was to describe the patterns and determinants of CMS distributions and assess whether its invasions have altered the composition of native snail assemblages using multiple spatial and temporal scales in their analyses. They tested for impacts of *C. chinensis* on native snails at the scale of both lake and sites within them. They combined their data with historical survey data from the 1930s to test whether contemporary assemblage structure or long-term changes in assemblages were related to the occurrence or abundance of *C. chinensis*. Their key findings were as follows:

- They found no evidence for a negative relationship between the site-level abundance of CMS and its closest relatives in these lakes, the viviparids *C. decisum* and *V. georgianus*.
- After controlling for chemical and physical variables and the presence of *O. rusticus*, a predator, and *V. georgianus*, there was no effect of *C. chinensis* on lake-level snail assemblages.
- They offer three explanations for the lack of strong evidence that *C. chinensis* invasion has adverse effects on native snail populations:
    - First, insufficient time had elapsed since the invasion to detect the effects of strong competitive interactions, which seems pretty unlikely given that no *C. chinensis* effects were observed in the re-survey analysis. Furthermore, the re-survey analysis could only detect *C. chinensis* effects if they result in lake-wide annihilation of a native species, whereas significant impacts could occur below that threshold.
    - Second, the lack of strong evidence for a negative impact is that the impacts are not substantial but rather are weak and localized.
    - Third, it may be that *C. chinensis* does not compete with native snails, suggesting either resource partitioning among the species or that resources are not limiting. Resource partitioning seems unlikely because all snails collected in their survey were co-occurring at fine spatial scales. CMS is both a filter feeder and deposit feeder, while pulmonate snails are scrapers of algae on surfaces. Their results from stable isotope ratios of *C. chinensis* collected from one of the study lakes suggest heavy reliance on benthic resources and little reliance on pelagic resources.
- While there were significant changes in snail assemblages between the historical surveys and their study data, there was no apparent effect of *C. chinensis* invasion on these changes.

- There is a likelihood that *C. chinensis* occurrence was influenced both by intrinsic properties of lakes (Secchi depth and conductivity) and by human activities (distance to a population center, shoreline housing density, and boat launches).
- Relationships between *C. chinensis* occurrence and distance to a population center, shoreline housing density, and boat launches indicate that greater human use of a lake is associated with a higher likelihood of *C. chinensis* establishment. The link between boat launches and within-lake distributions suggests that boater movements, in particular, play an important role in dispersal.

More recently, Ellman (2019) performed a two-week field exclusion study using cages of 1x1 m^2 fences in Michigan's Upper Peninsula. The cages were composed of a window screen to prevent any CMS from entering or exiting control (natural setting) and experimental (no CMS, allowing only native snails and bivalves to remain) enclosures. He hypothesized there would be more native snails and bivalves in experimental cages than in control cages because both native snails and bivalves were expected to have higher survivorship and reproduction in the absence of CMS as competitors. He predicted that because CMS have thick shells, they would survive invasive predators (rusty crayfish) better than native species of snails and bivalves. He found none of the native snails or bivalves had significantly higher populations in experimental cages than in control cages, suggesting that CMS's presence had neither a positive or negative effect on native snail and bivalve populations.

The contradictory results among Johnson, Olden, Solomon, and Vander Zanden (2009); Solomon, Olden, Johnson, Dillon, *et al.* (2010); and Ellman (2019) support the need for subtle and long-term perspectives promoted by Strayer (2006) for understanding the impacts, if any, on non-native species. As Lodge, Stein, Brown, Covich, *et al.* (1998, 53) professed, "unfortunately, no algorithms exist to guide scaling up from small-scale experiments to the whole-lake, long-term management scale."

Mesocosm studies rarely, if at all, examine the complex food webs that emerge from introducing an invasive species. Not all water bodies have exotic crayfish or native crayfish, for that matter. Many insects prey on snails. For example, Turner and Chislock (2007) conducted mesocosm treatments with two predacious species of dragonflies and found a pronounced negative effect on snail biomass and density. Given that both pulmonate snails and dragonfly nymphs are widespread and abundant in many freshwater habitats, snail assemblages in these water bodies are likely regulated in large part by dragonfly predation. Nyström, Svensson, Lardner, Brönmark, *et al.* (2001) found that the predatory and herbivorous signal crayfish, *Pacifastacus leniusculus*, had weak but significant adverse effects on predatory invertebrates' biomass, which greatly reduced the biomass of snails, the most abundant invertebrate grazers in their replicated field experiments.

Olden, Ray, Mims, and Horner-Devine (2013) reported *C. chinensis* exhibited an average filtration rate of 106-113 mL $\text{snail}^{-1}\text{h}^{-1}$ (1.45 mL mg DW^{-1} h^{-1}) and an individual maximum of 471 mL $\text{snail}^{-1}\text{h}^{-1}$. These filtration rates match those of the high-profile invasive zebra mussel (Mackie and Claudi 2010). Olden, Ray, Mims, and Horner-Devine (2013) found relationships between snail size and filtration rate of *C. chinensis* that explained an ontogenetic shift in feeding behavior from primarily radular grazing to increased filter feeding at a threshold size of approximately 44 mm shell height. High snail densities can result in small, significant shifts in bacterial community composition. Hence *C. chinensis* may influence microbial communities either directly by using bacteria as a food source or indirectly by producing sufficiently large quantities of fecal and pseudofeces to affect bacterial activity and growth. The overall ecological effects of these results remain unclear. Still, they suggest that these impacts may be large and should be further investigated to understand better its potential role in coupling benthic and pelagic food webs in lake ecosystems.

Abiotic factors affect snail diversity as well. Brönmark (1985) found a significant, positive regression between pond area and the number of gastropod species in the pond. Also, an increase in the number of macrophyte species increases the number of available microhabitats for feeding and refuges from predators, a significant biotic relationship.

David, Thebault, Anneville, Duyck, *et al.* (2017) profess that an introduced species may only persist if it can pass through environmental and biotic filters. Environmental filters range in abiotic conditions (e.g., temperature, chemistry, depth) that determine its fundamental niche needed to complete its life cycle. Biotic filters include the level and availability of resources, competition, and natural enemies, which define the realized niche. Species that have been able to pass through these filters may not come alone (David, Thebault, Anneville, Duyck, *et al.* 2017).

David, Thebault, Anneville, Duyck, *et al.* (2017) concluded that predation underlies the most spectacular damage in invaded systems, sometimes cascading down to primary producers. They illustrated the potential complexity of food webs after the invasion, shown in Figure 6-13. Two possible scenarios arise after the arrival of *C. chinensis* (Figure 6-13a, b): first, positive bottom-up effects on higher trophic levels (Figure 6-13a), and second, indirect trophic effects result from the exploitative or apparent competition (Figure 6-13b) that also affects native species but rarely provokes extinctions. A reduction in biomass of snails caused by native and exotic crayfish predation results in an indirect positive effect on periphyton biomass grazed selectively by snails (Nyström, Brönmark, and Graneli (1999). Overall, the exotic crayfish had a stronger impact on the biomass of macrophytes and grazers than the native crayfish. This result is an example of crayfish structuring food webs through consumption from many food levels.

Trophic interactions and non-trophic ones (e.g., mutualism, ecosystem engineering) after invasions can profoundly modify the structure of the entire food web. David, Thebault, Anneville, Duyck, *et al.* (2017) suggest that species richness, phenotypic diversity, and functional diversity limit the likelihood and impact of invasions by saturating niche space. They show how vulnerable communities have unsaturated niche space mainly because of isolated evolutionary history, dispersal constraint, or anthropogenic disturbance. Exotic and native species are essentially new to one another when first introduced. The invasion will retain alien species that inherently have an advantage over residents in trophic interactions. Resident species, therefore, need to evolve traits to two types of interactions rapidly; vertical interactions are shown in Figure 6-13a, and horizontal interactions in Figure 6-13b, but both exist simultaneously.

Referring to Figure 6-13a, vertical effects include direct top-down (R1) and bottom-up (R4) effects, and indirect top-down (R2) and bottom-up (R5) are trophic cascades. Horizontal effects (Figure 6-13b) are only indirect and include exploitative (R3) and apparent (R6) competition. Shown in Figure 6-13 are only one- and two-step potential impacts of *C. chinensis*, but effects may propagate further (open circles), such as the snail's feces and pseudofeces altering N-, P-, and S-bacteria cycles. The positive or negative direction of the impact depends on the relative positions of CMS and R in the food web. Considering the path from CMS to R, if it includes an even number of steps opposite to arrows, the impact should be positive; if the number of such steps is odd, it should be negative. Food webs are much more connected and complex than this idealization. Still, it demonstrates how mesocosm studies or closed field studies may fall short of explaining the impacts of invasive species.

Perhaps Allee effects (Allee 1931) determine the success of establishment by CMS and JMS propagules. Allee effects are positive relationships between any component of individual fitness and either numbers or density of conspecifics (Stephens 1999; Courchamp 2008). Stephens (1999) suggested it is essential to differentiate between two-component Allee effects (Allee effects manifested by a member of fitness) and demographic Allee effects (Allee effects manifested by a member of population structure).

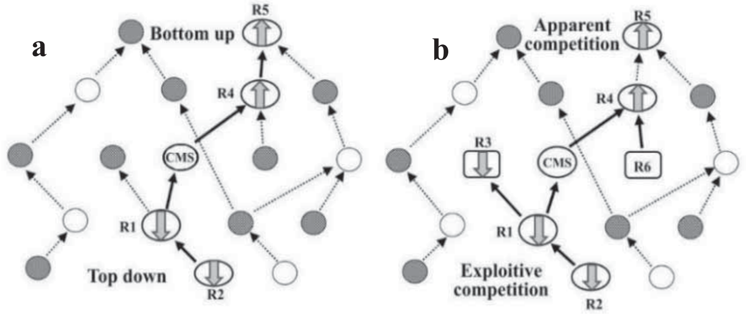


Figure 6-13. An idealized food web illustrating (a) direct and (b) indirect trophic links through which CMS (*Cipangopaludina chinensis*) can affect resident species (R). Arrows go from host to predator. Open circles = species that are expected to increase upon arrival of the invader; filled circles = species that are expected to decrease. See text for explanation. Redrawn from Figure 1 in David, Thebault, Anneville, Duyck, *et al.* (2017).

F. Parasitism

This section entails an exhaustive search of the literature to address the concerns of cottagers, aquarists, and authorities making risk assessments of mystery snails serving as vectors of diseases, or epizootics, an outbreak of a disease in an animal population, often extending to humans. An epizootic may be restricted to a specific locale, generally spread, or widespread (a panzootic).

The parasites of freshwater molluscs fall into three groups: protozoans (e.g., *Paramecium* and *Entamoeba coli*), trematodes (e.g., *Aspidogaster, Echinoparyphium,* and *Echinostoma* species), and nematodes (e.g., *Angiostrongylus* sp.). Trematodes are the most prevalent parasites of CMS and JMS, followed by nematodes.

The trematodes of viviparids are represented by two classes, Monogenea and Digenea. Monogeneans are a group of ectoparasitic flatworms found on the skin, gills or fins of fish. They have a direct lifecycle and do not require an intermediate host. Adults are hermaphrodites, having both male and female reproductive structures. Only one species of *Aspidogaster*, *A. conchicola*, occurs in freshwater molluscs of North America. Digenea refers to the alternation of generations between sexually reproducing adults and asexually reproducing larval stages. Digeneans have a definitive vertebrate host and a mollusc first intermediate host. Additional intermediate hosts may be involved.

i. Monogenea: *Aspidogaster conchicola*

Aspidogaster conchicola is a common parasite of freshwater bivalves found in Central Europe, Eastern Asia, North Africa, and North America (Dollfus, 1959). It is native to North America and typically infects unionid mussels (Michelson 1970; Huehner and Etges 1971, 1977; Alevs, Vieira, Santos, and Scholz, *et al.* 2015; Harried, Fischer, Perez, and Sandland 2015). It has been found sporadically in species of freshwater gastropods (Huehner, Hannan, and Garvin 1989), but Van Cleave and Williams (1943) consider infections in animals other than Unionidae accidental and transient. Alevs, Vieira, Santos, and Scholz *et al.* (2015) give this trematode 122 host–parasite associations of molluscs from the Nearctic and Palaearctic regions and occasionally vertebrate hosts. This species can complete its life cycle using just a mollusc as its definitive host (Huehner and Etges 1972, 1977). If a vertebrate eats an infected invertebrate, it can also become infected, as Gao, Nie, and Yao (2003) demonstrated with the Black Carp, *Mylopharyngodon piceus*.

The snail hosts reported for *A. conchicola* include *Paludina* (= *Viviparus*) *decisa* in Philadelphia, Pennsylvania, US (Leidy, 1905); *Viviparus lapillorum* and *V. catayensis* in China (Faust 1922); *V. malleatus* and *V. japonica* in Massachusetts (Michelson 1970); and *V. malleatus* in Ohio (Huehner and Etges (1971, 1977).

The mature *Aspidogaster conchicola* (Figure 6-14) is approximately 2.2 to 3.0 mm in length (Eckmann 1932; Bychowsky and Bychowsky 1934; Huehner and Etges 1977). The worm's body, not including the ventral sucker, is somewhat spindle-shaped and can be stretched to twice its normal length during locomotion. The distensible mouth, located at the end of the neck, is surrounded by an oral sucker. The pharynx, posterior to the oral sucker, is small, but it may be seen opening and closing in the living worm. The intestine is a blind sac that extends almost the entire length of the body; it is unbranched but broadens slightly distally.

The worm has a single, large ventral sucker, called the opisthaptor that takes up most of the ventral surface (Figure 6-14). The opisthaptor is divided into adhesive depressions (termed loculi or alveoli) formed by muscular septa, useful in classification; the two largest alveoli are the anterior and posterior (Figure 6-14). *Aspidogaster conchicola* has 64–66 loculi, arranged in four longitudinal rows. An exterior longitudinal septum, which is a horizontal flap of muscle, divides the body anteriorly. The function of the septum is unknown.

The life cycle of *A. conchicola* is well described and illustrated by Voeltzkow (1888) and Williams (1942), from egg cleavage to the adult. They include descriptions of all the organ systems, especially the reproductive, excretory, and circulatory systems. Williams (1942) described four larval stages. The first stage was 130–150 µm long and 50–55 µm diameter; the second was 275 µm long with a loss of body constriction and greater locomotory powers; the third was 880 µm long with a well-developed oral sucker; and the fourth was 1,200–1,400 µm long and 320 µm wide when extended. Figure 6-15 is based on his illustrations from the embryo with the yolk assimilated (Figure 6-14 A a), through the early development of the opisthaptor (Figure 6-15 A b,c) to the early adult stage with the anterior and posterior alveoli well developed (Figure 6-15 A d); the life cycle was based on examining embryo development in the unionid, *Anodonta*; the clam in Figure 6-15 is *Gonidea angulata*.

All life stages in Figure 6-15 occur in the two molluscs. Only the embryonic egg is found in the water. Both the clam and CMS are benthic, living mostly within the sediments, but CMS is also found grazing on algae and detritus attached to surfaces of rocks, plants, and other objects, including on shells of other CMS. Both molluscs are deposit feeders. Because the eggs are released at or slightly above the sediment water interface, many eggs will be consumed by grazing CMS. However, the physical damage caused by the radula likely causes damage or death to some of the embryos. CMS takes in

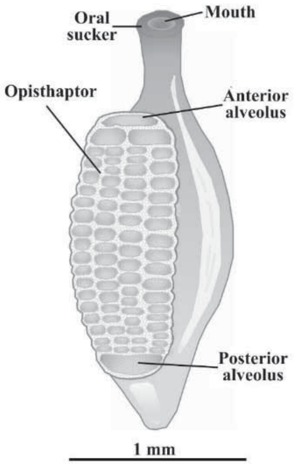


Figure 6-14. Illustration of a mature adult of *Aspidogaster conchicola* depicting diagnostic features.

some eggs through the incurrent siphon and by deposit feeding and avoids destruction by the radula.

Rohde (1994) found the life cycle of *A. conchicola* completed experimentally in 270 days at 20ºC in the snail *Viviparus (C. c.) malleatus*. Transmission by embryonated, unhatched eggs was demonstrated explicitly. Development of *A. conchicola* from egg to adult involves three growth phases displaying major shifts in allometric growth of the oral disc, ventral sucker, and the body: (1) worms < 0.65–0.70 mm long show growth with only slight changes in body proportions (negative allometric growth of oral disc, positive allometric growth of ventral sucker) and no alveolation of a ventral sucker; (2) strong positive allometric growth and alveolation of a ventral sucker; and (3) worms > 1.60–1.65 mm long, and the ventral sucker ceases positive allometric growth, which lessens negative allometric growth of the oral disc until growth rates of the body, oral disc, and ventral sucker become equal at a worm length of 2.25 mm.

Alveolar development in the ventral sucker was observed to begin at a growth zone behind the anterior lip of the juvenile posterior sucker. From this region, transverse alveoli were formed and pushed anteriorly by the formation of subsequent alveoli. Longitudinal septation of the ventral sucker did not occur until 11 or 12 transverse alveoli were formed. Development of the medial septum slightly preceded that of two laterally situated longitudinal septa. Development of *A. conchicola* in *Elimia livescens* appeared slightly more rapid than in *V. malleatus*. The name “aspidocidium” was proposed by Huehner and Etges (1977) for the non-ciliated juvenile stage of some aspidogastrid species.

Huehner and Etges (1971, 1977) reported the development of *A. conchicola* in Ohio populations of *C. chinensis malleatus.* Transmission of *A. conchicola* occurs through ingestion of embryonated eggs. Harried, Fischer, Perez, and Sandland (2015) reported meager rates of trematode parasitism rates of CMS in 22 Wisconsin lakes. Of 147 necropsied wild-caught snails from the lakes, only 2 snails harbored trematode parasites. The parasites that did successfully infect CMS were often found encased in the shells of the snails in a non-viable state. Harried, Fischer, Perez, and Sandland (2015) also conducted infections by the trematode *Sphaeridiotrema pseudoglobulus*, implicated in waterfowl die-offs. Using experimental exposures, they found that CMS infection levels were very low. The parasites that did successfully infect CMS were often found encased in the shells of the snails in a non-viable state. Huehner and Etges (1981) observed encapsulation of *A. conchicola* in six out of seven unionid bivalve species found to be infected. Encapsulated worms were most common, alive or moribund, anterior to the pericardium, the capsule probably

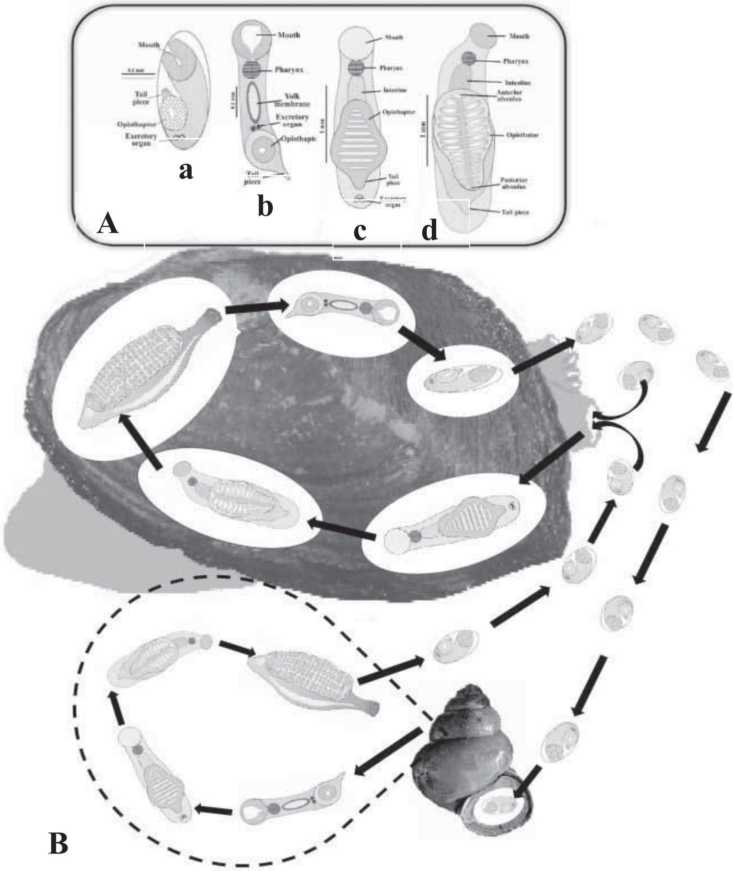


Figure 6-15. Life stages and cycle of *Aspidogaster conchicola*. (A) Details of four life stages (see text). (B) Life cycles in a native clam and *Cipangopaludina chinensis*. Stages within the dashed circle occur within *C. chinensis*. The only life stage in the water is the embryonated egg. All drawings of the stages are from Figures 37b, 41, 44, and 45 in Voeltzkow (1888).

contributing to the death of the worms. They suggest that the frequent occurrence of capsules anterior to the pericardium and dorsal to the digestive gland is the most likely route of infection.

In the Giant Floater, *Pyganodon grandis*, Gangloff, Lenertz, and Feminella (2008) related increased densities of *A. conchliola* to reduced mussel reproductive output and physiological condition. In three unionids, *Anodonta oregonensis*, *A. californiensis*, and *Gonidea angulata*, heavy infections occurred in the renal and pericardial cavities of the two *Anodonta* species but only in the foot of *G. angulata*, where the parasite was encapsulated (Pauley and Becker 1968).

Huehner and Eteges (1981) reported encapsulations commonly occurring in several unionid host species, particularly when *A. conchicola* leaves the relatively large pericardial and nephridial spaces for smaller hemocoels in other locations. They suggest that the frequent occurrence of encapsulated worms directly anterior to the pericardium and dorsal to the digestive gland is the most commonly utilized invasion route. Host defenses, including encapsulation, are first initiated here.

The tendency of molluscs to encapsulate a parasite or an unknown body is a typical host response and often occurs when a parasite invades an unnatural host (Cheng 1967; Pauley and Becker 1968). Halton and Lyness (1971) found worms inhabiting the pericardial and renal cavities of the mussel were bathed in host blood, ingested by the worm and later phagocytosed by the gut epithelial cells. Tubercles on the tegument of the parasite increase the free surface membrane surface for taking up nutrients.

The effects of *A. conchicola* on CMS and JMS are unknown, but Michelson (1970), contrary to Van Cleave and Williams' (1943) opinion of only incidental occurrences in snails, concluded that *A. conchicola* is a true parasite of *C. chinensis* and *C. japonica*, based on (1) a high frequency of infection (42%) in the snails studied; (2) a mean worm burden (14.5 per snail) comparable to or greater than that reported from various species of Unionidae (Van Cleave and Williams 1943; Hendrix and Short 1965, 1968); (3) the apparent absence of Unionidae in the sites from which the infected snails were collected; and (4) the continued presence of *A. conchicola* in snails from the collecting sites for more than seven years. However, when comparing the pathologies of three unionids studied by Pauley and Becker (1968), the responses of CMS and JMS were somewhat similar, but no clear interpretation of these reactions could be made because experimental infections of known chronology were not available (Michelson 1970).

Michelson (1970) found survival of the trematodes in vitro declined with temperature, from 92, 65, and 49 days at 4, 20, and 25°C, respectively; maximum survival at these respective temperatures was 135, 78, and 60 days. Curiously, although most eggs hatched in vitro and the resulting larvae remained alive for up to 28 days, no adults developed from them. High frequencies occurred in some snails: 21 of 23 positives for *C. chinensis*, and 9 of 10 positive for *C. japonica*.

Karatayev, Mastitsky, Burlakova, Karatayev *et al.* (2012) examined seven species of exotic molluscs for parasitological infestations from 27 sites located in 12 waterbodies, including the Lower Great Lakes and their tributaries, Finger Lakes, and Lake Oneida during 2009 and 2010. They did not find any trematodes in *C. chinensis* during the survey. However, a small sample size (only 30 snails were dissected) prevented them from speculating on the occurrence, prevalence, and intensity of infection by trematodes.

Mastitsky, Karatayev, and Burlakova, (2014) examined the parasites of exotic invertebrates and the potential risks posed to the Great Lakes. They concluded that the actual number of parasite species introduced into the Great Lakes, along with their invertebrate hosts, cannot be approximated, because very few studies have been conducted on this topic as of 2014. Certain relevant information is currently available only for *C. chinensis* by Michelson (1970).

ii. Digenea: Echinostome Trematodes

Echinostomatidae is the most prominent family within the class Trematoda. Members are parasitic intestinal flukes that infect many vertebrates, including humans, in their adult stage. These adult worms are distinguished by the presence of a circumoral head collar with one or two crowns of spines. Figure 6-16 shows the significant features of echinostomes, using *Echinostoma macrorchis* as an example. Butboonchoo, Wongsawad, Wongsawad, and Cha (2020, 504) describe the adults of this species (Figure 6-16a) as “flattened with an elongated body of about 4.9 mm average. “Tegument covered with small spines from the anterior of the body extended to the posterior portion of the body. An average of 45 collar spines in a semicircle around the collar, with 5 spines on each side, and 37 spines in double rows (18 oral and 19 aboral)” (Figure 6-16b). Also shown in Figure 6-16a are: A subterminal oral sucker that is subspherical in shape; a muscular pharynx; an intestinal bifurcation anterior to the ventral sucker, or acetabulum.

A muscular ventral sucker that is spherical in shape and larger than the oral sucker; two large, elliptical testes located in the posterior half of the body; a cirrus sac pyriform in shape, located dorsally between the levels of intestinal bifurcation and anterior level of the ventral sucker; a genital pore situated anterior to the ventral sucker and opens into the genital atrium; a spherical ovary located at midbody; a Mehlis' gland situated between the ovary and anterior testes; the uterus has numerous transverse loops between the ventral sucker and ovary and is filled with shelled eggs; a vitellarium occurring laterally on both sides and posterior to the ventral sucker, extending to the posterior end of the body; an excretory pore located at the posterior end of the body.

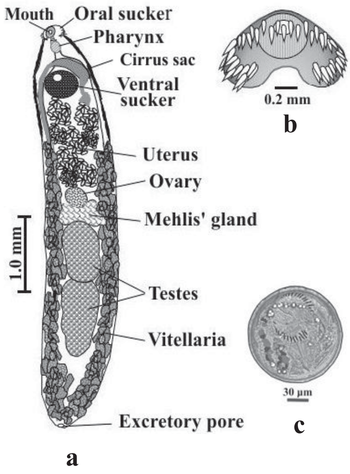


Figure 6-16. *Echinostoma macrorchis* features. (a) Adult worm; (b) head collar arrangement of spines; (c) metacercaria. All figures redrawn from Figures 1–3 in Butboonchoo, Wongsawad,

The oviduct emerges on the mid-lateral side of the ovary that enlarges to form the ootype (central portion of the ovarian complex), in which fertilization occurs. The ovum receives yolk (vitelline) material from the vitellaria in the ootype. The Mehlis' gland, also known as the shell gland, surrounds the ootype and furnishes the ovum with a shell. The ova are then passed to the uterus to tanning the shell, storage, and a causeway toward the genital pore.

Echinostomes have a complex life cycle involving hosts, a final or definitive host, and first and second intermediate hosts. There are seven developmental stages: adults, eggs, miracidia, sporocysts, rediae, cercariae, and metacercariae. Muñoz-Antoli (2009) describes the life cycle in the following six phases, asterisk stages being free-living in the water (refer to Figure 6-17):

1. Passage of eggs from the definitive host to the outside environment and their subsequent development
2. *Hatching of miracidia; search for and penetration of the first intermediate snail host
3. Development from sporocysts to rediae; multiplication of the parasites inside the snail

4. *Emergence of the cercariae from the snails; search for the second intermediate host
5. Penetration and encystment of the cercariae in the second intermediate host (e.g., fish, snails, herpetofauna)
6. Finally, ingestion of infective metacercariae by the final hosts; development into adult worms. Snails can act as either first or second intermediate hosts.

The first intermediate host is always a snail, most often a pulmonate. Several animals may serve as the second intermediate host, depending on the species, including other snails, bivalves, fish, salamanders, and tadpoles. In some cases, the snail may serve as both a first and second intermediate host, such as the planorbid pulmonate, *Helisoma trivolvis*, host of *Echinoparyphium rubrum* (Kanev, Sorensen, Sterner, Cole, *et al.* 1998). Fretter and Graham (1962) state that trematode parasites tend to settle in the sinuses and tubules of the digestive gland and gonad, the shortest routes to nutrients, which flow from the digest gland to the gonad.

Echinostomatidae is the most prevalent parasite group of freshwater gastropods. The encysted metacercaria, or cyst, is the dominant stage in the second intermediate host. The preferred site for encystment is usually the kidney or pericardium (Keeler and Huffman 2009). This encysted stage is thought to protect the parasite from the acidic digestion in the host's stomach.

Pace (1973) reported six species of echinostomes in *C. chinensis* from Taiwan: *Echinochasmus elongatus, E. redioduplicatus, E. rugosus, Eupariphium (= Echinoparyphium) ilocanum, E. recurvatum,* and *Echinostoma macrorchis*. Ahn, Ryang, Chai, and Sohn (1989) demonstrated infectivity of *C. chinensis* by C. *cinetrorchis* in Japan. Lo (1995) cites studies of *E. macrorchis* development in *C. japonica* from Japan and Taiwan. Chung and Jung (1999) showed *C. chinensis* to be a second intermediate host. Sohn, Chai, Na, Yong, *et al.* (2013) describe the infection rate of *E. macrorchis* in two rats and a cat using *C. chinensis* from Korea and report 6–17% adults formed after 14 days of infection with metacercariae, and 46.4% adults formed after 30 days of infection in a cat.

At least nine species of echinostomes use *C. chinensis* as a host in its native range (Asia): four species of *Echinostoma* (*E. cinetorchis*, *E. macrorchis*, *E. melis*, and *E. revolutum*); three species of *Echinochasmus* (*E. elongatus*, *E. redioduplicatus*, *E. rugosus*); and two species of *Echinoparyphium* (*E. recurvatum* and *E. ilocanum*) (Pace 1973, Keeler & Huffman 2009). The final hosts of these trematodes include fish, amphibians, turtles, waterfowl, and humans (Chai 2009; Keeler and Huffman 2009).

Although the first records of *C. chinensis* in North America date back to 1892 or earlier, and sometime between 1931 and 1942 in the Great Lakes Region (reviewed in Mills, Leach, Carlton, and Secor 1993), none of these trematodes has ever been reported from a North American population of *C. chinensis*. Even the cosmopolitan *E. recurvatum*, commonly reported from freshwater molluscs of North America, has never been found in Chinese Mystery Snails in the New World—and not for the lack of studies. Cort (1914, 1915) in his description of North American trematodes, described only two echinostomes: *Cercaria* (= *Echinostoma*) *trivolvis* infected *Helisoma trivolvis* from a small pond in Urbana, Illinois, and *Campeloma subsolidum* from Hartford, Connecticut; and *Cercaria rubrua* (= *Echinoparyphium rubrum*, according to Kanev, Sorensen, Sterner, Cole, *et al.* (1998), infected *H. trivolvis*, which serves as both first and second intermediate hosts for both *Echinostoma* species. Another echinostome reported in North America was *Echinostoma spinulosum* from a loon, but Ward (1917) rejected the identification and named it *Stephanoprora gilbert*, a member of the Echinochasmidae, not Echinostomatidae. Miller (1936) described numerous echinostomes from North America, but only six species had collar spines; all of them were marine. Stunkard (1938) described the life cycle of *Himasthla quissetensis*, (Family: Himasthlidae) using marine bivalves at Woods Hole, Massachusetts. Finally, exhaustive treatments of echinostome hosts and geographic occurrences of *Echinostoma* and *Echinoparyphium* species are given by Beaver (1937), Murrell and Fried (2007), and Fried and Toledo (2009), the latter two listing CMS and JMS as intermediate hosts, but only in Asia (Korea, Japan, Philippines, Taiwan) and Europe (Russia, Poland).

Several species of echinostomes are parasitic to humans. The first record of human infection with *E. hortense* in Korea was in a 21-year-old man in 1983, apparently from eating infected, raw freshwater fish (Seo, Hong, Chai, and Lee 1983). Two other cases of human infection were reported later by Lee, Chung, Ko, Ko, *et al.* (1986), one in a 38-year-old man who ate raw fish, the other in a 20-year-old man who ate raw salamander. Seo, Chun, Chai, Hong, *et al.* (1985a) infected volunteer humans with *E. hortense*; after infection, they were treated with praziquantel and purged with magnesium salt on the 26th–27th day, and stools were examined for eggs. The prepatent period of the fluke in humans was 16–17 days. The major subjective symptoms in human volunteers were abdominal pain and diarrhea likely were caused by eating raw freshwater fish from a local river.

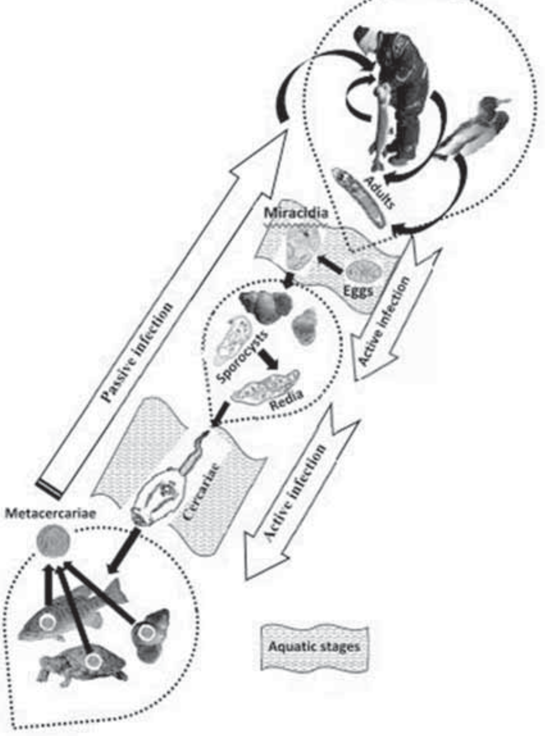


Figure 6-17. Life cycle of echinostomes as depicted by Fried and Toledo (2009) in their Figure 1.2.

Echinostoma cinetorchis is a human intestinal trematode in the Republic of Korea (Park, Hwang, and Chung 2008). Chung and Jung (1999, 2001) reported the first occurrence of *C. c. malleatus* serving as a second intermediate host of *E. cinetorchis* in Korea. Possibly, this gastropod could serve as a source of human infections. Of 68 specimens of *C. chinensis malleata* collected, 3 out of 12 local areas naturally harbored *E. cinetorchis* metacercariae. Of 44 specimens of *C. japonica* examined, none carried metacercariae. *Echinostoma macrorchis* was first described from naturally infected rats in Japan; subsequently, human infections were reported in Japan (Lo 1995). Metacercarial cysts were found in uncooked *Cipangopaludina malleata* and *Cipangopaludina japonica* specimens, presumed to be the source of human infections.

Human echinostomiasis is endemic to southeast Asia and the Far East. It is a food-borne intestinal parasite certified to at least 16 species of digenean trematodes transmitted by snails (Graczyk and Fried 1998). There are two separate life cycles of echinostomes: in humans and occurring in or affecting wild animals in endemic areas. Clinical symptoms of echinostomiasis include abdominal pain, violent watery diarrhea, and anorexia. Clinical symptoms are related to parasite load (Graczyk and Fried 1998). Light to moderate infections cause headache, dizziness, slight anemia, stomachache, gastric pain, and loose stools. Heavy infections are associated with abdominal pain, profuse watery diarrhea, anemia, edema, and anorexia. Pathological damage to the intestinal mucosa that cause extensive intestinal and duodenal erosions and inflammation of airway passages are also common.

iii. Nematodes

The rat lungworm, *Angiostrongylus cantonensis* uses *C. chinensis* as its natural intermediate host and has been incriminated in eosinophilic meningitis in an eight-year-old girl in Taiwan (Chang, Cross, and Chen 1968). The girl had obtained the snails from a rice field and ate some uncooked; one week later, she developed symptoms of meningitis. Seddon, Appleton, Van Damme, and Graf (2011) report angiostrongyliasis from northern, western and southern Africa and believe they have become widespread in Africa. When people ingest its larvae, either by eating infected snails or in mucus trails left by infected snails on salad material; they penetrate the central nervous system, resulting in eosinophilic meningitis.

Mastitsky, Karatayev, and Burlakova (2014) suggested that alternative exotic hosts can be used by 23% of the high-impact parasites detected in the Great Lakes. They list A. *cantonensis* as a high-impact parasite, along with *Echinoparyphium recurvatum*, *Echinostoma cinetorchis*, *Echinostoma macrorchis*, and *Euparyphium ilocanum*, all of which infect *C. chinensis*, and *E. macrorchis* in *C. japonica* outside of North America

To summarize the potential impact of parasites in North America, thus far, only one trematode, *A. conchicola*, has been reported in *C. chinensis*

(Michelson 1970). Mastitsky, Karatayev, Burlakova, and Molloy (2010, 2) described epizootics as occurring after the introduction of exotic species due either to “parasite spillover” (i.e., exotic parasites infecting novel hosts in invaded areas) or “parasite spillback” (i.e., an increase of the native parasites' impact because of their amplification in an exotic host). Their studies revealed that the spread of non-indigenous species is an important yet underestimated and insufficiently studied factor in the emergence of disease outbreaks. The conundrum is the inability to predict which native species will be susceptible to the introduced parasites or which native parasites will readily use exotic hosts for amplification. In addition, there are myriad snail species, both native (e.g., planorbids, physids, lymnaeids) and exotic hydrobiids (e.g., *Bithynia tentaculata*), already serving as first or second intermediate hosts in North American waters. Untangling, which is contributing to parasitic spillovers and spillbacks, is challenging. I subscribe to Taraschewski’s (2006) recommendation, who acknowledged that adaptations of some populations of the novel host to the alien parasite take several decades to a century or more. We can figure out tentative patterns and principles of host–parasite relationships, but individual case studies teach us those generalizations should be avoided.

G. Predation

Predators are defined here as animals that kill their prey, usually for nutrition. Predation of *C. chinensis* and *C. japonica* is not well reported, perhaps because, as prey, they are large, have thick shells, and inherited an operculum to defend their soft parts. Of the freshwater operculates, most predator studies have been done on *Bithynia tentaculata*. Predators and prey have a variety of behaviors to react to each other. Vermeij (1982, 705) proposed three phases to evaluate the effectiveness of a purported anti-predatory feature: “(1) the recognition or detection phase; (2) the pursuit or escape phase; and (3) the subjugation or resistance phase. As predator and prey approach each other, the predator may be unable to recognize the other party as prey, choose not to pursue the prey, or initiate an attack. The prey may escape, but if it is captured, the prey may still be rejected, either because subjugation was unsuccessful or because the prey was undesirable.”.

Here, I apply these phases to CMS and JMS:

1. They are easy to recognize because of their large size, or if detected, they withdraw and protect their soft parts by closing the aperture with its operculum.

2. Mystery snails, as prey, are not likely to escape and certainly not pursue, and they are not predators, they are herbivores or detritivores.
3. Subjugation may occur on juvenile snails but unlikely on adult snails, which will resist any attempt to crack their shells.

Six groups of predators are examined from invertebrates to vertebrates: triclads or turbellarians, leeches, crayfish, fish, waterfowl, and mammals. Among the latter are humans who are predators (e.g., of moose, deer, rabbits, etc.), sometimes referred to as super predators, but for snails, who use them as food (escargot); this is discussed later under beneficial impacts (Chapter VIII).

i. Triclads

Triclads (turbellarians with three-branched intestines) are known to prey on snails, at least in British waters (Reynoldson and Pearce 1979a; b). The food habits of triclads are classified as scavengers, carnivores, and opportunistic predators feeding on living and dead matter. If living, apparently only soft or disintegrating tissues are sucked up by the muscular and extendible pharynx, which questions the triclad's attribute like a true predator. Only Reynoldson and Pearce (1979b) included a viviparid, *V. viviparus* in their studies. *Dugesia polychroa*, *D. lugubris*, and *Planaria torva* preyed upon snails of differing morphologies, while the *Dugesia* spp. fed approximately in proportion to snail abundance; *P. torva* was more selective on the introduced operculate *Potamopyrgus jenkinsi* (Reynolds and Pearce 1979a).

Reynolds and Pearce (1979) used a serological technique to determine the extent of feeding upon snails by *Polycelis tenuis*. They compared snails in habitats lacking and containing *Dugesia polychroa,* the major triclad predator of snails; they found that *P. tenuis* ate significantly more snails when *D. polychroa* was absent. The viviparid was not a significant prey item in their study.

There appear to be no studies of triclads as predators of snails in North America, despite the occurrences of the cosmopolitan and usually abundant species *Dugesia tigrina* and the introduced *D. polychroa*, examined in the studies of Reynoldson and Pearce (1979a, b). Nevertheless, it is unlikely that triclads are major predators of CMS and JMS in North America because of their predilection for dead or moribund tissues. It seems that the snails must be dead or dying before triclads invade the soft parts, the death being caused by other reasons, like senescence, parasitism, etc.

ii. Leeches

Several species of leeches in two genera, *Glossiphonia* and *Helobdella*, feed on snails, especially pulmonates (e.g., *Physa*, *Lymnaea*, *Planorbis*, *Gyraulus*). The cosmopolitan species in these two genera is *G. complanata*, which feeds almost exclusively on snails (Sawyer 1972). Of the *Helobdella* species, *H. fusca* also feeds almost exclusively on snails. Chernin, Michelson, and Augustine (1956) and McAnnaly and Moore (1966) suggest some *Helobdella* species could help as a biological control agent for the snail-borne disease, schistosomiasis. The growth of the schistosome-bearing snail, *Austraborbis glabratus*, was effectively controlled by *H. fusca*, with small snails being exceptionally vulnerable to the leech (Chernin, Michelson, and Augustine 1956).

Brönmark and Malmqvist (1986) investigated the efficiency of anti-predatory adaptations in four pulmonate and two operculate gastropods to leeches and the conflict between demands for forage and avoidance. They analyzed the strategies involved in prey capture by the leech *G. complanata*, including search mode, encounter rates, attack and capture, patch use, and prey choice. For hunting and anti-predatory behavior, the leech showed a typical nocturnal activity pattern. The pulmonates, *Physa fontinalis*, *Planorbis planorbis*, and *Lymnaea peregra*, had elaborate responses by shaking the shell to the left and right when encountered by a leech, and the snails escaped after this behavior. Besides shaking, *L. peregra* and *P. planorbis* moved upwards on vertical surfaces and eventually left the water. The operculate prosobranchs, *B. tentaculata* and *Theodoxus fluviatilis*, withdrew into the shell for up to 743 minutes. The activity of *B. tentaculata* decreased with increasing leech activity but was relatively higher when food was present than when not. Leech handling times depended on the time elapsed since the previous meal was captured, which was related to the size of the previous prey. Leech handling time was also related to the size of both predator and prey. Leeches were unable to discriminate between patches of different prey density. The trend within each size class of *G. complanata* for decreasing proportions of fed leeches with increasing prey size was also reported by Martin, Seaby, and Young (1994).

Klemm (1975) examined leeches in natural associations with molluscs at 10 intensively analyzed stations and 25 supplemental sites in Michigan. He found a relatively wide variety of molluscs harbored an abundance of leeches as well as trematode larvae and symbionts. Leeches were especially abundant in *Helisoma anceps, H. trivolvis, H. campanulatum, Stagnicola exilis*, and *Physa gyrina*, but many pulmonates were not invaded by *G. complanata*. No operculates, including CMS, were found with leeches. He indicated that the leeches infesting snails in Michigan would not serve as a biological control against snails.

Kelly and Cory (1987) examined the defense reaction of operculum closure in response to the molluscivorous leech *G. complanata* and the non-molluscivorous leech, *Erpobdella octoculata*. They studied the responses of four freshwater prosobranchs, *B. tentaculata*, *Valvata piscinalis*, *V. cristata*, and *Potamopyrgus jenkinsi*. Both *B. tentaculata* and *V. piscinalis* could distinguish between the leeches, reacting only to *G. complanate*; the *V. piscinalis* was capable of detecting the leech's scent from a greater distance. *Valvata cristata* and *P. jenkinsi* did not react to either leech, but the former was not considered a potential prey item for *G. complanata*; *P jenkinsi*, on the other hand, was fed on by the leech, but the leech was a relatively new invader.

While no behavioral study between leeches and mystery snails have been reported, the lack of data reporting leech infestations in these snails suggests that leech predation is not likely to be a factor in limiting their population sizes.

iii. Crayfish

Unfortunately, there are only a few studies on predation of mystery snails by crayfish, but there are several studies of prey selection of other snails, including operculates. Olden, Larson, and Mims (2009) evaluated how native signal crayfish, *Pacifastacus leniusculus*, the non-native red swamp crayfish, *Procambarus clarkii*, and the northern crayfish, *Orconectes virilis*, utilized the Chinese Mystery Snail as a prey resource. Their mesocosm experiments revealed that crayfish could consume CMS, despite the snail's large size (the largest was 39.9 mm high), thick outer shell, and opercular defensive behavior. Crayfish exhibited size-selective predation whereby consumption levels decreased with increasing snail size; small and very large snails may represent the most profitable prey choice. By contrast, previous studies have reported the opposite pattern for crayfish consumption on thin-shelled snails. For all snail size classes, Olden, Larson, and Mims (2009, 1073) found "that native *P. leniusculus* and invasive *O. virilis* consumed greater numbers of snails than invasive *P. clarkii*. Moreover, *P. leniusculus* consistently handled and consumed snails at a faster pace compared to both invasive crayfishes across the range of snail sizes examined". These results suggest not only that *C. chinensis* is a suitable food source for crayfish, but also that native *P. leniusculus* may ultimately out-consume invasive crayfish for this new prey resource.

As a preamble for the following discussions of predatory–prey interactions, crayfish and fish have defensive traits that are induced by chemical cues produced during predation events (Petranka, Kats, and Sih 1987; Dodson, Crowl, Peckarsky, Kats, *et al.* 1994; Chivers and Smith 1998; Schoeppner and Relyea 2005; Ferrari, Wisendon, and Chivers 2010). These chemicals contain components from predators (termed kairomones) and injured prey (termed alarm cues). There is a potential sequence of stages between predator and prey through chemical information and the nature and imminence of risk. At the stage of initial detection, prey detect predators through the predator's unique odor, called a kairomone. A prey receives the kairomone released by the predator adaptively favorable to the prey but not to the predator, allowing the prey to evade the predator, the evasion behavior differing among species. Some responses of gastropods to chemical detection of predators include burial in the substrate, seeking refuge in vegetation, crawling out of the water (mainly pulmonates), delaying reproduction, altering growth patterns, and decreasing foraging and movement (Chivers and Smith 1998).

Dodson, Crowl, Peckarsky, Kats, *et al.* (1994) described the use of chemical signals by prey species to modify their morphology, life history traits, feeding, and predator avoidance behaviors, an advantage in dark or turbid environments by animals that do not have image-forming eyes. They argued that chemical signals are more persistent than mechanical signals (e.g., touching, attacking, hydrodynamic pressure waves or sound) and allow species-level identification of predator species. Many predators use chemical signals to stimulate or inhibit feeding and use species-specific mechanical signals to locate or track prey or potential mates. They suggest that the exact nature of non-visual signals depends on the ecological constraints of both the sender and receiver. Organisms often adjust their responses as ontogenic development changes size, diet, and habitat (Dodson, Crowl, Peckarsky, Kats, *et al.* 1994).

Crowl and Covich (1990) showed that in the presence of a chemical cue from *O. virilis*, snails grew more rapidly but exhibited little reproduction until they reached a size of about 10 mm after eight months. In the absence of the cue, snails grew to about 4 mm (3.5 months) and then began reproduction. They concluded that crayfish might increase the likelihood of coexisting with seasonal predators by increasing the variance associated with size and age of maturity.

Alexander and Covich (1991) examined predator avoidance behaviors of two freshwater pulmonate snails, *Physella virgata* and *Planorbella trivolvis*, to the crayfish *Procambarus simulans*. Both snails crawled above the waterline for several hours to escape the probability of an encounter with the crayfish. However, they found a significant size-dependent relationship between vertical escape and vulnerability to predation, with all size classes of *P. virgata* and small *P. trivolvis* crawling out in response to crayfish presence. The large *P. trivolvis* did not display any avoidance behavior, likely relying instead on strong shell architecture for defense. Alexander and Covich (1991) considered both escape behavior and size as adaptive responses to predation. Similar results and conclusions were reported by Turner, Fetterolf, and Bernot (1999) for the escape behavior of the snail *P. gyrina* from the crayfish *O. rusticus.*

Brown (1998) exposed four gastropods, *Amnicola limosa*, *Gyraulus parvus*, *Physella gyrina*, and *Helisoma anceps*, to predation by three crayfish species, *Orconectes rusticus*, *O. propinquus*, and *O. virilis*, in a laboratory setting to determine prey preference. Crayfish had a higher selection for the thin-shelled, planospiral pulmonate *G.* parvus despite its lower abundance in samples than the thicker-shelled but small prosobranch *A. limosa* and a large planospiral pulmonate, *H. anceps*. Crayfish selectivity appears to be a function of the resistance of shells to chipping by crayfish mandibles. Although different species are preferred, this is similar to selecting thin-shelled species by sunfish, described later.

Turner, Fetterolf, and Bernot (1999) conducted predation experiments using fish and crayfish on snails in 16 outdoor 525-L polyethylene pools. They placed corrugated vinyl sheets (68 x 61 cm), supported by four legs 4 cm tall, that covered about 1/4 of the benthic surface of each pool. In the presence of fish, the snails moved under the benthic cover, which provided safety from the fish predators. However, in the presence of crayfish, snails avoided benthic cover and moved to the water surface. Turner, Fetterolf, and Bernot (1999) concluded that the two species of predators exerted the same level of mortality on prey but induced very different behavioral responses. They predicted that these contrasting behavioral responses to predation risk have significant consequences for the interactions between snails and their periphyton resources.

Nyström, Brönmark, and Graneli (1999) in their mesocosm experiments with the exotic Signal Crayfish, *Pacifastacus leniusculus*, and a native crayfish, *Astacus astacus*, had a strong impact on grazers dominated by thin-shelled *Lymnaea* snails. Hard-shelled *Bithynia* snails were also reduced in numbers. The reduced biomass of snails had an indirect positive effect on periphyton biomass and grazed selectively on macrophytes. Overall, the exotic Signal Crayfish had a stronger impact on the biomass of macrophytes and grazers than the native Noble Crayfish. The results indicate that crayfish may structure food webs through consumption from many food levels.

Dickey and McCarthy (2007) compared behaviors of *Orconectes* juveniles and snail prey, *P. gyrina*, with and without exposure to injured-snail cues, in seven different sizes of arenas (aquaria). The crayfish were generally more active in larger arenas, but their response to injured snail cues decreased as arena size increased. Snails responded to the injured snail cue by seeking refuge but responded less strongly in larger arenas. Consumption time was lower in the presence of injured snail cue but was unaffected by arena size. They concluded that the effects of the injured snail cue are mediated by spatial scale, which affects the outcome of this predator–prey interaction.

There are numerous other studies of snail predation by crayfish (see references within the studies cited above). As Olden, Larson, and Mims (2009), demonstrated, crayfish could impact mystery snail populations with individuals ranging in size from 10 to ~40 mm in mesocosms. While studies of predator and prey interactions in mesocosms, arenas (aquaria), etc. can be easily manipulated to address specific objectives, they oversimply potential reductions in snail populations in nature. The impact of crayfish on mystery snails in a lake depends on habitat structure (e.g., presence of emergent macrophytes to crawl to the surface, submersed macrophytes to hide in), diversity of snails (e.g., thin shell vs. thick shells, size classes) and other preferred prey (e.g., easier to obtain), crayfish diversity (e.g., native vs. invasive species) and density, physical complexity of the habitat (e.g., prevalence of mud as a substrate favors large size of the offspring at birth in *Viviparus*, according to Ribi and Mutzner-Werli 1987), and spatial distance between snails and crayfish. All these factors determine the extent of the impact on mystery snail populations.

iv. Fish

Based on a literature review, at least three factors seem to affect food choice, especially in sunfish: food preference, period and extent of overlap during feeding, and seasonal variations in habitat preferences. Sadzikowski and Wallace (1976) examined the food habits of three species of sunfish: the pumpkinseed, *Lepomis gibbosus*, bluegill, *L. macrochirus*, and green sunfish, *L. cyanellus*. The latter two feed mostly on plant material and dragonfly larvae, but adult *L. gibbosus* made much greater use of gastropods. They concluded that the strong pharyngeal jaws, tooth morphology, and mouth size present in *L. gibbosus*, but lacking in the other two species, explained food habits differences. This molluscivorous jaw adaptation was supported by Lauder (1983) in his trophic specialization studies.

Keast (1978) compared the feeding and spatial ecology of the pumpkinseed with that of the bluegill. The two species and their equivalent year-classes were separated partially on a diet (the bluegill consuming a greater proportion of Cladocera and Trichoptera larvae, the Pumpkinseed, molluscs and isopods), and partly on habitat and the height at which they foraged in the water column.

Laughlin and Werner (1980), in addition to attributing the differences in mouth structure between the pumpkinseed and longear sunfish, *Lepomis megalotis peltastes,* found the former concentrated in deeper areas with heavy vegetation cover. The longear sunfish gathered in shallows with less vegetation. Both sunfish species consumed more food in the spring and exhibited greater overlap in diet during this period, which complicated the assessment of competition between species when food and habitat use are dependent on size.

Osenberg and Mittelbach (1989) suggested prey selection patterns by pumpkinseed sunfish (*L. gibbosus*), a specialized molluscivore in the family Centrarchidae. Field studies showed that pumpkinseeds fed primarily on gastropods (see Seaburg and Moyle 1964; Sadzikowski and Wallace 1976; Keast 1978; Laughlin and Werner 1980; Mittelbach 1984). However, dietary patterns and prey selection among gastropods were highly variable from time to time (or site to site). The strong pharyngeal jaws and molariform teeth allowed them to efficiently crush the shells of gastropods and extract their soft tissues (Lauder 1983; Mittelbach, Osenberg, and Wainright 1992). Globose, more crush-resistant shells are better adapted to prevent predation by fish (DeWitt, Robinson, and Wilson 2000).

Crowl and Covich (1990) demonstrated that predation induced shifts in life history traits of the freshwater snail *Physella virgata virgata*. Keller and Ribi (1993) tested this hypothesis using four fish species in field studies within grid closures. They used as predators the Common Barbel, (*Barbus barbus*), Roach, (*Rutilus rutilus*), Common Rudd, (*Scardinius erythrophtalmus*), and Tench (*Tinca Tinca*), all of which prey on viviparid snails in Lake Zürich. Their aims were (1) to determine which species of fish potentially eat the snails, (2) to estimate the survival rate of offspring in their natural habitat and to test whether the presence of shelters increases offspring survival, and (3) to document the seasonal migration of *V. ater* in Lake Zürich. They installed three plastic fences to reduce migration between adjacent areas. The fences ran perpendicularly to the shoreline from 1–4 m depth, one along either side of the grid, the third one running down the middle, dividing the grid into two sections of equal length, A and B, each being 40 x 40 m. Then, they placed 72 tiles, 30x30 cm, into section A between 2–4 m depth to provide shelters from vertebrate predation for juvenile *V. ater* migrating from shallow to deeper water. Each tile was held 2–5 cm above the ground utilizing wooden pegs. Section B was left unaltered and served as control. The use of the shelters was determined by the number of juvenile and adult snails underneath the tiles in equal-sized adjacent plots. Snails were counted in the morning and around midnight over three days. Following this, 78 male and 78 female snails were tagged using correction fluid to follow their growth and dispersal. Their position was recorded once a week in the grids. Offspring survival in the natural habitat was one order of magnitude lower than in the tiled section, suggesting that predation was a significant cause of mortality of newborn *V. ater*. In September, there was a migration from shallow (1-4 m) to deeper water (5-9 m). The average distance between weekly recordings of tagged *V. ater* was 4.7 m wk^{-1} in males and 3.0 m wk^{-1} in females. All four fish species ate the snails, cracking the shells while they held the snail in their mouths. Shell fragments were spat out, the fragments being largest in *R. rutilus* and smallest in *B. barbus*, but they never spat out any soft parts of the snails. During their first summer, the estimated survival rate of V. ater was 10.9% in section A of the grid, where tiles were placed to provide shelters for them, and 9.6% in section B, which served as a control. Age-specific survival rates were estimated from the total number of offspring born on the grid during summer and from the number of snails of different age groups found in October. Survival was 10% during the first few months after being born; age class 0 snails reaching the end of the first summer had a 54% chance, and age class 1 snails the end of the second summer had an 80% chance of living for another year. It is apparent from these data that younger, smaller, and more fragile snails are at a higher risk than older snail groups. Keller and Ribi (1993) interpreted the overlap in size between age groups due to some of the life history features of *V. ater*, reported by Ribi and Gebhardt (1986). Individual growth was fastest in the first year, while later in life, the growth rate became smaller on average, but the variation in growth rate between individuals increased.

For snails, DeWitt, Robinson, and Wilson (2000) proposed that resistance to one predator then implies susceptibility to the other because shells can be relatively rotund or elongate but not both. They provided three levels of evidence to support this trade-off:

1. Measurements indicated that rotund shells were relatively crush-resistant, whereas elongate shells were more entry-resistant.
2. Foraging trials showed that rotund shells required more handling time and were rejected more frequently by fish, whereas snails with elongate shells were more likely to survive with crayfish.

3. Field samples revealed rotund shell morphology in habitats where fish were common.

One other molluscivorous fish is the Freshwater Drum, or Sheepshead, *Aplodinotus grunniens*. It also has large pharyngeal arches. Lake and river-dwelling molluscs are more important in their diet (Scott and Crossman 1998), but the latter lives in deep water (12–18 m, 40–60 ft) and viviparids live in shallow water, making them unlikely prey for Freshwater Drum.

v. Waterfowl

Waterbirds are well-known vectors for overland dispersal of snails (Kobelt 1871; Kew 1893; Boycott 1936; Baker 1945; Malone 1965a, b; Boag 1986) and feed on them directly or indirectly as bycatch with other invertebrates. Kobelt (1871) thought it not unlikely that small, living fingernail clams and operculate snails could pass the intestinal canal undigested and can thus be transplanted. He added that one should look where the sunshine has warmed up the shore's shallow stretches where molluscs gather in large quantities in the warmth. Also, birds bashing the shell against stones is often observed in birds preying upon the *Viviparus* (Parisi and Gandolfi 1974).

Waterfowl are well-known predators of snails, especially *Viviparus* species. De Bernardi, Ravera, and Oregioni (1976) confirmed the mass mortality of juvenile *V. ater* in a northern Italy lake by examining the stomach contents of the mallard *Anas platyrhyncos* during spring feeding.

The importance of gastropods as prey for waterfowl was demonstrated by Reynoldson and Pearce (1979a) in their investigation of triclad predation on pulmonate and prosobranch snails. They reported a marked decrease in the density of the snail populations after a small pond was visited by a pair of mallard ducks, which virtually wiped out the snail populations before the triclad study began. Attempts to reestablish the snails were unsuccessful due to further depredations by the ducks.

Stanczykowska (1990) examined the possible effects of predation pressure from coots (*Fulica atra*) on mollusc communities. She found in most places where birds commonly foraged on an abundance of *Viviparus viviparus*, they did not forage on them when high densities of the zebra mussel and Sphaeriidae were present. This behavior suggests an active selection of specific foraging places by coots, even when there are many viviparids.

The great blue heron, *Ardea herodias*, also feeds on CMS, as shown in Figure 6-18 in a photo 8644341 by Sandy Wolkenberg (Appendix B, Great blue heron). The water body looks highly eutrophic with floating algae, a common habitat quality populated with the Chinese Mystery Snail.

Figure 6-18. Great Blue Heron preying on Chinese mystery snails. Photo 86443417, by Sandy Wolkenberg, see Appendix C for source.

The ring-billed gull, *Larus delawarensis*, also preys on CMS, accessing the soft parts without breaking the shell, as shown in a series of photographs by Andrea Wuenschel (Appendix B, Ringed-bill gull)

vi. Mammals

The Muskrat, *Ondatra zibethica*, and River Otter, *Lutra canadensis*, are known to prey on molluscs, the Muskrat being the major consumer compared to the Otter, with only about 0.1% to 6% molluscs in the latter (Gilbert and Nancekvell 1982), fish being their main prey (Knudsen and Hale 1968).

The Muskrat is one of only a few mammals to prey on freshwater mussels, capable of destroying mussel beds, altering species composition, and negatively affecting endangered mussel populations (Bovbjerg 1956; Convey, Hanson, and MacKay 1989; Hanson, Mackay, and Prepas 1989; Neves and Odom 1989; Tyrrell and Hornbach 1998). It also discards live unionids, as evidenced by muskrats selectively preying on zebra mussels rather than unionids (Sietman, Dunn, Tucker, and Kelner 2003). Much of this evidence is based on shell remnants in riverside middens. Gastropods may be prey for muskrats, but apparently, the shells are swallowed whole with plants and do not appear in middens (Errington 1941).

Parisi and Gandolfi (1974) examined predation by the Norway rat (also known as brown rat, sewer rat, common rat), *Rattus norvegicus*, on diverse terrestrial, freshwater and marine species molluscs in the Po River basin in Italy. Among the molluscs preyed upon were *V. ater* and *V. contectus*. The authors refer to other studies that describe the rats having to dive for these snails because the viviparids migrate seasonally from shallow to deep water.

Gordon, Wilding, and Aldridge (2016) examined bankside middens of the brown rat to provide evidence of predation on the native freshwater gastropod *V. viviparus* in a closed, lentic system in Ely, southeastern England. The reported high mechanical force required to break the shells suggested this was driven predominantly by maximizing nutrient gain rather than optimizing handling effort. They concluded that aquatic gastropods represented a potentially important nutrient resource for brown rat populations in the closed system.

H. Biogeology

This section is intended to explain the origins of water bodies in which viviparids live, which can be the most pristine, as dictated by their geological origins, or have deteriorated beyond that point, as hopefully elucidated by the processes offered herein. These processes include the ionic contributions by the parent bedrock, the delivery of these ions to the water bodies, the ionic composition (chemistry) of the water body, the internal (autochthonous) and external (allochthonous) processes that contribute to their temporal and spatial variations, and characteristics in the range of habitats that CMS and JMS have successfully populated. Only the fundamental ecosystem concepts are given here. Thorough treatment of all biogeological components (e.g., lake origins and morphometrics, water chemistry and physical, plants, plankton, and benthic organisms, water quality assessment, etc.) of freshwater ecosystems may be found in several textbooks, including Wetzel and Liken (1991), Horne and Goldman (1994), Wetzel (2001), and Mackie (2004).

i. Geological Contributions

The genesis of a water body's chemical framework is largely determined by the ionic contributions from the types of bedrock underlying and surrounding it. There are three types of rock formations: igneous, sedimentary, and metamorphic.

- Igneous rocks are of two types: intrusive and extrusive rocks. Intrusive igneous rock is internal, under the earth's crust, and magma cools slowly to create large, coarse-grained crystals. Extrusive rocks form when molten magma spills over on the top crust of the earth as a result of volcanic eruptions. Igneous rocks may consist of one mineral or various minerals (e.g., basalt, granite), and their shapes and sizes depend on the cooling process. They are insoluble, contain no organic material, and contribute few ions to waters flowing over or through them. Some relevant minerals include quartz made of silica (SiO_2), used by diatoms, also a common food item for viviparids; feldspar, a group of aluminosilicate minerals that contain calcium ($CaAl_2Si_2O_8$); sodium ($NaAlSi_3O_8$); or potassium ($KAlSi_3O_8$).
- Sedimentary rocks are formed secondarily from weathered and eroded previous rocks that have fractured and are from sedimentary deposits. They are subject to greater erosion, reshaped by abrasion and compaction, creating layers of minerals and materials. The cementation occurs by combining rock pieces with salt compounds or organic matter. Sedimentary rocks include limestone, sandstone, and mudstone. All are quite soluble and contribute many kinds of ions to water bodies. Among the most important are limestone ($CaCO_3$); gypsum ($CaSO_4 \cdot 2H_2O$), a sulfur source; apatite ($Ca_{10}(PO_4)_6Cl_2$), a phosphate mineral; pyrite (FeS_2), or "fool's gold"; sulfide; and iron mineral.
- Metamorphic rocks are created from other rocks, mostly sedimentary or igneous rocks that have been altered by extreme heat (150–800°C) and pressure. These "hot rocks" are formed due to widely distributed pressure and temperature changes created by tectonic movements. Gneiss is a metamorphic rock with a banded or layered structure, consisting mainly of feldspar, quartz, and mica. Some most notable metamorphic rocks are marble formed from limestone and slate formed from shale.

ii. Water Bodies

The bodies of water that viviparids live in are categorized here as permanent flowing waters (lotic systems), including creeks, streams, and rivers, and standing waters (lentic systems) that include permanent ponds and lakes. Viviparids also occur in ditches if the ditches have an endless water supply and may be classified as lotic or lentic systems, depending on whether the water is flowing or standing.

a. Flowing (Lotic) Waters

Most lakes have source streams that begin as headwaters or seeps. The ordering and functioning of streams described herein follow the river continuum concept (RCC) of Vannote, Minshall, Cummins, Sedell, *et al.* (1980). It describes characteristics of flowing waters, including width, depth, velocity, and sediment load, and uses indicator organisms to help classify individual sections. It shows how to map out biological communities and their sequence in individual sections of water, allowing the structure of rivers to be more predictable as to the biological properties of the water. The concept is explained in Mackie (2004), but it is essential to recognize the stream order (size) that viviparids are collected from. There are two stream ordering systems, but Strahler's (1964) method is most used, illustrated in Figure 6-19.

A topographic map is needed to determine stream order, preferably at a 1:25,000 scale. The mainstream/river in Figure 6-19 is shown as a dotted line. Stream order 1 is the seep or the source origin of the river. The stream order increases only when two streams of equal order combine; hence, while numerous streams of order 1 exist, the final order size is 4 in Figure 6-19. The RCC divides stream orders into headwaters (1 to 3), medium-sized streams (4 to 6), and large rivers (> 6); from headwaters to downstream, the physical variables within a stream system exhibit a continuous gradient of conditions, including width, depth, velocity, flow volume, and temperature. Unfortunately, stream order is seldom reported for *C. chinensis* and *C. japonica* occurrences, but they are unlikely to occur in the headwaters (orders 1 to 3).

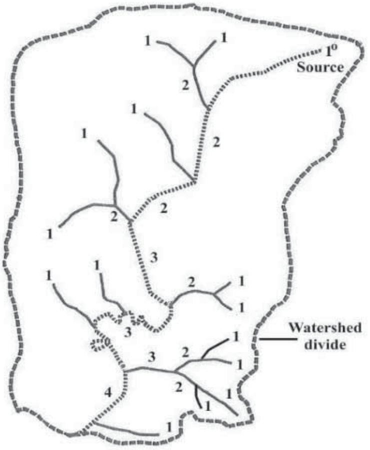


Figure 6-19. A hypothetical stream (dotted line) showing how stream order is assigned using the Strahler (1964) method (see text for details). Tributaries are shown as solid lines. The watershed boundary is shown in a heavy dashed line.

The headwaters are characterized by cool temperatures due to heavy canopies of trees shading the stream. Hence, with little sunlight, primary production by submersed macrophytes and algae is greatly reduced to absent; this leads to very little detrital material produced within this stream segment. However, the foliage of the trees seasonally provides organic matter that insects must shred before it becomes available to deposit feeders. The bottom is erosional, generally represented by gravel and stones, with little sediment or organic material between them. Meager amounts of macrophytes, algal food, and suitable substrate make very poor living conditions for viviparids.

b. Standing (Lentic) Waters

Often it is difficult to distinguish between a large pond or a small lake. Ponds are defined here as bodies of water with little depth (usually < 3–4 m), small enough that waves cannot be generated to leave wave-swept beach zones and deep enough for mystery snails to migrate into during winter. Temporary or vernal ponds are not included because viviparids require water permanent enough to establish a population. Ponds also are exclusively littoral, with submersed and emergent macrophytes at all depths.

Lakes are much larger than ponds and have distinct life zones, a littoral zone with emergent and submerged plants, a pelagic or limnetic zone with plankton, and a profundal zone, if deep enough with benthos (Figure 6-20). Viviparids occur mainly in the littoral zone in the summer, but many migrate in the fall into the deeper sublittoral zone where only submersed macrophytes occur and the water is deep enough not to freeze to the bottom. The literature (e.g., Stañczykowska, Magnin, and Dumouchel 1971) suggests that CMS's maximum depth is between 2 and 3 m. This depth sounds reasonable when one considers the thickness of ice on lakes between 42° and 47° latitude in Canada can vary from about 50 cm to 75 cm (based on personal ice fishing experience). One would expect the thickness to become less from 42° latitude and south, and snails migrate to less deep water in the winter.

Both winter and summer thermal profiles are shown in Figure 6-20; the temperature of maximum density is 4°C, which, being the densest, sits at the bottom of deep lakes. During the summer, the lake becomes thermally stratified, with the warmest part being the upper epilimnion. As long as winds mix the water in this region, the temperature drops only slightly from the warmest and least dense water at the surface, shown as ~20°C in Figure 6-20, until the maximum depth of mixing is at the metalimnion. Here, the temperature declines rapidly to 4°C (in deep lakes), at which point it delimits the metalimnion from the hypolimnion, where the water is at 4°C throughout.

As temperatures drop in the winter, the water gets denser and denser at the surface and begins to sink until it reaches 4°C, at which time the lake is at 4°C from top to bottom. At the surface, however, the water gets colder as air temperatures drop below 4°C, and the water gets lighter and begins sitting at the surface; ice eventually forms as the water temperature approaches 0°C and sits at the surface because it is the least dense. The winter thermal profile is referred to as being inverted because its shape is opposite to the summer thermal profile.

Profundal zones occur in the hypolimnion of deep lakes where light cannot penetrate deep enough to support primary production; the bottom limit of primary production is known as the compensation depth (Figure 6-20), where the rate of primary production equals the rate of respiration. The compensation depth is usually near or at the top of the metalimnion.

There are many kinds of lakes (about 12). Still, viviparids have been reported from glacial lakes (e.g., Great Lakes); fluvial lakes, or lakes formed in river systems (e.g., oxbow lakes); and anthropogenic lakes (e.g., impoundments and reservoirs). Lakes that are most productive in viviparids are somewhat enriched and have calcium levels > 15 mg^{-L} and pH > 7.5, although there are exceptions, as discussed in the next section. Some lakes are meromictic and have no inflows or outflows and have layers of water that do not mix; lakes that mix throughout, as just discussed, are holomictic. However, the littoral zones of meromictic lakes may be suitable to support viviparids. To date, neither CMS nor JMS have been recorded from meromictic lakes. The least productive and unlikely to support populations of viviparids are the so-called beaker lakes, lakes formed in granite or quartz bedrock, which contribute silica or glass particles and little nutrients.

i. Water Chemistry and Trophic Relations

Chinese and Japanese mystery snails occur in a wide range of water chemistry and trophic status (e.g., mesotrophic to eutrophic lakes). This section summarizes the ranges in critical ions to support populations of CMS and JMS. What are the critical ions? The most essential ones are those involved in the formation of calcareous shells. As stated in Chapter V. Biology, A. External Morphology, 1. Shell and Mantle, the shell consists of calcium carbonate in an organic matrix, called conchiolin. A calcium (Ca^{++}),

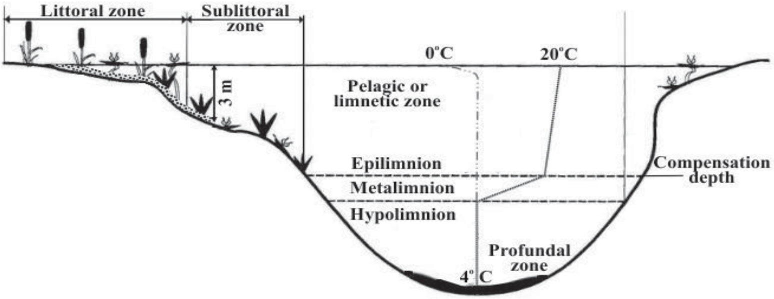


Figure 6- 20. Drawing illustrating regions and zones in a deep lake, with a typical summer thermal profile starting at ~20°C at the surface and dropping to 4°C at the bottom (dotted line) and the winter thermal profile (dash-dot-dot line) with ice about to form at 0°C but hypolimnion remains at 4°C. The depth limit of C. chinensis and C. japonica is shown as the stippled area extending from the littoral to the sublittoral zone. See text for details.

cation is taken up in solution and attached to a bicarbonate ion (HCO_3^-), an anion. A solution of bicarbonate is generated by acidifying monocarbonate (CO_3^{-2}). Combining $Ca^{++} + HCO_3^-$ produces $Ca(HCO_3)_2$; that is, it takes two negative bicarbonate ions ($^{-1}$) for every positive Ca ion ($^{+2}$). The total alkalinity is the sum of bicarbonate alkalinity (pH < 8.3) and monocarbonate alkalinity (pH > 8.3); hence, the total alkalinity of water with pH < 8.3 = bicarbonate alkalinity. The calcium comes from a solution of limestone bedrock; the bicarbonate is generated from carbonic acid (H_2CO_3) in precipitation (rain and snow), where carbon dioxide (CO_2) + water (H_20) $\rightleftharpoons$ $H_2CO_3^-$, which has a pH of 5.6 (i.e., rain and snow are acidic). Combining H_2CO_3 + CaCO3 will yield $Ca^{2+} + 2HCO_3^-$; skipping some reactions, ultimately, $Ca(HCO_3)^{-2} \rightleftharpoons CaCO_3\downarrow + H_2O + CO_2$, from which $CaCO_3$ precipitates out and CO_2 is used in photosynthesis by plants. However, when inorganic carbon (CO_2) is removed from the solution, the pH is raised further, altering the alkalinity and promoting more precipitation of $CaCO_3$ to a point where the floating crystals may induce “lake whiting.” Lake whiting has also been attributed to the resuspension of bottom sediments containing calcium crystals by fish activity and internal water currents (Larson and Mylroie 2014).

It should be clear from these reactions that pH and calcium and bicarbonate levels are essential to molluscs. Bicarbonate alkalinity is measured as part of total alkalinity, all of it being bicarbonate alkalinity when pH is < 8.3 (Mackie 2004).

Table 6-4 shows the ranges and means for the occurrences of the and JMS based on pH, calcium, alkalinity, conductivity, and total dissolved solids (TDS) levels in three studies. JMS occurred at only one of the eight locations (Black Pond) examined by Jokinen (1982). All locations were selected on the confirmed presence of at least CMS.

Conductivity is an early indicator of change in a water body. Conductivity is measured in µSiemens cm^{-1}, a measure of the electrical conductance (EC) of water, and can be used as a surrogate to estimate TDS (e.g., TDS = conductivity x 0.65). TDS is a summed measure of the dissolved content of all inorganic and organic substances present in a liquid in the molecular, ionized, or colloidal suspended form of both cations (e.g., Ca, Mg, Fe) and anions (e.g., Cl, HCO_3, SO_4).

Table 6-4. Ranges in values of six water chemistry variables with surface area as recorded from three authors cited in the table. Means are shown in parentheses.

Author	# Locations	Surface Area Ha	pH	[Ca] mg^{-L}	[Mg] mg^{-1}	Total Alkalinity mg^{-L}	Conductivity . µS cm^{-1}	TDS mg^{-L}
Stańczykowska, Magnin, and Dumouchel (1971)	3	ND	7.0–8.4 (8.3)	24–97 (65.3)	13–25 (23)	87–308 (212)#	ND	ND
Jokinen (1982)	8	1.8–227.6 (68.5)	6.4–7.6 (7.2)	7.1–35.0 (16.4)	2.0–22.0 (7.5)	22–111 (56)#	74–286 (191)	48–186 (124)"
Therriault and Kott (2002-2003)	11	0.04–2.5x10^6	7.9–8.7 (8.3)	50.8–102 (71.4)*	4.6–9.2 (6.5)*	147–255 (179)	615–1,505 (823)	310–978 (535)
Overall mean	7.3	227,280	7.7	43.9	7	118	270	330
Overall range	22	0.04–2.5x10^6	6.4–8.7	24–102	2–25	22–308	74–1,505	48–978

ND = no data; * estimated from total alkalinity; # estimated from [Ca] and [Mg]; " estimated from conductivity; ~ estimated from TDS

a. pH

The occurrence of CMS and JMS is not limited by pH above 6.4, and they do well in circumneutral (pH 6.5-7.5) waters. The pH level of the Black Pond in which JMS occurred in Jokinen's (1982) study was 7.6. The lower limit of pH cannot be determined from the three studies in Table 6-4, even from Jokinen's (1982) studies, which included lakes situated on highly insoluble metamorphic bedrock, like schist and gneiss. Stream organisms are susceptible to spring pH depressions due to migrations of H^+ to the bottom of the snowpack, causing pH to decline by two to three pH units, some with pH as low as 4.5. These acidic inputs occur from atmospheric contributions of sulfur (e.g., sulfuric acid, H_2SO_4) and nitrogen (e.g., nitrogen oxide that forms nitric acid, HNO_3), both as anthropogenic air pollution sources largely from fossil fuel combustion (Haines and Johnson 1982).

In contrast, Therriault and Kott (2002-2003) sampled lakes for CMS mostly in southern Ontario, which is dominated by limestone and dolomitic ($CaMg(CO_3)_2$) bedrock. Such lakes are very resistant to changes in pH because of the buffering capacity of associated high total alkalinities.

b. Calcium and Magnesium

All study locations were selected based on previous occurrences of CMS (and JMS in one of Jokinen's 1982 study locations), rather than selecting locations with ranges in values for each of the variables listed in Table 6-4. The latter is needed to determine each variable's upper and lower limits for both CMS and JMS. Based on the data presented in the table, CMS occurs in water with Ca > 7.1 mg^{-L}, the upper calcium value for CMS being 102 mg-L. The calcium level for JMS in Black Pond was 11.4 mg^{-L}. For magnesium, CMS occurred in waters with > 2 mg^{-L}. The magnesium content of the water for JMS in Black Pond was 4.5 mg^{-L}.

c. Total Alkalinity and Hardness

High alkalinity is of value to snails because the buffering of any acid additions is performed by the water, not the dissolution of their shells. Significant relationships between the buffering capacity of water and the morphology and calcium content of freshwater molluscs were demonstrated by Mackie and Flippance (1983a). They reported the main effect of a decrease in buffering capability and an increase in noncarbonate anion content was a short but heavily calcified shell in the prosobranchs *Amnicola limosa*, *Valvata tricarinata*, and *Campeloma decisum*.

Stańczykowska, Magnin, and Dumouchel (1971) and Jokinen (1982) did not measure alkalinity, but the values in Table 6-4 approximate the total alkalinity from the molecular weights of calcium and magnesium relative to the molecular weight of $CaCO_3$. Therriault and Kott (2002-2003) measured total alkalinity using titration methods. The total alkalinity is a measure of the acid-buffering capacity of water by its bicarbonate and monocarbonate ion levels.

The concept of hardness originated in the early days to express the soap-consuming power of water. The harder the water, the less soap lather forms because the soap precipitates as scale (calcium carbonate, $CaCO_3$) leaving a deposit, often referred to as ring-around-the-tub. Water hardness is also a useful surrogate for estimating the levels of calcium and magnesium attached to anions of carbonates and other anions, like sulfate and chlorides, which can be significant contributions of the two cations. However, molluscs can use calcium as only bicarbonate. The carbonate anions of calcium and magnesium are called temporary hardness because bicarbonates can be boiled off as CO_2; the difference between total and temporary hardness is known as permanent hardness, but its calcium is less available to molluscs than calcium in temporary hardness.

Only Therriault and Kott (2002-2003) measured total hardness in the three studies; of the 11 locations examined for CMS, all had hard water, with four very hard using these criteria: soft has a hardness of < 60 mg $CaCO_3^{-L}$, medium-hard water 61–120 mg $CaCO_3^{-L}$, hard water 121–240 mg $CaCO_3^{-L}$, and very hard water > 241 mg $CaCO_3^{-L}$. The hardness levels varied from 152 to 306 mg $CaCO_3^{-L}$, with a mean of 226 mg $CaCO_3^{-L}$ in their study of 11 locations. Mackie and Flippance (1983b) found intra- and interspecific variations in molluscs' calcium content concerning the water's calcium content. A decrease in calcium bicarbonate alkalinity relative to total hardness was correlated with short shells and decreasing shell calcium content in the prosobranch *Cincinnatia cincinnatiensis*.

d. Conductivity

Conductivity is expressed as either mhos (℧) or siemens (S), the units being μ℧ cm^{-1} or μS cm^{-1}, and although they are considered equivalent, the symbol S is easier to use than ℧. It is also expressed as EC with the same units as conductivity. The higher the conductivity, the greater the concentrations of cations (e.g., Ca, Mg, Na, K) and anions (e.g., CO_3, SO^4, Cl). Low conductivity (0–100 S cm-L) is an indicator of pristine water, as in oligotrophic water (see next section). Mid-range conductivity (200–1,000 μS cm^{-L}) is considered the normal background for most water bodies. Values above this range indicate either saline conditions (1,000–10,000 μS cm^{-L}), which are intolerable or may kill many freshwater organisms, or indicate pollution by industrial discharges (e.g., heavy metals like lead, cadmium, zinc, copper, nickel, chromium, and mercury). Runoff from roads high in sodium chloride, applied during winter and that runs off in spring, and calcium chloride, applied on dirt roads to reduce dust, also lead to high conductivities.

Conductivity can be used to estimated total alkalinity (TA) and hardness (TH), but knowing the bedrock composition of the watershed increases the accuracy of the estimates. For carbonate bedrocks under natural conditions, Kney and Brandes (2007) formulated the relationship between long-term median concentrations of each of conductivity, total alkalinity, and total hardness as follows:

$$EC = 2.161 * TA + 10.601,\ R^2 = 0.940$$

$$EC = 5.418 * TH + 13.625,\ R^2 = 0.990$$

If the watershed overlaid granitic bedrock with alkalinities < 30 mg^{-L} as $CaCO_3$, the relation was $EC = 2.044 * TA + 126.1$, with the upper and lower confidence intervals shown in Figure 3 of Kney and Brandes (2007).

Thompson, Brandes, and Kney (2012) collected data from streams in eastern Pennsylvania where there are cladistic sedimentary (sandstone, mudstone, shale) and crystalline bedrock of low buffering capacity to examine the relationship between EC and TH. Their relationship should be used for streams with alkalinity < 75 mg/L as $CaCO_3$:

$$EC = 2.579 * TH + 9.2689\ (R^2 = 0.993)$$

Table 6-4 indicates a range of pristine conductivity levels in Jokinen's (1982) study. The average conductivity of 191 μS^{-cm} suggests that most locations are surrounded by granitic bedrock; four are in the normal range (207–286 μS^{-cm} and expected for the occurrence of CMS and JMS. The conductivity in Therriault and Kott's (2002-2003) study was estimated from their TDS values using the relation TDS mg^{-L} = 0.65 x conductivity μS^{-cm}, and all fall well within the mid-range, again anticipated for the occurrence of CMS.

Conductivity (μS^{-cm}) can be converted to salinity (ppt) when only salinity values are given. Matthews, Collas, Hoop, van der Velde, *et al.* (2017) give the salinity range for CMS as 0.1–0.64 ppt, which converts to 205–1,285 μS^{-cm}. This range is well within the overall range for conductivity in Table 6-4.

e. Trophic Relations

Trophic status refers to the enrichment state of a body of water. Lakes are either oligotrophic, mesotrophic, or eutrophic, depending on the number of nutrients present. Oligotrophic (*oligo* = poor, *troph* = nutrients) lakes have little or poor nutrient levels; eutrophic (*eu* = true) lakes are truly enriched with excessive levels of nutrients; mesotrophic (*meso* = middle) lakes lie between these two extremes. The nutrient most commonly measured is phosphorous because it is the limiting nutrient (relative to nitrogen) to algae. Of all the phosphorous sources, only one, bedrock (as apatite, $Ca_{10}(PO_4)_6(OH,F,Cl)_2)$), is natural and is mostly insoluble and settles to the lake's bottom, as do aerial deposits. It is estimated that > 90% of phosphorous entering lakes is insoluble, leaving 10% soluble, and it enters through anthropogenic sources, such as detergents and fertilizers. Lakes are classified in their trophic status on the basis of total phosphorous values: oligotrophy = < 10 μg^{-L}; mesotrophy = 10–30 μg^{-L}; eutrophy = > 30 μg^{-L}. There are other methods to determine trophic status, like Secchi depth and chlorophyll-*a* level, but unfortunately, none of the three studies reported trophic status for their localities.

A crude estimate of trophic status can be made from Table 6-5, making most ponds reported in the literature likely in the mesotrophic to the eutrophic range. Those with conductivity levels < 200 $\mu S\ cm^{-L}$ are likely in the oligotrophic range.

Table 6-5. Some features of lakes of three trophic states. Modified from Mackie (2004).

Features	Oligotrophic lakes	Mesotrophic lakes	Eutrophic lakes
Lake basin shape	U-shaped, on granitic bedrock	V-shaped, littoral zone prominent	V-shaped, littoral and sublittoral zone established
Depth	Very deep with high O_2 in the hypolimnion	Moderately shallow, buildup of organic matter, low O_2 in the hypolimnion	Shallow, organic bottom, anoxic hypolimnion
Color	Blue or black	Greenish to brownish	Green (i.e., algal blooms) or brown from detritus buildup

iv. Habitats

Clench (1962) states that CMS thrives in cool- to warm-temperate climates in permanent ponds, lakes, and slow parts of rivers with mud, silt or sand substrate. According to Clench and Fuller (1965), CMS prefers areas with some vegetation. Stañczykowska, Magnin, and Dumouchel (1971) found CMS on a mix of soft mud, detritus, a variety of plants, concrete banks, silt, small, spring-fed ponds. Jokinen (1982) found all locations supporting *C. c. malleata* populations to be permanent bodies of water, ponds, lakes, reservoirs or slow-moving portions of rivers; the species was not found in any temporary water bodies. Based on my inventories and web photos, I have seen CMS on substrates ranging from the finest, inorganic silt and organic detritus, ooze, sand, rip-rap, and boulders in ditches, ponds, lakes, and creeks, all indicating that substrate type is not a limiting factor in their establishment (Figure 6-21). Unfortunately, few if any reports define the various grades of sediments. While everyone has a conception or definition of sediment types, these likely differ among individuals. The standard terms, arguably the most accepted, are those of Udden (1914) and Wentworth (1922), the latter of whom accepted much of the former's definitions; these have become known as the Wentworth Scale. Table 6-6 is a compilation of their terminologies and classifications with definitions. Mud is generally accepted as a mixture of water and soil, silt, and clay. Unless one carries sieves with openings down to 0.25 mm, one can probably eyeball the grade to 0.5 mm particle size. But classification requires sieving the sediments down to 0.5 mm or settling a core sample in a graduated cylinder for smaller (e.g., fine sand, silt, and clay) particles. Applying the grades and classes to Figure 6-21, I interpret a–h as follows: (a) predominately silt with some submersed vegetation; (b) predominately detritus with coarse organic material; (c) predominately sand with some gravel and large organic debris; (d) mix of boulders, cobble, and gravel with silt between, and some attached algae; (e) predominately filamentous algae covering cobble; (f) predominately silt and coarse organic materials; (g) boulders with submersed vegetation; (h) and boulders and cobble with sand and silt.

Table 6-6. Substrate particle size terms and classification schemes of Udden (1914) and Wentworth (1922).

Grade Terminology		Classification Scheme	
Particle size (mm/inches)	**Grade**	**Classification**	**% Composition**
>256/>10	Boulder	Coarse sand	>25% very coarse sand, <50% other grades
64/2.5	Cobble	Sand	>25% very coarse sand, coarse and medium sand, <50% fine sand
4/0.16	Pebble/gravel	Gravel	>50% fine sand, or <25% very coarse sand, coarse and medium sand
2/0.08	Granule	Very fine gravel	>50% very fine sand
1/0.04	Very coarse sand grain	Sandy loam	>25% very coarse sand, coarse and medium sand
0.5/0.02	Medium sand grain	Fine sandy loam	>50% fine sand or <25% very coarse sand, coarse and medium sand
0.25/0.10	Fine sand grain	Sandy clay	<20% silt
0.125/0.005	Very fine sand grain	Loam	<20% clay, <50% silt
0.0625/0.0025	Silt particle	Silt loam	<20% clay, >50% silt
0.004/0.00016	Clay particle	Clay loam	20–30% clay, <50% silt
		Silt clay loam	20–30% clay, >50% silt
		Clay	>30% clay

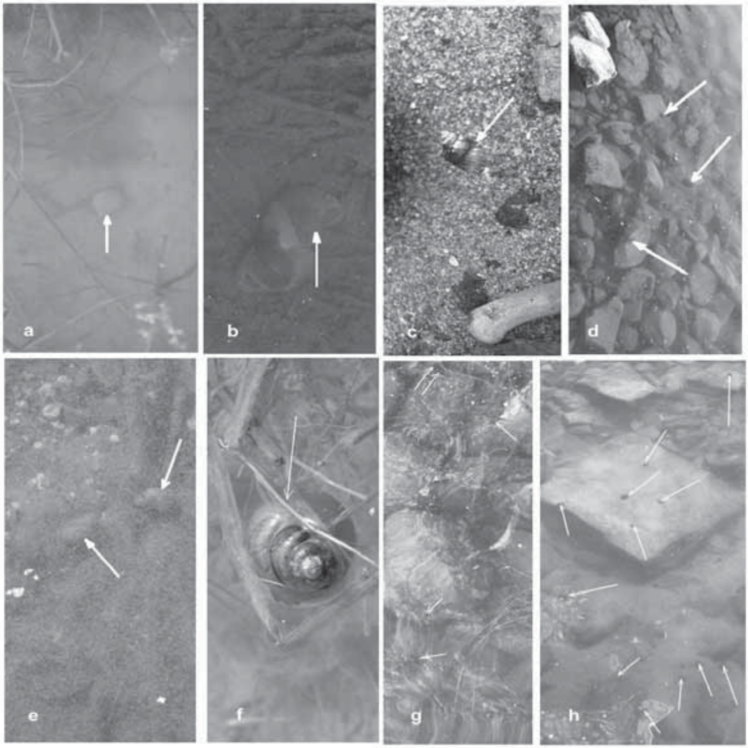


Figure 6-21. Range in substrate types occupied by *C. chinensis*. (a) murky water with flocculant silt, from photo 7888513, by Hyun-tae Kim; (b) organic detritus, from photo 38659436, by Hyun-tae Kim; (c) sand, from photo 99554948, by Erik Erbes; (d) boulders, cobble, and pebble, cropped from image courtesy of Jamie Delanie; (e) gravel covered with filamentous algae, from photo 43624667, by Rod; (f) coarse and fine organic matter, from photo 70953936, by Tia Offner; (g) boulders with *Potamogeton* between; and (h) boulders. (a, b, c, e, f) cropped from photos listed in Appendix C. (d, g, h) cropped from images courtesy of Jamie Delaney. Arrows point to *C. chinensis*.

Therriault and Kott (2002-2003) found minimal fluctuations in all water chemistry variables in all 11 CMS locations, and emergent plants were common at many sites in Southern Ontario. The Deer Creek CMS population was significantly larger than the Lakeside Park population, the difference attributed to the sizes of the bodies of water. They reasoned that Deer Creek Reservoir has a larger surface area and greater mean and maximum depths than Lakeside Park Lake, thereby providing more overwintering habitat. The difference in population densities did not appear to result from different eutrophication levels because Lakeside Park is much more eutrophic than Deer Creek Reservoir. Moreover, a comparison between population densities over rocky and sandy substrates at Deer Creek Reservoir indicated no significant difference in densities between the two substrates over the summer sampling period in the littoral zone. Other populations were found on mud, rock, sand, mud and clay, mud and muck, and rock and sand.

CMS is not limited by substrate type. Jokinen (1982) often recorded higher species diversity in lakes with large surface areas than smaller ones. Among all the variables listed in Table 6-4 and substrate type, Therriault and Kott (2002-2003) found the best correlation between CMS population density was with surface area. However, while the surface area is an expected significant correlation, it may be related more to the substrate area available for feeding and migrations to deeper water. Figure 6-22 illustrates the reasoning behind this hypothesis. The hypothetical bathymetries of two lakes are provided: (a) with some very steep slopes and little shoreline for CMS to populate, and (b) with the same surface area as (a), but very different bathymetry in the 1- to 3-m depths. Only the 1- to 3-m depths are relevant, assuming CMS occurs mainly in the 1- to 2-m depths in summer and fall and 2- to 3-m depths in fall and winter, and ice thickness is 0.5–0.75 m in winter (see earlier discussions). There is more area for CMS habitat in (b), even though it has the same surface area as (a). To reiterate, because ice thickness is < 0.75 m, even in the 47° North latitude in Canada, the reason for CMS to migrate into the 3-m depth in any water body to avoid freezing is questioned. The deepest that the snails need to move to avoid freezing is 2 m.

Kurihara and Kadowaki (1988) stated the *C. japonica* avoids soils that bear rice plants and weeds, preferring soils without higher plants. Their feeding experiments revealed that the snail consumes plenty of bacterial materials, such as detritus and sludge compost, suggesting that the snail's sewage sludge produced from wastewater-treatment installations could be decreased if it is applied to paddy fields sludge compost. The occurrence of

JMS in organic mud in Black Lake in Jokinen's (1982) study supports its predilection for muddy, organic substrates.

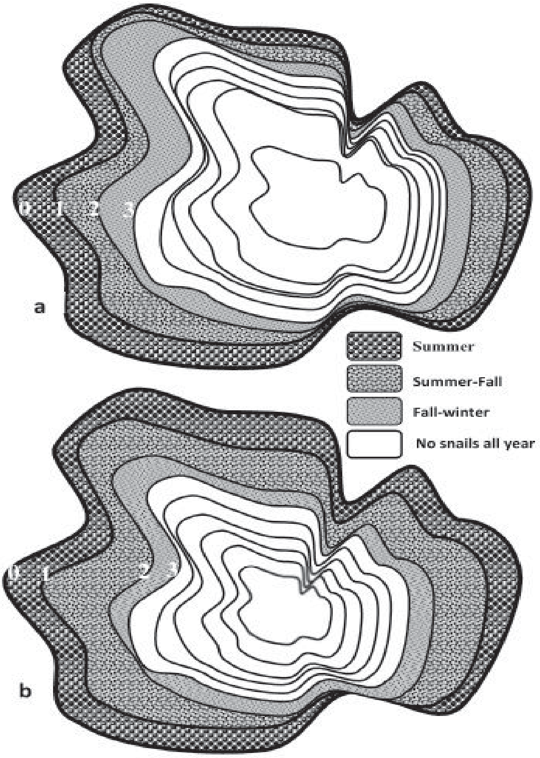


Figure 6-22. Hypothetical bathymetries of two lakes with the same surface area but different depth profiles. 0 to 3 m depths are shown; depths 4 to 8 m (not labeled) in both lakes are assumed to be devoid of *C. chinensis* all year.

I. Requirements

A requirement is defined herein as an element or compound and its amount vital to sustaining a viable population. It has a range of values, from a minimum (or lower threshold) to a maximum (or upper threshold), between which is the ideal level for the certainty of population establishment by its rank among levels of other variables. Inherent in this definition is that the requirements should be based on measurements under natural field conditions because each variable interacts with other variables. Consider the lake as a soup bowl containing a broth of elements and compounds. The broth is what makes the milieu "tasteful" (to invoke the snail's osphradial function) to the myriad organisms, although one element may override others. Also, there are temporal fluctuations in the values of many elements and compounds. pH (H^+, hydrogen ions) is a good example; pH rises during the day because of photosynthesis and drops during the evening. The respiration rate of organisms consumes DO faster than plants produce it.

Further, the amount of change in pH depends on the water's buffering capacity (alkalinity). The lower the alkalinity (e.g., bicarbonate ions), the greater the fluctuation in pH; the higher the alkalinity, the more stable the pH. Temperature also affects the solubilities of many compounds, like DO, which increases in solubility with decreasing temperature. The amount of DO affects the solubilities of other compounds, like iron (Fe); Fe^{+++} (ferric iron) is present in freshwaters as ferric phosphate ($FePO_4$), an insoluble oxidized compound, and Fe^{++} (ferrous iron) is present as ferrous phosphate ($Fe_3(PO_4)_2$), a reduced iron-soluble compound.

Because of the myriad potential interactions, like those just described, the results of laboratory bioassays that isolate particular elements or combinations of elements to determine thresholds usually cannot be extrapolated to the natural environment. These become tolerance values, as discussed in the next section. When the lower and upper threshold values are exceeded, the element or compound becomes toxic. The degree of toxicity depends on the amount and the rate of change of the element.

Applying these concepts to *C. chinensis* and *C. japonica,* no study demonstrates the unequivocal requirements of either species for their survival or establishment of populations. The studies described in the previous sections give lower and upper threshold values within which they have been found in North American waters, but caution needs to be exercised in interpreting them as absolute lower and upper threshold limits. More surveys are needed in waters to expand the ranges given in Table 6-4. For buffer variables (pH, calcium, magnesium, alkalinity, total hardness) the threshold values given in Table 6-4 are provisionally provided and should not be taken as absolute values because they change temporally (e.g., hourly) and spatially (e.g., depth), as previously forewarned. Harman (1974) gives lower and upper values for several gastropods. Still, the only viviparids listed are *V. georgianus* and *C. decisum*. Both fall within the pH and alkalinity values in Table 6-4 (no data are given for the other buffer variables).

The lower and upper threshold cation and anion values published for waters in Europe and Asia fall mostly within the ranges given in Table 6-4 (Collas, Breedveld, Matthews, van der Velde, *et al.* 2017; Matthews, Collas, Hoop, van der Velde, *et al.* 2017). Some exceptions for the occurrence of CMS in Asia (Taiwan) are pH 4.0–9.0, Ca < 2 mg^{-L}, and conductivity at < 30 µS cm^{-1} in Taiwan, all individuals within which were short-spired (Chiu, Chen, Lee, Chen *et al.* 2002; Matthews, Collas, Hoop, van der Velde, *et.al.* 2017), perhaps indicating sublethal effects.

No data, especially for total phosphorous and chlorophyll a, delimit the trophic requirements for either species. A useful metric for measuring trophic status is Secchi depth. Values < 2 m indicate eutrophy, 2–5 m, mesotrophy, and > 5 m, oligotrophy (Mackie 2004). Matthews, Collas, Hoop, van der Velde, (2017) listed a range of 0.3–0.95 m for the occurrence of CMS, indicating eutrophy. However, based on other trophic-related conditions described previously (e.g., Table 6-5), it appears CMS (and likely JMS) occurs in all trophic states. One remaining variable to discuss is the lower threshold value of DO for each species. Carbon dioxide is also a requirement, but it is more soluble in water than oxygen and can become indirectly toxic at high levels (e.g., by lowing the pH, thus increasing the H^+ content) in the water, or indirectly toxic in the sediments directly (e.g., production of methane gas CH_4) as discussed in the next section.

There are limited data on DO requirements for CMS and JMS. Jokinen (1982) gives 7.0–11 mg^{-L} for the range of DO in Connecticut waters. Two DO sources occur in freshwater: (a) from the atmosphere and (b) photosynthesis by algae and submersed vegetation, the former contributing much more than the latter. The diffusion rate of oxygen from the air into water varies with the pressure difference across the air–water interface. The greater the difference in partial pressures, the faster the rate of diffusion across the interface. The atmosphere has 21% oxygen, and carbon dioxide has about 0.0014%, yet carbon dioxide is 33 times more soluble than oxygen. Hence, carbon dioxide is more abundant in water than is oxygen. This inverse relationship results in more or less mirror image depth profiles; when CO_2 is high, DO is low. Implicitly, removal of CO_2 will result in higher DO, as in the process of photosynthesis, which can be expressed simply:

$$CO_2 + H_2O \rightleftharpoons CH_2O + O_2$$

Because the atmosphere has very low levels of CO_2, most of it is generated from the decomposition of plants and other organic materials in freshwater. The greater the amount of organic matter, the greater the production of CO_2 and the less DO because bacteria use it in the decomposition process. Temperature greatly affects the solubility of both gases, their solubilities increasing with decreasing temperature, and vice versa. These relationships result in different vertical profiles in lakes with different trophic statuses, as illustrated in Figure 6-23. Oligotrophic lakes, with little to no organic accumulations, have a DO profile exhibited in Figure 6-23a. The slight decrease in DO is due to increased temperature but is still 100% saturation at all depths. As shown in Figure 6-23c, eutrophic lakes have anoxic hypolimnia due to massive accumulations of organic material. Oxygen levels increase above the metalimnion, rising to higher levels. Supersaturation in the epilimnion of eutrophic lakes can occur due to higher algal productivity. The DO profile in mesotrophic lakes (Figure 6-23b) is intermediate between oligotrophic and eutrophic lakes. The significance of all this is that DO content should not be limiting to mystery snails in lakes of any trophic status because the epilimnion, where CMS and JMS live, is usually 100% saturated or even supersaturated with DO.

The minimum level of DO for CMS and JMS has not been determined, but in most littoral and sublittoral zones of lakes, DO should be readily available during the summer. During the winter, DO levels in these zones may drop to lethal levels in eutrophic lakes with substantial macrophyte biomass; this will depend on the activity levels of the snails and the exposure time. However, the DO levels in streams and ponds may vary considerably throughout the year, depending on stream productivity and land use. Haak (2015) examined the effect of temperature on the oxygen consumption rate (mg O_2^{-Kg-Hr}) of CMS (adults > 22.4 mm) and found the highest rate at 20°C (187.9), the lowest at 27°C (74.0), and snails were still active at 12°C (173.2). He did not test the rates at temperatures lower than 12°C.

Of the physical attributes, temperature is a key driver of the solubilities of chemicals and the onset and termination of reproduction; rates of growth and metabolism; and levels of activity, behavior, and competition. According to Li, Wu, Lu, Zhang, *et al.* (2013), the optimal water temperature for *C. chinensis* to grow and develop is between 20–28°C; it hibernates while the water temperature is lower than 10–15°C or higher than 30°C.

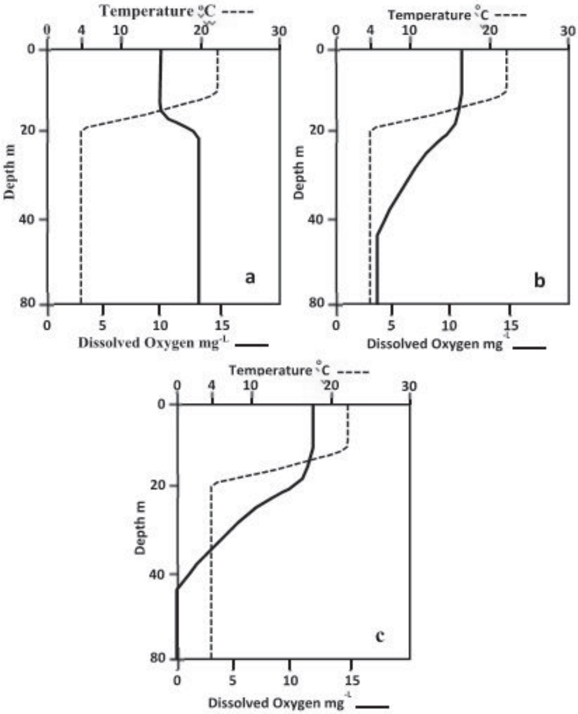


Figure 6-23. Dissolved oxygen profiles in (a) oligotrophic, (b) mesotrophic, and (c) eutrophic lakes with the same depth and temperature profiles.

J. Tolerance and Toxicity

If the lower and upper threshold values of an element (or compound) are exceeded and half the number of organisms dies within 96 hrs (i.e., LC_{50}), the element is considered acutely toxic. If the threshold values are marginally exceeded, the element may become chronically toxic by slowly eroding the physiological processes to the point where the organism eventually succumbs; this process may require several weeks. Chronic toxicity can be directly lethal but is more commonly sublethal by interfering with growth, reproduction, respiration, excretion, behavior, etc. For freshwater snails, which must maintain shell integrity, the buffer variables, especially pH, are the most proximate constraints.

The tolerances discussed below include chemical stressors, such as excessive levels of H^+, low alkalinities, DO, and levels of nutrients, metals, and organic pesticides. Physical stressors include temperature, desiccation, and silt loading.

i. Chemical Stressors

a. pH and Alkalinity

The importance of pH and alkalinity to molluscs has been recognized for several years (e.g., Wurtz 1962; Harman 1974, and references therein). Alkalinity and pH studies on freshwater molluscs (pulmonates, prosobranchs, and bivalves) by Rooke and Mackie (1984), Servos and Mackie (1986), and Mackie (1987) demonstrated direct effects, such as H^+ toxicity and metal toxicity, and indirect effects, such as changes in shell morphology, shell composition, decreased growth, and decreased reproduction. These have community-level effects (e.g., elimination of sensitive species, decreased diversity and production, changes in functional feeding groups). The impacts to lakes include reductions in the biotic carbonate pool, cycling of $CaCO_3$, and the lake's buffering capacity.

The effects of pH on molluscs were well demonstrated during the height of acid precipitation deposition studies in the 1970s and 1980s. McKillop and Harrison (1972) showed that most pulmonates had high densities in hard and medium water. In contrast, the prosobranchs *A. limosa* and *C. decisum* showed a reverse pattern, with the highest densities in pH 5.9–6.7. water and very low densities in pH 6.8–8.4. Most pulmonates showed a slower individual growth rate in soft water and a lower proportion of large individuals.

Servos, Rooke, and Mackie (1985) held the prosobranch *A. limosa* through the summer in cages in acidic lakes (pH 5.78–5.89) and reported slower growth than those held in less acidic lakes (pH 6.03–6.84). Moreover, egg development by *A. limosa* in the laboratory was impaired at and below pH 5.0 and delayed at pH 5.5 relative to pH 6.0. Hence, the recruitment failure and elimination of *A. limosa* in acidifying lakes may be a result of reduced summer growth and/or impaired development of the eggs.

Servos and Mackie (1986) examined the effects of natural pH depression using artificial channels to manipulate pH levels while minimizing confounding factors such as metal mobilization from aquatic sediments. The addition of sulfuric acid extended and exaggerated the natural pH depression (from pH 5.8 to 4.8) to as low as pH 3.5 over 5 days. The survival and reproduction of *A. limosa* were not affected by exposure to short-term pH depressions (e.g., 5.8 to 4.8; 4.8 to 4.3) in three south-central Ontario streams during spring snowmelt. However, short-term spring pH depressions appear to have minimal effects, at least on some prosobranchs. Their results suggest that recruitment failure and elimination of *A. limosa* from acidifying lakes noted in other studies do not directly result in short-term pH depression during snowmelt.

Ribi, Mutzner, and Gebhardt (1986) evaluated the relationship between soft water in Lake Maggiore (3.5 mg $CaCO_3^{-L}$) and shell morphology and population dynamics of the operculate *V. ater* compared to those in Lake Zfirich (11.5 mg $CaCO_3^{-L}$), Switzerland. The low calcium concentration of the water resulted in shell dissolution in Lake Maggiore. The snails in Lake Maggiore were smaller, suffered higher mortality, and had a shorter life span than those in Lake Zfirich.

While the impacts of lake acidification on molluscs have been demonstrated, molluscs contribute or return some alkalinity from dead, dissolving shells. Rooke and Mackie (1984) demonstrated dead mollusc shells (*A. limosa*, *Campeloma decisum*, *Euglesa casertana*) resulted in more stable alkalinity concentrations than the same species in other aquaria with no molluscs when all received additions of natural acid rain (pH 4.1). Non-molluscan invertebrates liberated acid-neutralizing materials from the sediments, but the source was quickly depleted; they purported a potential role for molluscs in the sources and cycling of carbonates in acidifying environments.

Definitive studies to examine the impact of high H^+ concentrations (low pH) and low alkalinities on CMS and JMS have yet to be done and are needed to help determine the potential for population establishment and spread in low-pH and low-alkalinity waters. Jokinen (1982) reported CMS and JMS at pH 6.4, but the effect of this pH level on growth and recruitment needs to be determined, along with their tolerance to lower pH levels. As stated earlier, pH in low alkalinity waters fluctuates widely during the day and would be elevated if measured in the afternoon.

b. Dissolved Oxygen

Fox and Taylor (1955) demonstrated that organisms tolerant of hypoxia (e.g., pollution indicators *Chironomus* larvae and *Tubifex* worms) are quickly killed in waters receiving pure oxygen, but many gastropods proved to be tolerant of 100% oxygen at atmospheric pressure (0), living as long as in aerated water with 21% oxygen. Unfortunately, the lower and upper threshold levels of CMS and JMS have not been determined. Harman (1974) lists the DO range of the viviparid *V. georgianus* between 1 and 8 mg^{-L}, suggesting it could survive lower than 1 mg^{-L} for at least a short term. My observation of *C. chinensis* in my fishpond (1.5-m, 5-ft deep) revealed the species could not survive anoxia under the ice for one to two months. The pond went anoxic sometime in January after a squirrel chewed the air supply hose to the pond. This was not noticed until mid-February, and several dead individuals (as well as about 30 goldfish) were found in March after the ice had melted. However, at least three survived (see the largest in Figure 5-4b).

c. Carbon Dioxide

Carbon dioxide exists in most freshwaters only between pH 3.6 and 8.4; between this range, as pH decreases, CO_2 increases, and as pH rises, carbonate alkalinity rises. Below pH 3.6, CO_2 is evolved; above pH 8.4, it forms monocarbonates. Implicit in these reactions is that the CO_2 level in water is rarely directly toxic to organisms. Not surprisingly, snails occur throughout the entire range of CO_2 levels in the water, between 0 and 43 mg^{-L} (Harman 1974). However, the solubility of CO_2 depends on water temperature and atmospheric pressure (Wiebe and Gaddy 1940).

CO_2 levels in the sediment can be indirectly toxic, depending on the amount and depth of organic matter and decomposition by carbon bacteria, which can evolve methane gas directly toxic to benthic organisms. This decomposition process is often accompanied by sulfur bacteria, which reduce sulfates to hydrogen sulfide, H_2S, which is also toxic to benthic organisms. One of the main pathways for sulfide toxicity is the inhibition of cytochrome *c* oxidase, the terminal enzyme in aerobic respiration (Bagarinao 1992). Mackie (2004) describes and illustrates the carbon and sulfur cycles and the reduction processes and species of bacteria involved in anaerobic sediments; he describes sulfide as an environmental factor, where sulfide tolerance and adaptations limit sulfide toxicity in benthic aquatic organisms

David, Pettit, and Edmund (2020) assessed the effects of CO_2-induced acidification on *V. georgianus* in terms of growth, mortality and shell repair over 12 weeks. They hypothesized that at the lower pH treatments, *V. georgianus* should exhibit lower growth rates, higher mortalities, and longer shell repair times. They found snails required a longer time to complete shell repair at pH 6, yet these individuals exhibited similar growth rates to their cohorts in control (pH 7.3) and pH 6.8 treatments, which ended their shell repair faster, concluding no relationship between growth rate and shell repair.

d. Metal Toxicity and Bioaccumulation

An increase in hydrogen ion concentration in lakes usually increases levels of metals, especially cadmium, aluminum, zinc, and lead (Wurtz 1962; LaZerte 1984). These metals can be toxic to molluscs at high enough concentrations (Wurtz 1962; Mackie 1989) and directly eliminate them from contaminated lakes. Mackie (1986) found *Euglesa casertana* to be more tolerant of Cd, Al, and Pb than *Amnicola limosa*. However, LC_{50} values for each metal are at least an order of magnitude greater than measured in any acidifying lakes in Ontario. Moreover, the metals (Al, Cd, and Pb) used in the laboratory bioassays were mainly inorganic forms, which are more toxic than the organic forms that dominate most low-alkalinity lakes (Lazerte 1984). Wurtz (1962) concluded that snails containing hemoglobin (e.g., pulmonates) are more tolerant of Zn than those with hemocyanin (e.g., viviparids).

Kurihara, and Suzuki (1987a), and Kurihara, Suzuki, and Moriyama (1987b) examined the incorporation of heavy metals on the growth of newborn CMS due to the application of reed-sewage sludge (composted *Phragmites* sp.) compost on rice paddy fields. The biomass and growth of the young snails in paddy soil with compost were greater than those in soil without compost. Zn and Cu levels in the body tissues were extremely high compared to paddy soil surrounding the snails. They reasoned the snails ingest sewage sludge, which is a main organic component of the compost. The sewage sludge often contained large amounts of Zn and Cu, suggesting CMS may help eliminate sewage sludge and Zn and Cu in paddy soil with applications of composted sewage sludge.

Tornimbeni, Galvez, Triffault-Bouchet, Gaëlle, *et al.* (2013) estimated concentrations of heavy metals in *C. chinensi*, to describe their relationship to values of metals in sediments. The overall common trend in the heavy metal concentrations (mg^{-Kg} dry tissue) was of the following order: Fe > Mn > Zn > Cu > Ni > Pb > Cd > Cr, or 224.3 > 68.8 > 56.9 > 10.8 > 1.05 > 1.0 > 0.6 > 0.3, respectively. Biota-sediment accumulation factors showed that *C. chinensis* cannot be used as a bioindicator of heavy metal pollution and exposure in the Canadian lakes where it is present. The lack of correlation between tissue levels in CMS from rice-paddy fields was also reported by Kurihara and Suzuki (1987); the ratios of paddy soil levels to tissue levels recorded were (in µg^{-g} dry tissue) in almost similar order: Fe (29,700:271), Mn (365:31.3), Zn (108:703), Cu (20.1:703), Cr (18.3: trace), Ni (11.6:trace), and Cd (0.40:0.73).

Elements are classified as toxic, beneficial, or essential for living organisms, including humans. The metal elements considered essential to humans are Na, K, Mg, Ca, Mn, Fe, Co, Cu, Zn, and Mo (Zoroddu, Aseth, Crispon, Medici, *et al.* 2019). Zoroddu, Aseth, Crispon, Medici, *et al.* (2019) classify H, C, N, and O as bulk and organic elements. Trace elements are essential elements and include Mn, Fe, Cu, Zn, Se, Co, Mo, and I. Macro-minerals are also essential and include Na, K, Mg, Ca, Cl, P, and S. Essential elements for human life can be toxic if the dose is too high. Regarding toxicity, elements can be divided into two groups: those for which abundance or bioavailability is low, making them not necessary for life, and those elements for which adverse effects have been reported, which includes Tl (thallium), Pb, Hg, and Cd. The toxicity of the levels of elements to humans reported above for CMS depends on the dose, number of snails consumed, and many other factors too numerous and complex to be included here. See Zoroddu, Aseth, Crispon, Medici, *et al.* (2019) for these complexities.

Haak, Stephen, Kill, Smeenk, *et al.* (2014) tested the efficacy of copper sulfate and rotenone as potential control chemicals for eliminating adult CMS using laboratory bioassays. All 10 snails survived exposure to 1.25 mg^{-L} copper sulfate solution, 90% survived exposure to 2.50 mg-L copper sulfate solution, and 80% survived exposure to 5.0 mg^{-L} copper sulfate solution. See discussion for rotenone under pesticides.

e. Pesticides

Studies on the effects of pesticides on mystery snails are limited. Haak, Stephen, Kill, Smeenk, *et al.* (2014) tested rotenone as a control agent. They found all 50 snails survived 72-hour exposure to rotenone-treated lake water, and 96% survived 72-hour exposure to predetermined rotenone concentrations of 0.25, 2.5, and 25.0 mg/L. Rotenone and copper sulfate are unlikely to be successful unless they penetrate the operculum or the shell at higher concentrations than were tested.

ii. Physical Stressors

a. Temperature

Haak (2015) cites unpublished thermal tolerance data of *Bellamya chinensis* having a wide temperature tolerance with adults surviving acute heating to approximately 45ºC and freezing water temperatures for > 24 hours. He observed no reproduction at water temperatures ≤ 12ºC. Collas, Breedveld, Matthews, van der Velde, *et al.* (2017) gives 0.0 to 30ºC as a range for the establishment of CMS in North America and encompasses a range of 19.0 to 21.4ºC in the Netherlands.

Koopman, Collas, van der Velde, and Verberk (2016) followed up on the hypothesis that higher oxygen levels should raise the heat tolerance of an animal. In contrast, lower oxygen levels reduce its heat tolerance. They assessed the heat tolerance of four lung-breathing pulmonates and two gill-breathing operculates under hypoxia, normoxia, and hyperoxia as well as the extent to which oxygen can lower or increase heat tolerance under different modes of respiration. They found hypoxia lowered the heat tolerance in three of the four pulmonates, and hyperoxia did not increase the heat tolerance in any of the four pulmonates. *Bithynia tentaculata* closed their opercula during heat treatment and survived. These results suggest hyperoxia may increase heat tolerance in gill-breathers, like viviparids.

Burnett, Pope, Wong, Haak, *et al.* (2018) attempted to identify both lower and upper thermal tolerance limits of *C. chinensis* in a laboratory setting. They exposed groups of wild-caught *C. chinensis* to either extremely high or low-temperature treatments. Despite exposing individuals to freezing temperatures for extended periods, they were unable to identify a lower temperature limit. The upper-temperature tolerance limit was between 40 and 45°C. Burnett, Pope, Wong, Haak, *et al.* (2018) suggested this result indicates that some hot water management techniques may successfully prevent the spread of *C. chinensis* among waterways. However, the lethal temperature range far exceeds the upper thermal tolerances of most aquatic organisms. Among the few applications of hot water treatment to control invasive species is for Zebra Mussels, but only in industries capable of using thermal backflushing (Claudi and Mackie 1994; Mackie and Claudi 2010).

Kurniawan, Sato, and Yasuda (2018) showed that the rate of excreta by CMS was affected by temperature, which influenced rice plants’ performance.

Although the effects of the snails and temperature differed among different plant performance measures, high temperatures (26.5–28.9°C) led to decreased rice performance due to reduced production of excreta by snails.

b. Desiccation and Air Exposure

Strachan, Chester, and Robson (2015) describe different mechanisms for invertebrates to survive periods of desiccation, namely physiological adaptations and or behavioral responses. A common behavioral response is dormancy, which they define as slowing metabolism to overcome a harsh environment, including long-term cessation of development, growth, and breeding. One type of dormancy used among gastropods is quiescence, which they define as a period of slowed metabolism to survive a period of limiting factor that resumes as soon as conditions become favorable. Another type of dormancy among gastropods is diapause, which slows the metabolism cued by seasonal cues and biological clock, driven by hormones, and this will not end when favorable conditions return but rather when diapause is broken.

Strachan, Chester, and Robson (2015) provide the key to identifying the dormancy type, the dormancy state, and the adaptation(s). Two cues are provided for quiescence (i.e., ends when conditions return): temperature and non-temperature. For temperature, estivation is the state for hot weather with two physiological adaptations, cryptobiois and anhydrobiosis, only the latter of which applies to mystery snails, which are able to dehydrate and rehydrate to survive. The other state is hibernation during cold temperatures; no physiological state is provided.

Havel (2011) reported *C. chinensis* as highly resistant to air exposure and can survive exposure to air for at least 28 days. They examined the tolerance of juveniles to air exposure in a series of field and laboratory experiments. The field and laboratory experiments indicated that individuals could survive exposure to air for at least four weeks, but larger juveniles were more resistant than smaller juveniles. The tolerance of small juveniles to air exposure appeared to be unaffected by temperature but was affected by humidity, with higher survival at 64% than 34% relative humidity. These results suggest that boats moving between lakes can readily transport CMS, particularly in cool, mesic environments.

Haak, Chaine, Stephen, Wong, *et al.* (2013) reported high mortality of CMS in a Nebraska reservoir following an extreme drought event, which coincided with abnormally hot weather. Still, they gave no details on the exposure period or temperatures. Unstad, Uden, Allen, Chaine, *et al.* (2013) tested the ability of individual *B. chinensis* to survive long periods of air exposure due to impoundment drawdowns using a laboratory setting. They found survival in air exposure of more than nine weeks with survivorship greater among adults (41–56 mm) than juveniles (< 40 mm). Several *B. chinensis* specimens responded to desiccation by sealing their opercula or burrowing into the mud substrate. They recommended that drawdowns alone may not be an effective means of eliminating *B. chinensis*.

Havel, Bruckerhoff, Funkhouser, and Gemberling (2014) performed simulated boater transport by placing snails individually in mesh bags, hung outdoors, and confined in a screen tent. The screen roof allowed exposure to both sun and rain. An on-site weather station recorded temperature, precipitation, and humidity. CMS survived 63 days and released viable young after 54 days of exposure. These results indicate that CMS should readily survive nine weeks of transport over land largely because of their thick shell and an operculum to seal off their internal tissues.

c. Silt Loading and Turbidi*ty*

Silt enters freshwater through various processes, including land uses, road runoff, erosion, recreational boating, wind and wave action, impoundments, and ice scouring (Kerr 1995). The impacts of silt on snails are varied: changes in water quality (e.g., taste, odor, temperature, DO levels); reduced light penetration, which impacts aquatic plants and invertebrates as reflected in species' tolerance levels, feeding activity, and nutrition; toxicity though direct and indirect mortality; movement; species composition and abundance; physiology; growth rates; etc. (Goodrich 1940, 1941; Heard 1970; Stansbery 1970; Kerr 1995). The impacts on CMS and JMS are unknown but likely are similar to those described by Goodrich (1941), Chutter (1969), Heard (1970), and Stansbery (1970), namely a reduction or loss of gastropod species.

K. Chapter VI Summary

The chapter begins with the life history assets of *C. chinensis* and *C. japonica*, beginning with direct larval development. *Viviparus viviparus* has three early stages through gastrulation and four later stages through early juvenile development. The embryonic development of *C. chinensis* and *C. japonica* have yet to be described in the details of early embryologists (1800s) on other viviparids. Development of all organ systems is described, including the nervous system and its torsion with loss of some organs, including one ctenidium, kidney, and gonad.

Different aspects of population dynamics of *C. chinensis* and *C. japonica*, begin with methodologies (e.g., quadrats vs. CMR, tagging, PIT tags), which have a lack of uniformity that affects the interpretation of results, especially when comparing traits of native, invasive, and nuisance species. The traits and their variations within each mystery snail examined are listed here.:

Density is estimated at (1-40 m^{-2}) for *C. chinensis*, no estimates *for C. japonica*, with nine factors identified that affect density.

Growth in width (W) and height (H) relationships for *C. chinensis*: Log W = 0.17 + 0.84 Log H; for *C. japonica*: Log W = 0.23 + 0.78 Log H

Biomass (W) and shell height (H) relationships for *C. chinensis*: Log W = -3.3829 + 2.4863 Log H, same for males, females, and juveniles. For *C. japonica*: None found

Life span is three to four years for male and four to five years for female *C. chinensis*; there are no estimates for *C. japonica*.

Fecundity (number of eggs), brood size (number in a brood sac), and natality (number of embryos surviving and born) are examined. Still, some data are not clear if numbers are for fecundity, brood size, or natality. Embryogenesis appears to begin at ~12°C. Numbers range up to 201 female^{-1} for *C. chinensis*; no estimate for *C. japonica*.

Survival is: 4–98% of eggs for *C. chinensis*. Adult survival for *C. chinensis* is 10–23% for females, 7–12% for males, but amount of immigration and emigration from study sites are largely unknown. Drought is a major factor in survival; many viviparids, including *C. chinensis*, emigrate to deeper waters during drought and immigrate back during wet periods. There are no estimates for *C. japonica*.

Mortality is estimated at 17–39% of previous population size during a drought event, but the specific duration was not specified. The mortality of viviparids has also been attributed to hypoxia.

Food and nutrition of *C. chinensis* are similar between males and females, except during spring breeding season when females eat more food. Food consists of primarily epiphytic algae and organic and inorganic elements with fatty acids.

Studies and reviews on the effect of the invasive *C. chinensis* on native species of gastropods and ecosystem properties have received mixed conclusions on its extent and kind of impact. Some conjecture impacts, some conjecture no impacts, a few experimentally concluded no negative impacts, and a few experimentally concluded negative impacts. The impact of *C. japonica* on native species has not been investigated. The topic of impacts needs to be revisited with experimental designs in natural habitats rather than laboratory mesocosm studies that isolate a select set of variables.

The parasites of *C. chinensis* in North America include trematodes (e.g., *Aspidogaster*, *Echinoparyphium*, and *Echinostoma* species) and nematodes (e.g., *Angiostrongylus* species), all of which are native to North America, and none of which are of concern to human health. The life cycles of each are reviewed and illustrated. All parasites that use *C. chinensis* and are harmful to humans are reviewed, and all are currently restricted to Asian populations of *C. chinensis*. Parasites of *C. japonica* as yet need to be identified.

The predators of mystery snails are grouped into triclads (turbellarians), leeches, crayfish, fish, birds, and mammals. Of these, the least concerning are triclads and leeches, both of which prey primarily on thin-shelled pulmonates that lack opercula for protecting internal soft parts. The remaining predaceous groups are capable of crushing the thicker shells of viviparids. Both invasive (e.g., *Orconectes rusticus*) and native (e.g., *Orconectes virilis*) crayfish prey on viviparids, up to ~4 cm shell height. Fish with molariform teeth (e.g., pumpkinseed sunfish, *Lepomis gibbosus*) are capable of crushing shells of young viviparids. While mesocosm studies demonstrate the ability of these groups to decimate viviparid populations, it has to be demonstrated in nature. Mallards appear to be one of the main bird predators of *C. chinensis*; while waterfowl have decimated *C. chinensis* in Europe, their ability to limit viviparid populations is unlikely. The brown rat is the small mammal demonstrated to prey heavily on viviparids, but it is unlikely to limit *C. chinensis* populations.

The biogeology of mystery snails describes the geological contributions to water bodies, the kinds of water bodies, and the main physical and chemical criteria that appear to support mystery snails based on their current distributions in North America. Several water chemistry variables are examined and discussed concerning the current distribution of *C. chinensis* in Canada and the United States. The habitat types and features that relate to occurrence and density are discussed. Lake area has been proposed as a correlation of population densities. Within this area, the area of available habitat within the shores of lakes is proposed as a better variable to explain occurrence and density in large lakes.

The elements and compounds required by mystery snails and their importance are explained. Six variables were selected, and their minimum and maximum values are offered as provisional lower and upper thresholds of the requirement for their occurrence in North American waters (Table 6-7). The tolerances and toxicities of several stressors are examined: pH, alkalinity, DO, carbon dioxide, metals and their bioaccumulation, and pesticides. Physical properties include temperature, desiccation and air exposure, and silt loading and turbidity. Unfortunately, nothing of the kinds and range of variables affecting *C. japonica*'s requirements and tolerances are known and need to be investigated before predicting the extent of invasion.

Table 6-7. Perceived minimum (lower threshold) and maximum (upper threshold) requirements of *Cipangopaludina chinensis* for six chemical variables and temperature in North American waters.

Thresholds	pH	Ca, mg^{-L}	Mg, mg^{-L}	Alkalinity, mg CaCO$_3$$^{-L}$	Conductance µS cm^{-1}	TDS, mg^{-L}	Temperature °C
Lower Threshold	6.4	7.1	2	22	74	48	0
Upper Threshold	8.7	102	25	308	1,505	978	30

CHAPTER VII

DISPERSION

A. Introduction

Dispersion is used here to mean dispersal or movement of organisms or propagules (embryos and juveniles in the context of prosobranch gastropods) between different localities or populations within water bodies or overland. Dispersal fosters range expansion when species successfully colonize new sites. Mollusc examples include the Chinese and Japanese mystery snails, the New Zealand mud snail (*Potamopyrgus antipodarum*) (Zaranko, Farara, and Thompson 1997), the Faucet Snail (*Bithynia tentaculata*) (Mills, Leach, Carlton, and Secor 1993), and the renowned zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis rostriformis*) mussels (Claudi and Mackie 1994; Johnson and Carlton 1996; Johnson, Ricciardi, and Carlton 2001; Johnson, Bossenbroek, and Kraft 2006; MacIsaac, Herborg, and Muirhead 2007; Mackie and Claudi 2010; Karatayev, Burlakova, Mastitsky, and Padilla 2015). Kelly, Lamberti, and MacIsaac (2009) use the Laurentian Great Lakes as an ideal example of the history, ecological impacts, economic effects, and social responses to biological invasions.

Dispersal is essential for establishing and preserving many species; it allows populations to pursue changes in the location of suitable habitats. Mackie (2004) and Enfjäll and Leimar (2009) attribute the dependence of dispersal strategies to several factors: species-specific traits, such as morphology (e.g., size of shell, operculum); social structure (e.g., “staying and helping,” Le Galliard, Ferriere, and Dieckmann 2005); life history traits (expounded below); environmental factors, such as climate (e.g., desiccation resistance traits); habitat quality (e.g., reservoir features, tolerance to pollution); and local densities of conspecifics (i.e., viviparid species). The ability to perceive and acquire information about different environmental characteristics varies greatly among organisms, which is likely to affect the evolution of dispersal (Enfjäll and Leimar 2009).

Myriad factors determine a species’ success in its newly found environment. These fall under three categories: (1) its inherited traits, or natural factors; (2) its opportunities or mechanisms for dispersal, which involves transporters, or vectors, both natural (e.g., water currents, birds, mammals) and anthropogenic factors, either intentional, unintentional, or malicious introductions; and (3) appeal or repulsion, in which further expansion of the species depends on its positive and negative impacts.

The species' inherited traits are developed over time in their native environment. Inherited traits influence life history characteristics. These characteristics include the species' reproductive habits (e.g., ovoviviparity or oviparity), life span, number of cohorts, natality, and surviving young, all of which contribute to population size. The species' physiological tolerances and requirements and the presence and density of competitors contribute to the species potential for establishment.

The opportunities for dispersal can be categorized as either natural dispersal vectors or anthropogenic dispersal vectors. Natural dispersal vectors include waterfowl, fish, and currents; the accessibility and frequency of the agents; and distance of dispersal by each vector. The species would benefit from having adaptations for both passive and active dispersal. Anthropogenic vectors are somewhat unpredictable, being concocted by the ingenuity of the human mind, whether selfish or required.

No freshwater gastropod species have a planktonic larval stage. Instead, embryonic development occurs within the egg, usually in a brood chamber, and a mobile juvenile emerges. In contrast, the eggs of pulmonate molluscs can be dispersed passively, but the eggs of prosobranch molluscs are either brooded by the female or deposited in large capsules. Hence, dispersal capabilities are even more restricted (Davis 1982).

Yamada (1989) found both direct and planktonic developers exhibited geographic differentiation in life history features (growth, egg mass, mortality). However, differentiation in the direct developer (*Littorina sitkana*) of embryos occurred over distances shorter than 30 km. In comparison, differentiation in the planktonic (*Littorina scutulata*) larval developer occurred over the 500 km distance that he examined. The planktonic developer exhibited similar seasonal patterns in individual growth and mortality, producing egg capsules containing a similar number of eggs in two of three populations; however, one population differed significantly in all these features from a distance (500 km) population. In contrast, *L. sitkana* from all three populations exhibited consistent population differences in growth and egg mass production. Yamada (1989) concluded that the planktonic disperser *L. scutulata* was physiologically similar over short distances (30 km) but not at distances of 500 km encountered in his study and that the direct developer *L. sitkana* is physiologically differentiated even over short distances.

Katoh and Frotz (2014) cite several studies suggesting that prosobranch populations may be genetically differentiated from pulmonate populations. They proposed the possibility of dispersal rates and levels of gene flow are potentially lower in freshwater prosobranchs than in freshwater pulmonates. This high genetic differentiation suggested to them that dispersal rates in freshwater prosobranch species are low, allowing populations to adapt to local environmental conditions without being swamped by gene flow (Yamada, 1989). Gene flow may also help explain the higher degree of endemism in prosobranchs than in pulmonates (Davis 1982).

The success of a species' dispersal to a new habitat depends on the quality of both the water and the sediment, the type of water body (ditch, marsh, wetland, pond, river, lake), food quality and quantity, predators, and competition. The dispersal range can be either intercontinental or intracontinental. Within intracontinental dispersal, one can expect extended introductions or expansion within its new habitat, especially in chains of lakes and tributaries of increasing order size (i.e., downstream dispersal). Expansions consist of the dispersion of organisms by natural vectors. In the past two centuries, introductions increasingly occurred by human transporting activities, intentionally or unintentionally, to an area where they did not occur (Souza 2010). Belatedly considered in some species success is their appeal for food (Mackie 2000b) as well as aquarium enthusiasts (Mackie 2000b) and fishpond enthusiasts that often result in banning the sales and exportation of the species. Repulsive species often impact the environment and economy, resulting in mortality of native species, alterations of community structure, costly revised industrial processes, or human health and recreational activities.

B. Dispersal Potential or Prowess

The dispersal potential is a species' prowess because of its inherited traits that increase its competency for expanding its range. It is based on natural factors that are easier to predict than anthropogenic factors because the human mind can often be devious, unintentional, or unpredictable. In addition, as Souza (2010) pointed out, in the 18th and 19th centuries, human beings achieved significant technological advances, accelerating the time for spatial and temporal distribution of organisms from one area to the next. Natural processes occur when native vectors cross biogeographic barriers, and geological scales can happen in short periods of a few years (Souza 2010). Species have been transferred over long distances by human innovations that facilitate eliminating or reducing natural barriers that previously separated ecosystems and maintained their integrity.

1. Natural Factors and Traits

Mackie (2002) examined the distribution of inherited traits among invasive species of molluscs and compared them to molluscan species at risk in North America. The traits included its reproductive potential, life span, size, physiological and ecological tolerances and requirements, dispersal mechanisms, or opportunities to determine a species' ability to establish populations, become abundant and widespread, and tolerate fluctuations in its new environment. Table 7-1 lists life-history and ecological traits. It ranks traits from a potentially invasive nuisance species to an invasive but benign species, modifying the traits in Mackie (2002) to distinguish between the two. For example, species that are dioecious, oviparous or ovoviviparous and parthenogenetic, iteroparous, and multivoltine with high fecundities and natality rates are more likely to become an invasive nuisance than species that are monoecious, ovoviviparous without parthenogenesis, semelparous, and univoltine, with low fecundities and natality rates. The key to the invasive traits, however, is dispersal ability. The greater the variety of dispersal mechanisms, the more likely a species will be invasive and a nuisance (Mackie 2004). Hence, based on reproductive traits alone, the potential for a species' dispersal ability can be ranked from high (e.g., ovoviviparity, high fecundity, high natality, multivoltine) to moderate (e.g., ovoviviparity, low fecundity, high natality, bivoltine) to low (e.g., oviparity, low fecundity, low natality, univoltine) (Mackie 2004). The dispersal mechanisms of the invasive molluscs are discussed in the next section. The life history traits are examined further in Chapter VII, Impacts, 1. Competition, to determine their potential role in explaining invasive species' invasiveness and nuisance levels in North American waters. Older invasive species are sometimes referred to as ex-invasive species relative to new invaders.

Table 7-1. Traits of invasive species that are potentially a nuisance or benign.

Trait no.	Life-history and ecological traits	Ranks from potentially invasive and a nuisance to potentially invasive and benign (> indicates survives as a benign invasive species)
1	Life span	(a) Short-lived (1–2 years) > (b) moderately long-lived (> 2–5 years) > (c) long lived (> 5 years)
2	Sex	(a) Hermaphroditism > (b) separate sexes
3	No. of generations per year	(a) Multivoltinism > (b) bivoltinism > (c) univoltinism
4	Lifetime no. of generations	(a) Reproduces twice or more in its lifetime > (b) reproduces only once in its lifetime
5	Parental care	(a) Oviparity > (b) ovoviviparity > (c) viviparity
6	Fecundity	(a) High numbers (> 162) > (b) low numbers of eggs (< 162)
7	Natality	(a) High survival of embryos (> 50%) > (b) low survival rate of surviving embryos
8	Development duration and rate	(a) Short development time (weeks) > (b) long development times (months or years)
9	Age at sexual maturity	(a) Early sexual maturation (same summer) > (b) late sexual maturation (≥ one year)

10	Adult size	(a) Adult size (< 2 cm) > large adult size (> 2 cm)
11	Ecological tolerances and requirements	(a) Hardy and tolerant (e.g., eutrophic indicator, wide range in buffer variables (e.g., pH 6.5–8.8) > (b) moderately hardy and tolerant (e.g., mesotrophic indicator), narrower range in buffer variables (e.g., circumneutral pH) > oligotrophic indicator, narrow range in buffer variables (e.g., ≤ pH 6.0)
12	Dispersal potential based on numbers of vectors	(a) Many dispersal mechanisms using a variety of natural and anthropogenic vectors > (b) mostly unintentional and intentional vectors > (c) mostly natural vectors

a. Reproductive Potential

Mackie (2002) and Mackie and Claudi (2010) examined and rationalize seven reproductive traits for dispersal potential:

- Its sexual state (e.g., separate sex, hermaphrodite, or parthenogenetic). Hermaphroditism and parthenogenesis reduce the risk of a species being eliminated during periods when it is difficult to find a mate and therefore increases its invasive potential.
- Its egg-laying habit (e.g., oviparous, ovoviviparous, viviparous). Oviparity generally results in larger numbers of eggs than ovoviviparity or viviparity, the latter of which is absent in freshwater molluscs.
- Its fecundity (number of eggs produced). The numbers of eggs produced by ovoviviparous and viviparous forms are limited by the internal volume of the female.
- Brood size (number of eggs surviving as embryos). Some eggs do not survive due to a lack of nutrition in yolks or failure of some organ systems to develop.
- Its natality (number of embryos surviving). Eggs can be fertilized either internally in the female and then laid or externally in the water. In freshwater molluscs, external fertilization occurs only in bivalves, and millions of eggs are produced, or at least orders of larger numbers than by oviparous forms with internal fertilization, or ovoviviparous forms, regardless of whether they are monoecious, dioecious, or parthenogenetic.
- Its annual frequency of egg-laying: univoltine (once per year), bivoltine (twice per year), or multivoltine (many times per year). The more times a species reproduces each year, the greater the potential for increasing its population size and providing more dispersal opportunities.
- Its lifetime frequency of egg-laying habits: semelparity (once in its lifetime) or iteroparity (more than once in its lifetime). Again, the more times a species reproduces in its lifetime, the greater the potential for increasing population size.

To put this into perspective, and based on these seven traits, the most likely successful dispersal for a species would be one that is hermaphroditic, oviparous, highly fecund, has a high natality rate, is multivoltine, and iteroparous. The species predicted to be least likely to achieve wide dispersal would be one that is dioecious, ovoviviparous, has a low fecundity and natality rate, is univoltine, and semelparous. These traits are examined later to assess the dispersal potential of CMS and JMS. Implicit among these traits, this needs to be emphasized: *the snails do not have a swimming stage.*

b. Life Span and Size

A species' life span and size affect dispersal potential because a longer-lived species has a greater opportunity to disperse, but its size limits this because smaller individuals are usually easier to transport than larger ones, at least within a taxon. However, smaller animals have shorter life spans than larger ones, at least in the Mollusca (Mackie 2002). Hence, small, short-lived molluscs have a greater dispersal potential than large, long-lived molluscs. For example, fingernail clams (family Sphaeriidae) have a greater global distribution than freshwater pearly mussels (family Unionidae). Mackie (2002) attributes two reasons for this trend. First, big is more noticeable than small, and the dispersal agent is more likely to unload a large hitchhiker sooner than a small one. Second, big also means heavy, and a vector would have to spend more energy, risk its own life, and transport itself and its "baggage" great distances. Perhaps the only exception to the size rule is intentional introductions by humans, as discussed above. In this instance, large is an advantage if the introduction is for food (e.g., CMS and JMS) or aquarists.

c. Physiological and Ecological Tolerances and Requirements

Guidance for the establishment of *C. chinensis* and *C. japonica* are provided in Table 6-7. Mackie (2002) suggests that each species has its physiological requirements; for molluscs, the critical variables are calcium, pH, alkalinity, DO, temperature, and turbidity. Similarly, each species has its ecological requirements for food and habitat. CMS and JMS have two feeding modes, filtering food from the water column immediately above them and feeding on deposited organic material (deposit feeding) within the sediments surrounding them. Waters that are relatively free of predation and parasitism ensure better survival. Substrates with organic detritus and waters with phytoplankton will enable the two modes of feeding. Physiological and ecological constraints vary within and from one environment to the next, and the ability of the species to tolerate the extremes in these variations will determine its population dynamics, and especially its nuisance potential—see Chapter VIII. Impacts, which uses physiological and ecological tolerances and requirements for risk assessments.

2. Anthropogenic Factors

Human activities are well-known factors in determining a species' dispersal, especially to nearby waters, usually unintentionally, such as overland transport by boats not adequately cleaned of attached vegetation.

a. Intentional Introductions

There is usually some rationale, right or wrong, for introducing a species. Some have success and meet their objectives with little or no impact on the environment and economy; some meet their goal but have collateral damage to the environment and economy. Courtenay and Taylor (1986) include in this category releases made to supplement extant species (i.e., stocking) to establish species beyond their historical ranges of distribution and other introductions made for some specified purposes (e.g., sport, forage). Usually, natural resource managers (and often federal, state, and provincial authorities) become involved. There are few statistics on intentional introductions of CMS and JMS, but considerable for fishes. Of the 743 native fishes known to inhabit the fresh waters of Canada and the continental US, at least 168 species had been transplanted via human activities beyond their natural ranges of distribution (Courtenay and Taylor 1986). Courtenay and Taylor (1986) reported as many as 58 species were probably moved as game species and perhaps were released unintentionally from bait buckets. A significant issue was the movement of mixtures of target species and non-target species into different drainage systems. Non-target species often were transplanted in this manner as incidentals, and Canadian waters were intentionally introduced as game species or unintentionally released bait fishes, underlining the importance of recreational fishing in the US and Canada (Courtenay and Taylor 1986).

Mills, Leach, Carlton, and Secor (1993) give an example of a "patriotic" citizen introducing common carp into the Hudson River and causing significant collateral damage, which Badiou, Goldsborough, and Wrubleski (2011) summarized as (1) increasing total suspended solids, sedimentation and erosion, (2) increasing water column nutrient concentrations, (3) increasing the biomass and altering the community structure of phytoplankton, (4) decreasing submerged macrophyte abundance, (5) decreasing large zooplankton, (6) decreasing benthic invertebrates, (7) reducing native fish diversity and abundance, (8) competing with waterfowl for food resources, and 9) altering contaminant cycling.

There are mollusc examples as well. Kew (1893) attributed the introduction of species of *Campeloma*, *Goniobasis* (= *Elimia*), *Somatogyrus*, *Bithynia*, and *Viviparus* into the Erie Canal, Mohawk River, and Schuyler's Lake by naturalists who saw a perceived need to improve diversity in the systems. As discussed earlier, CMS was collected in rice fields near Yokohama, Japan, brought to America by sailors, and then given to marketers in Chinatown, San Francisco (Stearns 1901). Their spread has already been described, and their impact is discussed later in Chapter VIII Impacts.

b. Unintentional Introductions

Courtenay and Taylor (1986) used unintentional introductions to include releases made unwittingly, probably the most problematic kind of introduction to control because the introducers are usually unaware of such releases' environmental implications. They included releases of unwanted aquarium species, and bait fishes, generally perceived as humane acts by the introducers. Some even dispose of the aquarium as litter simultaneously (Therriault and Kott 2002-2003).

Mills, Leach, Carlton, and Secor (1993) list four categories of unintentional releases: (1) aquarium (e.g., Banded Mystery Snail, *Viviparus georgianus*), (2) cultivation (e.g., water cress, *Nasturtium officinale*), (3) fish (e.g., goldfish, *Carassius auratus*); and (4) accidental (e.g., brown trout, *Salmo trutta*). Mackie (2000a) examined several species of freshwater gastropods and bivalves introduced through the aquarium trade and described their ecological and economic impacts but did not include any mystery snails.

Artificial impoundments, or reservoirs, are built for one or more reasons, including supplying drinking water; generating hydroelectric power; providing flood control downstream; implementing water storage to augment flow downstream during summer low-water discharges; providing irrigation for farmlands; and recreational activities such as swimming, boating, fishing, etc. (Mackie 2004). Impoundments are riverine systems superimposed on a terrestrial one; the river provides the initial materials—the water, the flora, and the fauna—for the new ecosystem. Reservoirs generally have a dendritic pattern to them, with many tributaries contributing water to the dammed area. The deepest area of a reservoir is generally near the dam, which may have one or more discharge levels. They slowly become functionally stable in ecosystem but not as stable as lakes because of seasonal or annual drawdowns and altering physical, chemical, and biological processes.

Reservoirs often feature novel combinations of native and introduced species, the latter becoming established, naturalized, or invasive. For example, viviparids are common in reservoirs (Chaine, Allen, Fricke, Haak, *et al.* 2012; Yanygina 2012, 2019; Stephen, Allen, Chaine, Fricke, *et al.* 2013; Haak, Chaine, Stephen, Wong, *et al.* 2013; Haak, Stephen, Kill, Smeenk, *et al.* 2014; Miller and Sytsma 2014). It has not been established whether they negatively affect native biota or ex-invasive species that might also be present or occupy niches made available during the transition of habitat conditions as reservoirs develop a stable ecosystem. Catford, Vesk, Richardson, and Pyšek (2012) demonstrated that relative richness and abundance of alien species indicate the contribution that alien species make to a community, explaining why invasive species thrive and often become dominant in ecosystems modified by humans. Pyšek and Richardson (2010) maintain that introduced species largely contribute to biodiversity loss, ecosystem degradation, and ecosystem service impairment. Johnson, Olden, and Vander Zanden (2008) showed that reservoirs harbor more invasive species than natural lakes and rivers in the nearby areas. While impoundments are anthropogenic conceptions with sound purposes for their creation, they have unintentionally become a causeway for dispersing native and alien species (Johnson, Olden, and Vander Zanden 2008). Havel, Lee, and Vander Zanden (2005) describe reservoirs as stepping-stones, acting to dispersal exotic species across landscapes. A variety of passively dispersing species has invaded reservoirs, spread through interconnected waterways, and then transported to nearby disconnected habitats.

Clements, Kohb, Lee, Meiera, *et al.* (2006) ascribe the importance of features for conserving the diversity of freshwater molluscs in China: (1) different habitats (e.g., catchment reservoirs, forest and rural streams, ponds, and canals), (2) key environmental factors (e.g., pH) that affect molluscan distribution, (3) biogeographical determinants (e.g., surface area) of molluscan richness within each habitat, and (4) habitat affinities of introduced species. They determined that area was the best predictor of molluscan richness across all habitats, inferring that the larger freshwater habitats require higher conservation priorities than smaller ones and that introduced species had high affinities for reservoirs.

For North American reservoirs, Havel, Lee, and Vander Zanden (2005) supported much of what Clements, Kohb, Lee, Meiera *et al.* (2006) ascribed for Asian reservoirs. They are more readily invaded than natural lakes because of their physiochemical properties, greater connectivity, and higher levels of disturbance. They argue that reservoirs typically have a high level of physical disturbance, solute loading, and unstable food webs that should enhance the invasibility of reservoirs over that of natural lakes. In addition, reservoirs may bridge gaps between standing water systems, thus facilitating movement across landscapes by homogenizing habitats and serving as stepping-stones for invasive species (Havel, Lee, and Vander Zanden 2005).

c. Malicious Introduction*s*

Chomel and Sun (2010) include invasive species as part of bioterrorism attributed to accidental or malicious introductions of foreign animal disease threats, such as avian influenza, foot and mouth disease, hog cholera, and West Nile virus. SARS-CoV-2, defined as the causal agent of the current global impact of COVID-19, allegedly introduced from China, is the most recent example of a malicious introduction.

Many freshwater molluscs are hosts of trematode parasites. Perhaps the most infamous is schistosomiasis, or snail fever, prevalent in developing countries but not in North America. However, a schistosome present in North America is *Trichobilharzia regenti*, which causes swimmer's itch in humans. The life stage that affects humans is the cercariae released from its snail intermediate host that uses its forked, tail-like appendage to swim and find its final definitive host, a duck. The larvae may accidentally encounter a swimmer's skin, penetrate the skin, and die in the skin immediately. In other words, humans are a dead-end in the life cycle of the trematode.

C. Dispersal Vectors or Opportunities

The vectors, or agents, of dispersal, can be passive or active, both of which have influential consequences for colonization, gene flow, and evolutionary processes (Bilton, Freeland, and Okamura 2001). Passive dispersal is movement using an external agent, like water currents or downstream drift. For gastropods, it results in the transfer of individuals to spatially discrete locations downstream. Hunter, Maitland, and Yeoh (1964, 27) describe an "authenticate case" of passive dispersal by the occurrence of a living marine operculate, *Littoritia littoralis*, in freshwater some 13 miles (21 km) from the sea.

Numerous vectors are available to organisms for dispersal over short to long distances. Some have a potential for dispersal; regionally, for example, by moving from lake to lake to eventually disperse throughout a province or state; intracontinentally, for example, within North America or Europe; or intercontinentally for example, from Asia to North America. Table 7-2 gives a comprehensive list of dispersal mechanisms, modified from Mackie (2002), to address the Viviparidae. Table 7-2 gives brief to detailed explanations of each mechanism's potential vagility in order of their alphanumeric coding.

1. Passive Vectors

Or, “go with the flow,” either by water currents or birds and insects to local water bodies or by flyways for migratory birds. Under A. Natural Mechanisms in Table 7-2, A1–3 are abiotic mechanisms, and A4–5 are biotic mechanisms.

a. Abiotic Mechanisms

Water currents and drifting are the most likely vectors for moving many invertebrates downstream. Mackie (2001) describes three kinds of drift: constant, catastrophic, and behavioral. Constant drift occurs at low flows and is represented by most taxa (e.g., amphipods, isopods, mayflies, stoneflies, caddisflies, and occasionally molluscs, such as limpets). Many insects can walk on water due to surface tension, the force that causes a layer of liquid to behave like a thin sheet. Similarly, small juvenile mystery snails can adhere by surface tension to the underside of the surface of the water. They can be transported short distances by laminar flow but lose contact in turbulent waters and fall back to the substrate.

Passive behavioral drift is an innate behavior usually with some diel periodicity (e.g., typically at night) associated with it and includes mostly insects and amphipods (Mackie 2001). Adams (1929) reported CMS in a pond in Fairmount Park, Philadelphia, Pennsylvania, that was probably introduced into the pond near Horticultural Hall with some goldfish. He suspects CMS migrated (e.g., attached to floating plants or logs) down a small stream that leads from the pond to the Schuylkill River, where it is now quite common near the mouth of this stream. This snail has been observed as far down the river as the Fairmount Dam, two miles below. Active behavioral drift involves the intentional movement of organisms due to density (Fonseca and Hart 2001) and competition for food and space (Richardson 1991). Some life history stages are drift-prone (Corkum 1978), avoidance of predators (Kratz 1996), and seasonal variations (Richardson 1991), with less drifting in winter than in summer (Naman, Rosenfeld, and Richardson 2016). Otherwise, moderate water currents are unlikely to move large viviparids downstream. The wind also comes into play, perhaps under cyclonic or hurricane forces. Waterspouts would include plankton organisms, but unlikely benthic organisms.

Catastrophic drift results from erosion of sediments with its organisms due to ice scour during large spring spate events or floodwaters. Included in the drift are logs and plants with attached invertebrates, including mystery snails.

Some invertebrates can migrate upstream, but usually under moderate flow conditions. Bishop and Hynes (1969) examined the extent of upstream movement by insects, especially mayflies. They attributed the mechanism for upstream movement by mayflies as largely positive rheotaxis (a response to the mechanical stimulus of a current of water) but positive skototaxis (movement of a motile organism to a dark area), the release of phototactic control probably governed the distance covered. In addition, they found greater movement occurred in areas adjacent to the banks than in midstream during the winter, but in summer, the midstream areas contributed most of the migrants. The upstream movement was of sufficient quantity and species diversity to recolonize dried-out or erosion-denuded areas. Rivera (2008) investigated whether an increase in water current created by culverts limits *C. chinensis* from invading further upstream; he found the current velocities in the culvert can hold the snails from moving upstream. However, his field studies found the snails were not as abundant as expected downstream in the creek and concluded no preference for upstream or downstream migration.

Table 7-2. Dispersal mechanisms available to Viviparidae for short-range (e.g., from nearby waters or water bodies within a province or state), mid-range (e.g., from waters within all provinces in Canada), and long-range (e.g., from ships or planes arriving in Canada or the US from Europe, Asia, South America, etc.) transport.

Dispersal Mechanisms	Potential Vagility
A. Natural Mechanisms	
1. Currents	Possible, if attached to floating debris or logs
2. Waterspouts	No
3. Wind	No
4. By insects, waterfowl, or mammals	Waterfowl are highly likely, some birds, e.g., gulls, mallards. See text
5. By fish or semi-aquatic vertebrates	Not likely

B. Unintentional Anthropogenic Mechanisms	
1. Ocean and freshwater vessels	No
Interiors (e.g., ballast tanks, fish wells) or exteriors (e.g., hulls) of large vessels and crafts of rivers and lakes	Possible if mud with snails is taken in ballast water; see text
2. Canals (irrigation and vessels)	Possible but not likely; see text
3. Reservoirs, artificial impoundments	Probable, as stepping-stones to natural bodies of water
4. Navigation and marker buoys and floats	Possible but not likely; see text
5. Marina and boatyard equipment	Not likely
6. Fisheries equipment (e.g., cages, nets, bait buckets), stocking, fishing activities	Possible but unlikely; related somewhat to trailered boats
7. Transport overland of boats, trailers, motors, anchors	Possible among attached plants and mud on anchors; see text
8. Amphibious and firefighting planes	No
9. Firetruck water	No
10. Commercial products (e.g., aquatic plants)	Possible, if disposed of in the wild
11. Aquarium releases	Yes; see text
12. Recreational equipment (e.g., floating docks, scuba equipment)	No
13. Litter (e.g., tires, grocery carts, aquaria)	Possible but unlikely
14. Scientific research	Possible
C. Intentional Anthropogenic Mechanisms	
1. Food	Yes, if cultured for food
2. Fishponds	Yes

b. Biotic Mechanisms

External transport (for example, feet and feathers) of the biotic vectors (A4, A5, Table 7-2), external transport (e.g., feet and feathers) is generally a more effective dispersal mechanism than internal transport via the digestive tract. Some fingernail clams can survive passage through the intestinal tract of waterfowl as extra-marsupial larvae, but internal transport is likely not prevalent (Mackie 1979). Large insects can carry small molluscs, like hydrobiids (Kew 1893) but are unlikely for viviparids unless a tarsal claw is wedged between a closed operculum and the shell of a newborn or juvenile snail. Also, only small size classes, possibly ~5 mm (newborn to young juveniles) of CMS and JMS, could be dispersed.

Cadée (1994) witnessed living *Hydrobia ulvae* emerging from feces of the shellduck *Tadorna tadorna*, indicating they survived the passage of the digestive tract. The numbers of *Hydrobia* observed alive in the shellduck's feces numbered in total 140 living specimens and 960 empty and/or broken *Hydrobia* shells. Viana, Santamaría, Michot, and Figuerola (2012) reported LDD of ingested propagules is an important determinant of population dynamics, community structuring, and biodiversity distribution at the landscape scale. They found that propagule dispersal patterns are determined by the migratory strategy of the disperser species, the region (or flyway) through which the disperser population moves, and the propagule characteristics (e.g., cysts vs. seeds). Waterbirds in particular may frequently link wetlands separated by hundreds of kilometers, contributing to the maintenance of biodiversity (Viana, Santamaría, Michot, and Figuerola 2012). The large geographic scale of the dispersal events may explain the distributions of CMS and JMS in remote marshes and ponds in North America.

Boag (1986) examined the dispersal pre-requisites of three pond snails, *Lymnaea stagnalis*, *Stagnicola elodes*, and *Helisoma trivolvis*, on birds' feathers. He examined four traits: (1) the size range of snails adhered to waterfowl plumage, (2) length of time snails remained to cling in a simulated flight situation, (3) survival time under such various flight conditions, and (4) differences among species of gastropod in these attributes. He found that those snails that adhered to the feathers were < 2.5 mm long in all three species; the proportion that remained to cling to the feathers declined sharply with time, with 6% (*L. stagnalis*) to 18% (*S. elodes*) remaining attached after 15 min of exposure; survivability declined with time exposed to the simulated flight conditions after 15 minutes, with 50% (*L. stagnalis* to 15% (*H. trivolvis*) still alive. Larger individuals tended to survive better than smaller ones for any given exposure time. Still, they also managed to fall off the feathers sooner than smaller ones with no snail more than 3-mm long recorded adhering to the feathers for more than four minutes. His results suggest that despite a low proportion of the snail population clinging to the feathers (< 1%) and the relatively high rates of loss or death after attaching, the probability of successful dispersal for distances up to 10 km remained high.

Wesselingh, Cadée, and Renema (1999) concluded avian dispersal of aquatic taxa is facilitated by a variety of factors, including mass occurrence in resting/foraging places of migrating birds, ways to attach to the birds and to overcome desiccation during flight, and easy reproduction from a single specimen when introduced into a new habitat. Birds, especially waterfowl, are the most probable natural vectors of CMS and JMS of the biotic mechanisms. As discussed in Chapter V under periostracum, smaller specimens of CMS and JMS have periostracal hairs (e.g., Figure 7-1), sometimes so dense that the rows are bristle-like and could function like Velcro strips. These hairs can attach to the barbs of the bird's feathers as they swim by or search for food among vegetation with snails attached. The dispersal by waterfowl would explain the occurrences of these snails in small ponds, marshes, wetlands, and other bodies of water that humans do not frequent. A search through the more than 2,200 observations of CMS and JMS in North America reveals an apparent preponderance of these snails in very small bodies of water. Indeed, they are the only other possible vector for their occurrence in my backyard fishpond (i.e., besides myself), which is visited frequently by mallard ducks (Figure 7-2a). The snails could also attach by wedging the tip of the feather between the shell and operculum. Three factors need to be considered. First, the distance traveled would depend on how firmly wedged the snail is on or among the feather; the more firmly wedged it is, the longer the dispersal distance. Second, larger classes would likely be dispersed a shorter distance than smaller classes because the "baggage" becomes heavier with the snail's increasing size (mass). Third, the distance dispersed would depend on whether the bird is seeking different habitats for food, nesting, mating, or migrating—migrations are a much greater distance for dispersal than "pond hopping" for food. If pulmonates can survive transport among birds' feathers for 10 km (Boag 1986), both CMS and JMS could survive much greater distances, surviving periods of desiccation for much more extended periods by closing their opercula.

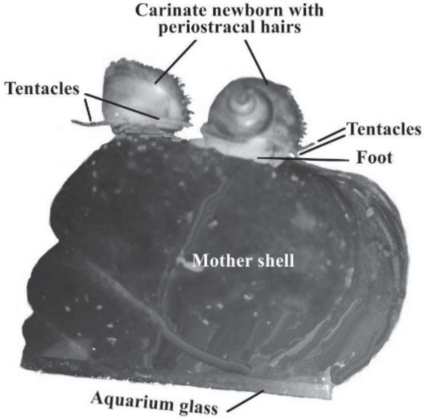


Figure 7-1. A female Chinese Mystery Snail with two newborn attached, both presumably grazing on attached detritus. Each newborn has a conspicuous row of hairs on their carinate body whorl.

Harried, Fischer, Perez, and Sandland (2015) support the dispersal of CMS by waterfowl. They found a general lack of infections by the trematode *Sphaeridiotrema pseudoglobulus*, which were encased in the shells in a nonviable state. They reasoned that waterfowl may have consequences for the establishment and spread of the snail in the region. Trematode infections can reduce reproduction and survival in native snails (Sandland and Minchella 2003; Lafferty and Kuris 2009). Therefore, lower parasite numbers in CMS relative to other members of the gastropod assemblage may lead to the invader having a fitness advantage relative to infected snail species. Higher reproductive output in CMS through reduced infection levels may help explain this species' relatively wide range across Wisconsin. Sandland and Minchella (2003) found snails infected with *Echinostoma revolutum* produced few eggs and tended to grow to larger sizes than uninfected snails regardless of diet; in addition, infected snails exhibited reduced survival relative to snails in control treatments. Lafferty and Kuris (2009) found parasitic castrations occur in many snail hosts. It is often achieved through the selective targeting of reproductive energy and can also simply be the consequence of a nutritional drain. The hosts might be programmed to make up for the energetic loss by first sacrificing reproduction. They reported that larval digenean trematodes are the most common castrators of gastropods and some bivalves, and the parasites can be abundant and substantially depress host density. This castration implies reduced competition from native snails.

Figure 7-2. Mallards frequenting waters with Chinese Mystery Snails. (a) Backyard fishpond, April 2, 2021 (GLM photo); (b) cottage shoreline in the Muskoka district, Ontario (June 2019, courtesy of Jamie Delaney).

Van Leeuwen and van der Velde (2012a) and Van Leeuwen, van der Velde, van Lith, and Klaassen (2012b) categorized dispersal of aquatic species according to active dispersal across the land over long distances or as suitable for passive transport by human vectors (anthropochory), wind (anemochory), water (hydrochory), or other animals (zoochory). Of these, zoochory is a potential dispersal vector of freshwater gastropods overland. Of the latter, birds have been captured while carrying aquatic invertebrates between their feathers or on their bill or feet (ectozoochory) (e.g., Kew 1893; Boycott 1936; Baker 1945; Malone 1965; Bilton, Freeland, and Okamura 2001; Van Leeuwen and van der Velde 2012). Green and Figuerola (2005) reported birds might have a major role in expanding exotic species, and the feeding process is likely to carry on their feathers, feet, bills, etc. Additionally, birds have been found to carry viable molluscs in their digestive system (endozoochory) (Mackie 1979; Van Leeuwen and van der Velde 2012). The snail *Hydrobia* (*Peringia*) *ulvae* was found to survive passage up to five hours through the digestive tract of mallards as fully functional adults. They estimated a maximum potential transport distance of up to 300 km, although the actual dispersal distance greatly depended on additional factors such as the behavior of the vectors (Van Leeuwen, van der Velde, van Lith, and Klaassen 2012b). Martin, Johnson, Bowerman, and Li (2020) found that most genetic variation in *Planorbella trivolvis* was associated within and among populations, suggesting LDD promoted gene flow between populations.

The overland dispersal of some species may depend on their association with other species. Maguire (1963) described the dispersal likelihood of organisms as dependent on the vagilities (the degree to which they can or do move or spread within their common environment) of associated species of airborne micro-organisms. He expressed the vagility of organisms dispersing from ponds (or other sources) as a function of distance carried by their viable propagules from the source and the frequency of such transports. His distance vagility index is formulated as:

$$\text{Distance Index} = \text{Log}_{10} \sum (n_i d_i^2)/ND$$

where n_i = number of times the organism was found at the ith station; d_i = distance (in yards) of that station from the edge of the pond; N = total number of times that the organisms were found in any of the original sites; and D = number of days over which there was an opportunity for aquatic organisms to reach its site; the summation includes values for all stations.

Distance is squared in the computation of the index because it is the most important factor and should contribute most heavily to the size of the index. In addition, areas at given distances from a pond increase roughly as the square of that distance. Therefore, if propagules spread radially from the pond, the probability of one of them getting to a site by chance decreases approximately as the inverse square of the distance from the pond. The total number of times (N) the organism reaches a site includes observations at 0 yards. Maguire rationalized the index as reflecting, to some degree, the distance traveled as a function of the number of organisms that were transported out of his pond site.

2. Unintentional Anthropogenic Vectors

Of the 14 unintentional anthropogenic vectors (i.e., B1–14, Table 7-2), only a few likely contribute to the dispersal of viviparids. Large ocean ships and freighters (i.e., B1, Table 7-2) are not a likely vector of strictly benthic viviparids unless the ballast water takes on mud, sand, or gravel substrate. Like those used in commercial fisheries, large freshwater vessels are unlikely to disperse viviparids on their hulls because the hulls do not contact the bottom. Some fishing vessels may capture viviparids in gill nets, seines, or trawls. Some nets are equipped with a “tickler chain” that scoops up some substrate with molluscs, like *C. japonica*, as observed in Sandusky Bay of Lake Erie by Wolfert and Hiltunen 1968); see discussion in Chapter VIII, Impacts. If the mud is not entirely removed from the gear, the snails may be dispersed elsewhere in the lake or other lakes. Otherwise, the gear may be included in B4, Marina and boatyard equipment.

B2, Canals, is attributed considerable discussion (Table 7-2), mainly because of the huge networks connecting European countries, as discussed under D. Intracontinental vs. Intercontinental Dispersal later in this chapter.

B3, Reservoirs are discussed earlier for aiding in dispersing both native and alien species acting as stepping-stones for spreading species across landscapes.

B4, B5, Navigation and marker buoys and floats (Table 7-2), are a potential dispersal vector for viviparids; some buoys are removed before winter ice conditions and replaced the following navigation season (Canadian Coast Guard 2012). In less severe ice conditions, the unlighted summer buoys may be left in place, or unlighted winter buoys may replace lighted buoys. Any anchors for the buoys with mud may harbor viviparids, but any snails will perish before reinstalling if they are stored on land during the winter. If summer buoys are removed and replaced, mud on replacement anchors of such buoys could harbor viviparids, but cleaned anchors are usually used.

B6, B7, Overland transport of boats and trailers with bait buckets, nets, etc., are well-known invasive species vectors (Johnson, Ricciardi, and Carlton 2001; Johnson and Carlton 1996; Rothlisberger, Chadderton, McNulty, and Lodge 2010). Adult *C. chinensis* and *Viviparus georgianus* move into shallow water in the summer (Jokinen, Guerette, and Kortmann 1982; Jokinen 1992), increasing their susceptibility to being picked up by boats and trailers, especially in masses of macrophytes caught in the propellers. Havel, Bruckerhoff, Funkhouser, and Gemberling (2014) observed juvenile *C. chinensis* and *V. georgianus* in macrophyte collections after field sampling of trailered boats. They tested the desiccation tolerance of three species of invasive aquatic snails widespread in Wisconsin, *Bithynia tentaculata*, *C. chinensis*, and *V. georgianus*, in 2011 and 2012. All three species exhibited high survivorship, with some individuals alive at the end of most experiments (e.g., 42 days for *B. tentaculata* and *V. georgianus* and 63 days for *C. chinensis*). *C. chinensis* released viable young after 54 days of exposure. These results indicate that the three invasive snails could readily survive long periods of transport overland.

Havel (2011) showed Chinese Mystery Snails of two size classes surviving for long periods of air exposure, > 3 days for small individuals (6–8 mm high) and > 28 days for large individuals (> 25 mm high). These durations indicate the snails could likely survive transport between lakes on overland vectors such as trailered boats.

A boat landing was a significant predictor of both *C. chinensis* (Solomon, Olden, Johnson, Dillon, *et al.* 2009) and other aquatic invasive species in Wisconsin lakes (Johnson, Olden, and Vander Zanden 2008). The second source of indirect data on the association between Chinese Mystery Snails and boats is the snail distribution within lakes relative to boat launches. In an earlier study of 42 northern Wisconsin lakes with snails, Solomon, Olden, Johnson, Dillon, *et al.* 2009 (2009) found *C. chinensis* widespread (21 lakes) and were more likely to occur at sites near launches than at sites more distant from launches. If the snails are moving slowly from their point of introduction, as observed for invasive rusty crayfish (Wilson, Magnuson, Lodge, Hill, *et al.* 2004), such a pattern is consistent with boaters as the source of colonizing snails. However, boat launches are also likely for aquarium dumping because of their ease of access, so transport by this alternate vector may also occur.

A final link to recreational boats is direct surveys, which have revealed boats to carry live zebra mussels (Johnson and Carlton 1996) and zooplankton (Kelly, Wantola, Weisz, and Yan 2013). But mystery snails do not produce planktonic larvae, easily transported in various settlement stages within water droplets. Harken back to two traits emphasized earlier: snails cannot swim or jump from the substrate to boat hulls, motors, or intakes. They cannot attach to the hull of boats unless the hull sits onshore. Most boats, however, are tied to a dock or weir well above the bottom to prevent damage to the hull.

If CMS and JMS are concealed in cavities in the hull or trailer, boater transport of aestivating snails would seem plausible. However, as expounded upon later (Chapter IX, Control, 3. Dispersal Options), boater transport is an unlikely primary mechanism of dispersal of these snails for these reasons:

- Trailers, after being stored for a long time on dry land, are pushed into the water at a boat launch for very short periods of 5, 10, or 15 minutes.
- All snails creep, crawl, or slither very slowly and thus are highly unlikely to attach to the trailer in the short term of trailer submersion because snails cannot swim (marine gastropods, like nudibranchs, swim, but not freshwater gastropods).

- If one or more snails do attach with their foot, they detach as the trailer is pulled from the water. To prevent water loss, the snail pulls its head and foot into its shell, sealing the aperture with the operculum, thereby losing its attachment.
- When pulling the trailer out of the water, some snails will likely be crushed by the trailer's wheels. Still, careful inspection of the trailer for attached vegetation should remove all of it.
- If the trailer pulls through a bed of submerged vegetation harboring snails, the trailer could transport snails. Moreover, many boat launch areas have concrete runways, limiting the growth of submersed plants.

The boat and outboard motor are also unlikely to harbor snails for additional reasons:

- Although most boats have been in the water for a long time (> 1 month) and snails could attach to the hull and motor if the bow is sitting onshore, even juveniles of CMS and JMS are not able to enter the water intake, water pump or impeller, or live wells and bait wells. Snails cannot swim or jump from the substrate to motors, hulls, intake ports, or other floating parts.
- If somehow snails were to attach to the hull and motor shaft, they could be transported out of the water but not overland; as soon as the boat is pulled out of the water, the snails withdraw their head and foot, close their "trap door," then drop off after losing their attachment with the foot.
- Any snails attached to the hull that contact and ride over the felted rails of the trailer would be crushed.
- As with trailers, any vegetation attached to motors would likely be removed and discarded, with any snails among them.
- There are no crevices or channels that could protect juveniles from falling off the boat when removed. Only then could CMS and JMS be transported overland by trailered boats.

Only vegetation or mud caught on the boat or trailer and anchors could conceal snails, at which point humans are responsible for not cleaning or removing the debris. Muddy anchors, particularly, are a potential refuge for snails, but the anchors are generally stored inside the boat.

B8, Amphibious and firefighting planes and B9, Firetruck water (Table 7-2) take on water with plankton, not benthic organisms.

B10, Commercial products including plants (Table 7-2) applies mostly to the aquarium trade and is discussed below as part of B11, under Introduction for the Aquarium Trade.

B12, Recreational equipment is not a potential vector if the equipment floats; if scuba divers stir up mud, some snails may get caught up in their gear, but the gear is usually washed clean before storing. If not cleaned immediately and the gear is used in another body of water, snails will likely survive and be dispersed.

B13, Litter, such as tires and grocery carts, is an unlikely dispersal vector because it is litter. If recovered, it would likely be considered garbage and go to landfill or recyclable materials. If recoverable, such as new grocery carts, they would be cleaned before the next use. Even aquaria, discussed shortly, would likely be broken and considered garbage or recycled for its glass.

B14, Scientific research, would bring to question the conscientiousness of the scientist, but probably in most cases, scientific permits allow the collection of invasive species for research and must follow strict guidelines for their disposal afterwards.

a. Introduction for the Aquarium Trade

Aquarium releases (B10, Table 7-2) are a proven vector for the dispersal of invasive species, including viviparids. Moon (1956) found the distribution of *Potamopyrgus jenkinsi* showed no correlation with physical or chemical conditions. No explanation of its distribution was offered, except for the eastern side of Windermere Lake, UK. It occurred in more developed commercial and residential areas where human activities prevail. Such a relationship is synanthropic—an undomesticated organism, usually a pest, that lives in close association with people and benefits from their surroundings and activities. Both CMS and JMS would likely qualify as synanthropes, based on the main anthropogenic vectors.

There can be little doubt that maintaining snails, fish, plants, etc., in aquaria is not an issue, even if they are invasive, as long as they, and the water, are kept in the aquaria. The problems arise when the contents of the aquaria are released into the wild with native species. The motivations for the releases are several, among the most likely being weariness of cleaning the aquaria, weariness and cost of maintaining the pets, and high reproductive traits, leading to overloading of the aquarium that results in excessive waste products (ammonia, bacteria, etc.). Most aquaria enthusiasts like or even adore the animals. Rather than kill them, they release them into the wild, not thinking of the potential impact on native species or the ecosystem.

Courtney and Stauffer (1990, 145) reported that of the "46 species of foreign fishes known to be established as reproducing populations in open waters of the contiguous United States, approximately 65% are known or presumed to have originated from the aquarium fish trade.” Many species escaped or were released from aquarium fish culture or retail facilities, and some were introduced intentionally by aquarists.

Schmeck (1942) purchased specimens of CMS from Beldt’s Aquarium of St. Louis, raised them in aquaria, then released them into the Niagara River (Cayuga Island), Niagara Falls, New York, and found them well established there eight years later. They were often sold by tropical fish dealers in Ottawa in the 1940s; La Rocque (1948) suggested the introduction of the species at Patterson Inlet in Ottawa was a result of an amateur aquarist becoming tired of his pets and dumping the entire contents of his tanks into the inlet. Bousfield (1955) indicated the CMS colony along the St. Lawrence River, below Quebec City, resulted from recently released aquarium stock.

Therriault and Kott (2002-2003) sampled many locations in southern Ontario, most close to inhabited areas where it would be relatively easy to dump unwanted aquarium stock. For example, Lakeside Park near Kitchener, Ontario, had a well-established population of CMS, and while sampling the lake, they saw many old aquaria on the bottom.

Karatayev, Burlakova, Karatayev, and Padilla (2009) attribute shipping in the northern part of the US as the most critical vector for introducing many invasive species, including their arrival through the aquarium trade. In Texas, they inculpate the introduction of exotics to the aquarium and ornamental trade that dominated unintentional vectors for introducing all freshwater exotics, citing three water bodies colonized by a CMS in the last 45 years.

Therriault and Kott (2002-2003) believe the distribution of *Cipangopaludina chinensis malleata* in North America suggests a series of point introductions. For example, Johnson (1915) suggested the CMS introduction to the Muddy River in Boston, Massachusetts, might have occurred during the addition of goldfish to the stream for mosquito larvae control. Likewise, in Tolton’s Pond, a private pond in which Japanese water lilies were transplanted, Therriault and Kott (2002-2003) suggested the possibility that the Chinese Mystery Snail may have been inadvertently introduced to the pond by “hitching a ride” on the lilies.

Rixon, Duggan, Bergeron, Ricciardi, *et al.* (2005) analyzed invasion risks posed by the aquarium trade and live fish (including molluscs) markets using three simple criteria from Ricciardi and Rasmussen’s (1998) model based on trends identified from previously successful invasions: (1) dominant geographical donor regions and dispersal vectors, (2) biological attributes of invasive species (e.g., wide environmental tolerances, broad diets, and high reproductive capacities), and (3) invasion history elsewhere in the world. They also assessed and compared the probability of establishment from the aquarium trade using Kolar and Lodge's (2002) model, which developed quantitative models that correctly categorized established, quickly spreading, and nuisance fishes with 87–94% accuracy. After visiting six live fish markets in Toronto and Windsor (Ontario), and Montréal (Québec), Rixon, Duggan, Bergeron, Ricciardi, *et al.* (2005) recorded 308 freshwater fish species belonging to 50 families from the 20 stores visited, the mean number of species recorded per store being 62.6. Only four molluscs were included in their survey; three were ampullarids that would unlikely survive Great Lakes winter temperatures, and the Oriental mystery snail had already invaded this system. Several additional snail species were observed associated with macrophytes or other substrates in aquaria but were not intended for sale, partly because of their small size or being hidden amongst macrophytes and substrate. Their research suggested that both the aquarium industry and live fish markets represent potential sources of future invaders to the Great Lakes, including several aquarium fishes and macrophytes as well as Asian carp species sold in fish markets. Currently, few regulatory mechanisms exist to control these potential vectors in Canada.

Lucena-Moya and Duggan (2011) and Duggan, Champion, and MacIsaac (2018) suggested that macrophytes with complex architecture (e.g., *Elodea*) commonly hold greater species richness and abundance of invertebrates than less complex plants (e.g., *Vallisneria*). While their studies examined microfauna associated with the plants, the plant complexity offers three attributes to invertebrates, including mystery snails: a greater variety of habitat, a greater concentration of food, or greater protection against predators. In addition, less mobile benthic species were found to discriminate among substrates, whereas the abundance and richness of planktonic species (mainly rotifers) were not affected by complexity level. These results perhaps explain the appearance of zebra mussels with moss balls (e.g., Marimo moss, actually filamentous algae), which were recently being outlawed in many aquarium retailers in the United States and Canada because they harbor invasive species. (See Chapter VII. Impacts, C. Beneficial Impacts, Section 3. Aquarium Trade).

3. Intentional Anthropogenic Mechanisms

a. Introduction for Food

Of the two intentional vectors listed in Table 7-2, deliberate introduction (C1) of snails as escargot is well known. Molluscs are common food items for humans, but most are marine species belonging to several classes. Included are cephalopods (e.g., squid, octopus), bivalves (e.g., oysters, scallops, cockles, clams), chitons, and gastropods (e.g., abalone, limpets, winkles, conchs, whelks). Many land snails are also used as food, especially species of *Helix*, cooked as escargot. Very few freshwater molluscs are used for food by humans. The only freshwater bivalve used for food is Asian clams (e.g., *Corbicula* species). The family groups of freshwater gastropods used for food include Pachychilidae, (e.g., *Brotia*), Paludomidae (e.g., *Paludomus*), Ampullariidae (e.g., *Pila*, *Pomacea*), all mostly in tropical and subtropical areas. Gastropods in the temperate zone include only the Viviparidae (e.g., *Bellamya*, *Filopaludina*, *Cipangopaludina*). *Bellamya* is a species-rich genus of freshwater snails occurring in Asia, India, and Africa (Gu, Husemann, Wu, Dong, *et al.* 2019), mostly subtropical to tropical climates. *Filopaludina* is a southeastern viviparid occurring in tropical wetlands of Vietnam and Thailand (Köhler, Do, and Jinghua 2012b). The occurrence of the Chinese and Japanese mystery snails in North America honors them with a distinguished position as the only freshwater gastropods used as food in North America, albeit in the temperate climate.

Viviparids are common food items in many Asian countries (Deshayes 1874; Tripathy and Mukhopadhayay 2015). Deshayes (1874) lists many common species on the sandbanks of rivers in Cambodia; many of the species are sought after by the natives. If interested in preparing viviparids for food, see Chapter VIII. Impacts, B. Beneficial Aspects, 1. Food.

Most alien fish species have food, sport, and aquarium value in North America. Molluscs such as CMS and JMS have no sporting value but do have food value, having been introduced into Chinese food markets in San Francisco (Wood 1982a, b; Pilsbry 1894; Stearns 1901; Hannibal 1901, 1908, 1911), as discussed in Chapter IV. The first record of CMS (as *Paludina japonica*) in Canada was in the Chinese Markets at Victoria, British Columbia, where they were "accounted dainties by the Chinese and are sold to them at 25 cents a pound" (Pilsbry 1894, 144). La Rocque (1948) mentioned the introduction of CMS at Harrison Mills, British Columbia, was a result of a purposeful introduction to provide food for workers at a large sawmill.

b. Fishponds

Perhaps many of the alien species introduced to backyard fishponds are unintentional, but most plants and animals placed in the ponds are purchased from pet stores or the internet. Among the common pond plants are water hyacinths, *Eichhornia crassipes*, and water lettuce, *Pistia stratiotes*. The most common exotic fish is goldfish, *Carassius auratus*, with koi, *Cyprinus rubrofuscus*. It is illegal to sell or buy Chinese or Japanese mystery snails in Canada, but one or both species appear in some ponds, including the CMS in my fishpond. The snail was likely introduced as several small juveniles or a gravid female because it was not noticed for four to five years. However, it was an accidental introduction with some native plants from a local stream.

D. Intracontinental vs. Intercontinental Dispersal

It is interesting to note that the extent of spread in the continent of North America is much greater than the extent of spread in the continents of Europe and Asia. CMS has invaded 39 states in the US, yet Europe, a much smaller continent than North America has had limited spread, with only four countries (Denmark, The Netherlands, Belgium, and Russia, having CMS (Table 4-15**)**. CMS invasibility is much smaller than the zebra mussel, which I estimate to be in about 25 countries. One reason for the wider distribution in much of the US is likely related to the extensive Missouri River, Mississippi River, and all the Great Lakes (Superior, Michigan, Huron, Erie, Ontario). The Missouri River is the longest river in the US, with a total length of 4,088 km (2,540 miles), and it covers an area of about 1,371,000 km^2 (529,350 miles^2). The Missouri River watershed includes four states that lack CMS and seven with CMS (Table 8-2). The Mississippi River is about 3,734 km (2,320 miles) long, and its drainage basin covers an area of 2,981,076 km^2 (1,151,000 miles^2) (Briney 2019). Two other river watersheds that contribute to the distribution of CMS are the Ohio River and the Arkansas River. The Ohio River is 1,579 km (981 miles) long, with an area of 528,319 km^2 (204,000 miles^2). The Arkansas River is 2,364 km (1,469 miles) long, with a watershed area of 260,039 km^2 (10,409 miles^2). The Great Lakes drainage basin is about 765,830 km^2 (295,710 miles^2), including the lakes' areas and their connecting waterways. Of the 32 states shared or restricted to the five watersheds, only seven are not occupied by CMS: Arkansas, Montana, New Mexico, North Dakota, South Dakota, Montana, and Wyoming; three, North and South Dakota and Montana are in the Missouri River watershed (Table 7-2). Of the remaining 26 states occupied by CMS, six (Iowa, Illinois, Kentucky, Missouri, Minnesota, and Indiana) share three watersheds (color-coded in Table 7-2); four (New York, Ohio, Pennsylvania, and Wisconsin) share two watersheds (underlined and colored in Table 7-2).

Table 4-14 shows Wisconsin has the most locations in the US with CMS (1,149), and it shares the Mississippi River and Great Lakes watersheds. Wisconsin is in the headwaters of both watersheds, suggesting that many of the locations may be from drift, likely on debris during high discharge events. Aquarium releases and other unintentional releases likely also contribute to many locations.

Table 7-3 lists the states in all five watersheds (Mississippi River, Missouri River, Ohio River, Arkansas River, and the Great Lakes watersheds) that encompass most of the areas occupied by CMS. Iowa and Minnesota share the Mississippi River, Missouri River, and the Great Lakes watersheds. Indiana and Illinois share the Mississippi River, Ohio River, and the Great Lakes watersheds. Kentucky shares Missouri, Mississippi, and Ohio River watersheds. New York, Ohio, and Pennsylvania share two watersheds, the Ohio River and the Great Lakes; Wisconsin shares the Mississippi River and the Great Lakes watersheds. If it is assumed that downstream movement is at least partly responsible for the distribution of CMS in these watersheds and that the snail does not move significant distances upstream, implicit in these assumptions is that the snail would have to be introduced upstream in each watershed to establish itself downstream.

Using the Strahler (1964) method that CMS is likely to establish itself, the lowest stream order is between stream orders 3 and 4, where the forest canopy thins and light can penetrate to increase the water temperature and biomass of algae on rocks. The coarse particulate organic matter of leaves breaks down to fine particulate organic matter. The biomass of plankton becomes available for grazers and deposit feeders (Mackie 2001), all suitable conditions for CMS.

The US also has a huge network of canals, a total of 18,241 (Table 7-4, based on Appendix B, USA canals. Many of the canals are shipping canals located primarily on coastal states. All others are irrigation, industrial, or drainage canals.

Mills, Leach, Carlton, and Secor (1993) attribute the entry of exotic species in part to canals, at least until 1959, after which ships became the primary entry mechanism. Karatayev, Padilla, Minchin, Boltovskoy, *et al.* (2007) argue that the spread of exotic species has not been a continuous process but rather punctuated by periods of rapid long-distance spread or jumps. Species can then greatly expand their geographic ranges. These jumps are interpreted here as the vectors, (e.g., unintentional releases). They claim that each jump was associated with changes in pulses of some human activities, such as the construction of shipping canals for trade, the building of reservoirs for water storage and power production, and political boundary changes or changes in political systems. Karatayev, Padilla, Minchin, Boltovskoy, *et al.* (2007) remark that these activities affect the permeability of national borders as well as human emigration and immigration, changes in the methods and volume of international trade, or modern industrial practices and environmental mandates.

Thus, the rate of dispersal of alien species is related to the spatial scale of distribution and rates of human activities. In general, exotic aquatic species may quickly spread along connected waterways in a new continent they invade and soon reach their maximum range at the intercontinental scale (Karatayev, Padilla, Minchin, Boltovskoy, *et al.* 2007). However, alien species take much longer to colonize isolated regions at an intracontinental scale and longer spread to all isolated lakes and river systems at a more local scale. The difference in the rate of colonization across scales may be several orders of magnitude (Karatayev, Padilla, Minchin, Boltovskoy, *et al*. 2007).

Table 7-4 lists all the canals and the number of locations of CMS in each of the 52 states. Most of the shipping canals are wide and deep, and shipping traffic is difficult to sample. A simple correlation test shows that there is a negative but not significant correlation ($P > 0.05$) (Table 7-5), implying that canals may even hinder fostering the establishment of CMS in the US.

The canals of Europe are also extensive and attributed to the expansion of zebra and quagga mussels and several other alien species (Gollasch and Nehring 2006; Ram and Palazzolo 2008; Leuven, van der Velde, Baijens, Snijders *et al.* 2009; Keller, Geist, Jeschke, and Kühn 2011). But they are not instrumental in the spread of CMS and JMS, except potentially for only five locations, Belgium, Denmark, The Netherlands, Russia, and perhaps France, where the two species now occur. The canals of Europe serve the same purpose as in North America—navigation, crop irrigation, water supply, or drainage—and appear to lack CMS or JMS for similar reasons. The main one is canals used for navigation, which are large and deep to accommodate ships. According to Davies and Marsh (2019), the growth of transport in Europe after World War II was coordinated by various international authorities. The result was an enlarged, integrated network of canals brought up to a minimum common standard for the craft of 1,350 tons. The Rhine and the Moselle and their tributaries dominated the German system and provided outlets for the Dutch and Belgian systems and were connected with the French network. The main improvements were concentrated on the international Main-Danube Canal and on improving the north–south route of the Nord-Sud Canal (or Elbe-Seitenkanal); the latter canal joins the Mittelland Canal near Wolfsburg, Germany, reaching a total of 711 miles and shortening the route between Hamburg and the Ruhr by 134 miles.

Ships are an unlikely vector for CMS in Europe or anywhere because the viviparid is a benthic species in shallow water and not a likely component of water being taken on board for ballast. External transport of viviparids is also unlikely because they cannot tolerate the salinity of water in many canals, or, if in freshwater, would not be carried long distances. Hence, vectors other than canals would explain the remoteness of the European localities with established populations of CMS. The most likely transport to remote localities is human-mediated, either intentionally or unintentionally. Some irrigation, industrial, and drainage canals are likely highly eutrophic and/or carry toxic materials from runoff or industrial processes.

Several models predict the distribution of exotic species; most are for the zebra mussel. Bossenbroek, Kraft, and Nekola (2001) suggest that gravity models may be useful in predicting LDD when dispersal abilities of species and the attractiveness of potential habitats are known. Their results were highly correlated with the actual pattern of colonized lakes by zebra mussels in southern Michigan and southeastern Wisconsin at the end of 1997. However, CMS has no specific requirement for habitat type or quality compared to the zebra mussel, which is limited by pH (> 8.0) and calcium content (> 25 mg Ca/L), suggesting that their gravity model may not work for CMS, or at least has to be tested.

Wisconsin has the largest number of locations (1,199) for CMS (Table 4-14), which raises this question: Is this related to boater traffic? For zebra mussels, Buchan and Padilla (1999) estimated spatial and temporal patterns of boating traffic among Wisconsin's inland water bodies using the results of an extensive, randomized survey of recreational boaters. Of the survey respondents, 90% of boaters traveled locally, within a county, or adjacent counties; 8.4% moved 50 km; and only 0.8% moved extreme long distances (261 km). Extreme long-distance boater movements were correlated positively with greater numbers of registered boaters in source and destination counties and with greater surface area and numbers of named lakes in destination counties.

Table 7-3. Distribution of the Chinese Mystery Snail in states with the Missouri River, Mississippi River (Upper and Lower), Ohio River, Arkansas River, and the Great Lakes watersheds. States with the Chinese Mystery Snail are indicated with an asterisk. All states are sorted alphabetically for each watershed. States with CMS in three watersheds are bolded across watersheds; states with CMS in only two watersheds are underlined and bolded.

Missouri R. States	**Mississippi R. States**	**Ohio R. States**	**Arkansas R. States**	**Great Lakes States**
Colorado*	Arkansas	Alabama*	Arkansas	Michigan*
Idaho*	**Idaho***	Georgia	Colorado*	**Illinois***
Iowa*	**Illinois***	**Illinois***	Kansas*	**Indiana***
Kentucky*	**Indiana***	**Indiana***	Louisiana*	**Iowa***
Minnesota*	**Iowa***	**Kentucky***	**Missouri***	**Minnesota***
Missouri*	**Kentucky***	**New York***	New Mexico	**New York***
Montana	Louisiana*	North Carolina*	Oklahoma*	**Ohio***
Nebraska*	Maryland*	**Ohio***		**Pennsylvania***
N. Dakota	**Minnesota***	**Pennsylvania***		**Wisconsin***
S. Dakota	Mississippi	South Carolina*		
Wyoming	**Missouri***	Tennessee*		
	Montana*	Virginia*		
	North Dakota	West Virginia*		
	Texas*			
	Wisconsin*			

Table 7-4. Numbers of canals in the 50 states of the United States, listed by descending numbers (Briney 2019). States with the Chinese Mystery Snail are indicated with an asterisk.

State	# of Canals	State	# of Canals
California*	2,903	New Mexico	69
Indiana*	2,239	North Dakota	69
Colorado*	1,888	Kentucky*	62
Michigan*	1,668	Tennessee*	61
Idaho*	1,540	Virginia*	59
Minnesota*	1,451	Delaware*	54
Wyoming	1,085	Louisiana*	45
Montana	858	Maryland*	44
Oregon*	661	New Jersey*	41
Utah*	575	South Carolina*	33
Iowa*	299	Kansas*	27
Texas*	299	Massachusetts*	26
Arizona*	289	Georgia*	25
Missouri*	287	Alaska	23
Illinois*	278	Ohio*	22
Nevada	263	Alabama*	21
Florida*	245	Pennsylvania*	11
Washington*	237	New Hampshire*	10
Nebraska*	209	Oklahoma*	9
Mississippi*	185	Connecticut*	8
North Carolina*	151	Maine*	7
Hawaii*	125	Arkansas	6
New York*	116	Rhode Island*	3
South Dakota	91	West Virginia*	2
Wisconsin*	89	Vermont*	1
Total number of canals			**18,241**

Table 7-5. Relationship between the number of canals in each state and the number of locations of the Chinese Mystery Snail in the United States. The list is sorted by descending number of canals.

State	# of Canals	# of CMS Locations	State	# of Canals	# of CMS Locations
California	2,903	91	New Mexico	69	0
Indiana	2,239	46	North Dakota	69	0
Colorado	1,888	1	Kentucky	62	4
Michigan	1,668	77	Tennessee	61	2
Idaho	1,540	10	Virginia	59	65
Minnesota	1,451	264	Delaware	54	2
Wyoming	1,085	0	Louisiana	45	2
Montana	858	0	Maryland	44	26
Oregon	661	6	New Jersey	41	93
Utah	575	5	South Carolina	33	12
Iowa	299	12	Kansas	27	14
Texas	299	18	Massachusetts	26	78
Arizona	289	8	Georgia	25	0
Missouri	287	16	Alaska	23	0
Illinois	278	222	Ohio	22	87
Nevada	263	0	Alabama	21	1
Florida	245	7	Pennsylvania	11	73

Washington	237	34	New Hampshire	10	30
Nebraska	209	12	Oklahoma	9	3
Mississippi	185	0	Connecticut	8	27
North Carolina	151	19	Maine	7	44
Hawaii	125	4	Arkansas	6	0
New York	116	87	Rhode Island	3	6
South Dakota	91	0	West Virginia	2	17
Wisconsin	89	1199	Vermont	1	9
Totals	**18,241**	**20,379**	**Correlation Coefficient, r^2**	**-0.095**	
Average	**695**	**373**	**St. Dev.**	**777.84**	**236.77**

E. Range Expansion

Propagule pressure, also called introduction effort, is arguably the most critical factor influencing the establishment of invasive species (Leung, Drake, and Lodge 2004; Colautti, Grigorovich, and MacIsaac 2006; Duggan, Rixon, and MacIsaac 2006; Leung and Mandrak 2007; Lo, Levings, and Chan 2012). Propagule pressure is an aggregate measure of the absolute number of individuals released into a region in any one event (Lockwood, Cassey, and Blackburn 2005). The number of discrete release events is a measure of the propagule number. As the number of releases and/or the number of individuals released increases, propagule pressure also increases. Increasing propagule pressure is also relevant in explaining the rate of the geographical spread of an invasive species. Bossenbroek, Kraft, and Nekola (2001) provide evidence that once a non-native population has established, proximity to a source of dispersing individuals increases the likelihood the invasive species will expand its geographical range because sites nearby receive many more propagules than those remote from a seed population. This theory was demonstrated by Bossenbroek, Kraft, and Nekola (2001) in predicting the distribution of zebra mussels by the proximity of each newly invaded lake to one that was already infested by small recreational boats.

Brockerhoff, Kimberley, Liebhold, Haack, *et al.* (2014) maintain that the size and composition of species pools arriving from source regions affect the probabilities of establishing and affecting pathway (vector) infestation rate. Propagule pressure encompasses variation in the quantity, composition, and rate of supply of non-native organisms resulting from transport (Ricciardi, Jones, Kestrup, and Ward 2011). These criteria suggest the spatial scale and mechanisms determining propagule pressure are inextricably linked to the developmental process in producing propagules, which is indirect development versus direct development. The more propagules produced, the greater the likelihood of the establishment of non-indigenous species.

To illustrate the importance of development types in contributing to propagule pressure, compare the indirect development of zebra and quagga mussels (Claudi and Mackie 1994; Mackie and Claudi 2010) and the golden mussel (Mackie and Brinsmead 2017) to the direct development of Chinese and Japanese mystery snails. Indirect development results in several larval stages, some planktonic and swim, and some benthic. The benthic juveniles and adults possess byssal threads for firmly attaching to solid substrates. The numbers of planktonic forms are enormous, several thousand per liter, and the numbers of adults are usually 1,000 to 100,000 m^{-2}. Direct development results in embryos born alive, the numbers usually < 50 per female, adult densities usually < 40 m^{-2}. The numbers of propagules arising from indirect development are orders of magnitude greater than those from direct development.

The consequence of this disparity in propagule numbers is a greater probability of establishing populations from indirect development than from direct development. In addition, propagules from indirect development can be dispersed in both water and on solids (i.e., attached by byssal threads). In contrast, propagules from direct development can be dispersed primarily in mud or on benthic plants. Dispersal in both water and solid substrates results in greater dispersal vectors from indirect development than direct development. Therefore, the vagilities differ between the two types of development. While both types may result in similar ranges of distribution, the sizes of the vectors vary, as illustrated in Figure 7-3, even if the distances between target lakes are identical. The vectors (open arrows) for indirect development are greater than for direct development (solid arrows). For example, byssate mussels have greater vagilities (e.g., attach to hulls, the anchor holds, ballast, humans, aquaria) for transfer between continents (e.g., Asia and North America) than do mystery snails (e.g., humans, aquaria). I'm not trying to be melodramatic, but zebra mussels disperse in a mere drop of water; mystery snails need a bucket of water. Once within a country, dispersal vectors are much more numerous (e.g., humans, trailered boats, water currents, wind, canals, fisheries equipment) for indirect development than direct development (e.g., humans, aquaria, food). The dispersal range of both types of development is illustrated as a pyramid scale of vagility complexity in Figure 7-3. The length of the vectors indicates the relative distance for dispersal; the width indicates the relative vagilities available to the invading species. The intercontinental source is usually single, but the sources increase at each level, intra-waterbody sources generally being the greatest, with water bodies nearby receiving more propagules. States can be interpreted as either provinces (as in Canada) or countries (as in Africa and South America). Dispersal within watersheds can be enhanced if the propagules are planktonic and can swim, unlike direct developers, such as mystery snails. One can expect a similar pyramid for the degree and extent of impacts.

Before summarizing this chapter, it is relevant to propose the potential functioning of Allee effects, introduced by Allee (1931), on establishing CMS and JMS propagules. Allee effects are positive relationships between individual fitness components and either numbers or density of conspecifics (Stephens 1999; Courchamp, Gascoigne, and Berec 2008). Stephens (1999) suggested it is important to differentiate between component Allee effects

(Allee effects manifested by a component of fitness) and demographic Allee effects (Allee effects that manifest at the level of total fitness). These effects suggest that populations will be depressed at very low levels of abundance, and small populations (below a lower threshold) are proportionally more prone to extinction (Stephens and Sutherland 1999). Lewis and Kareiva (1993) showed that Allee effects will slow the advanced rate of invasive species and that invasions cannot propagate unless they initially exceed a critical area. Native species' ranges may be truncated, even where suitable habitat is available, should their populations fall below a threshold due to competition with an invasive species. The rate of spread of a species can be affected by processes at the fringe of a population. For many populations, Pulliam (1989) suggested that a large fraction of the individuals may regularly occur in "sink" habitats, where within-habitat reproduction is insufficient to balance local mortality. Populations may persist in such habitats if they can be locally maintained by continued immigration from more productive source areas nearby. Pulliam (1989) concluded that when a surplus population of the source is large, the per capita deficit in the sink is small; only a small fraction of the total population will occur in areas where local reproduction is sufficient to compensate for local mortality, equilibrium with both source and sink habitats occupied can be both ecologically and evolutionarily stable.

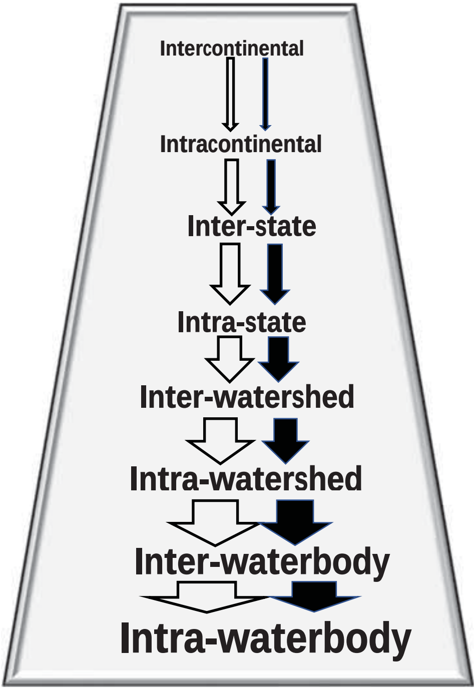


Figure 7-3. Pyramid scale of vagility complexity, illustrating the increasing diversity of dispersal vectors with decreasing distance between target bodies of water; propagules from indirect development (open arrows) have relatively greater vagilities than those from direct development (solid arrows). See text.

F. Chapter VII Summary

Several factors are examined to determine a species' success in its newly found environment: (1) its inherited traits, or natural factors; (2) its opportunities or mechanisms for dispersal, which involves transporters, or vectors, both natural (e.g., water currents, birds, mammals) and anthropogenic factors, either intentional, unintentional, or malicious introduction; and (3) its appeal or repulsion, in which further expansion of the species depends on its positive and negative impacts, respectively. The inherited traits examined in this chapter were life span, number of cohorts, natality (number of surviving young), size, reproductive habits, and physiological tolerances and requirements. Based on these six traits, the most likely dispersal for a species would be one that is hermaphroditic, oviparous (lays eggs), highly fecund with a high natality rate, is multivoltine (reproduces many times a year), iteroparous (reproduces many times in its lifetime), and has wide environmental tolerances and requirements. The species predicted to be least likely to achieve dispersal would be one that is dioecious, ovoviviparous (produces live young), has low fecundity and natality, is univoltine (reproduces once a year), and semelparous (reproduces only once in its lifetime), and has narrow environmental tolerances and requirements. Based on these characteristics, both *C. chinensis* and *C. japonica* have traits that predict low to moderate invasibility.

Of the numerous mechanisms for dispersal of *C. chinensis* and *C. japonica*, humans are the most important vector for its dispersal from Asia into and throughout North America. The main value of mystery snails is in the aquarium trade, and to a lesser extent, their value as food. Evidence is presented to show that many locations are close to inhabited areas where the snails can be easily dumped with unwanted aquaria. There is a weak negative correlation between the numbers of occurrences of *C. chinensis* and the number of canals in North America, suggesting canals may even hinder the spread of the mystery snail. The presence of a boat landing was shown to be a significant predictor of *C. chinensis* occurrences (and other aquatic invasive species). The second source of indirect data on the association between Chinese Mystery Snails and boats is the distribution of this snail within lakes relative to the position of boat launches; the snails are more likely to occur at sites near launches than at sites more distant from launches. Boat launches are also likely for aquarium dumping because of their ease of access, so transport by this alternate vector may also occur. However, arguments are presented to show that overland transport of trailered boats is an unlikely dispersal mechanism because of the behavior of the snails to withdraw their foot into their shell shortly after air exposure.

The distributions of the Chinese and Japanese mystery snails are associated in some way with human activities. They have a synanthropic relationship: an undomesticated organism lives in close association with people, apparently benefiting from their surroundings and activities. Both CMS and JMS qualify as synanthropes, primarily based on the two main human-related activities of the snails' values as aquarium pets. The aquarium is often released into nearby water bodies when snails are no longer valued as pets and food. Much of the incentive for releasing aquarium pets (snails, fish, etc.) lies in the fact that people do not like to kill animals and prefer to release them into areas where they can continue to survive. Add to these associations' proximities of boat launches—the potential for snails to be dispersed in plants and mud attached to the trailer and boat was discussed.

A pyramid scale of vagility complexity was devised to illustrate the effect of development type (i.e., indirect vs. direct) on propagule numbers. The vagilities embody variations in the quantity, composition, and rate of supply of propagules along each vector, all being greater for indirect development (e.g., zebra, quagga, and golden mussels) than for direct development (e.g., mystery snails).

CHAPTER VIII

IMPACTS

A. Introduction

A comparison of modern to background extinction rates reveals that gastropods have the highest current extinction rate observed to date, 9,539 times greater than background rates (Johnson, Bogan, Brown, Burkhead, *et al.* (2013). Among the many reasons for the increased extinction rate are the introduction of invasive species of gastropods and invasive predators and their inculpating impact on native species of gastropods.

The literature refers to native, resident, and invasive species, among others. The convention followed here is largely that of David, Thebault, Anneville, Duyck, *et al.* (2017): native species are those that have been present since prehuman time—they have a pre-Pleistocene geological record, mainly from the Palaeozoic and Precambrian eras (e.g., Starobogatov 1992; Karrow and Mackie 2013; Bajc, Karrow, Yansa, Curry, *et al.* 2015). Resident species include ex-invasive species that have become established locally and have potential competitive significance (e.g., Table 8-1). Invasive species are any non-resident species, intentionally or accidentally introduced, that can maintain, spread, and reproduce in the new habitat.

Also often used in the literature are the terms *exotic* and *introduced*. Sax, Stachowicz, Brown, Bruno, *et al.* (2007) define exotic species as those that have been introduced to a place or have otherwise become established there because of human activities but have not dispersed much beyond the watershed in which they were introduced. Exotic species could be embraced by introduced species, which herein are any non-resident species that were intentionally introduced and can maintain, spread, and reproduce in the new habitat; exotic species are considered unintentionally introduced. Intentionally introduced species include the brown trout, *Salmo trutta*, which was introduced to support recreational fishing, being first introduced to Canada in 1883 in Newfoundland. The rainbow smelt, *Osmerus mordax*, was introduced from the Atlantic coast and eastern waters of North America and was first recorded in Lake Ontario in 1931; they came from some inland water of New York, where they were intentionally introduced in 1917.

There are other terms and definitions. Gallardo, Zieritz, and Aldridge (2013) define invasive non-native species as non-native species that adversely affect the regions and habitats it invades environmentally, economically, and/or ecologically. This definition, therefore, excludes non-native species that do not pose any significant threat to biodiversity conservation. In this context, the invasive non-native species group is here embraced in resident species. According to Gallardo, Zieritz and Aldridge (2013), non-native species are those that have been introduced through human action outside its natural present or historical range. They include species whose main pathway of introduction is human-related, although they have entered RINSE (Reducing the Impacts of Non-native Species in Europe) countries, which includes Great Britain, France, Belgium, and The Netherlands) through natural spread from neighboring countries. However, the term excludes species expanding their range without direct human action, as in migration or because of climate change or habitat modification, even if humans cause these changes. The non-native species group is included here as introduced species. The terms are relevant here because CMS is present in both the Netherlands and Belgium, and *Viviparus* species are present in all three countries.

Some introductions have proven to have undesirable impacts, such as the alewife, *Alosa pseudoharengus*, which were transplanted into large reservoirs in the southeastern United States to serve as aquatic forage species. The fish is anadromous and had initially been limited to the Great Lakes and small glacial lakes in the northeastern United States (Kohler 1984). Alewife's earlier transplantations occurred in 1968 in Claytor Lake, Virginia, where it had several negative consequences, the most serious of which included predation on larval sport fishes. Alteration of the zooplankton species and size composition by selective predation and rapid growth beyond a size vulnerable to most predators also was observed (Kohler 1984). Only pelagic predators such as white bass, *Morone chrysops*, and walleye, *Sanders vitreus*, benefited from the introduction, although walleye recruitment coincidentally declined following alewife establishment (Kohler 1984).

As for molluscs, exotic species would include some sphaeriids, like *Sphaerium corneum*, *Euglesa supina*, *E. henslowana*, and *Pisidium moitessierianum*, which have expanded their ranges outside of the Great Lakes drainage systems since being introduced, some more than 100 years ago. While *C. chinensis* and *C. japonica* have been in North America for more than 130 years and qualify as ex-invasive species, they are here considered invasive species to compare their life history traits to those of ex-invasive (resident) species listed in Table 8-1.

Table 8-1. Ex-invasive (resident) gastropods and bivalves in Canada (CA) and United States (US) of potential competitive significance to the Chinese and Japanese mystery snails. The likely countries of origin also given.

Resident Gastropoda	Country	Origin	Resident Bivalvia	Country	Origin
Bithynia tentaculata	CA, US	Europe	*Corbicula fluminea*	CA, US	Europe or Asia
Elimia virginica	US	US	*Dreissena polymorpha*	CA, US	Europe
Gilia altilis	US	Eastern US	*Dreissena rostriformis bugensis*	CA, US	Europe
Melania tuberculata	US	Southern Asia	*Euglesa* (formerly *Pisidium*) *amnica*	CA, US	Europe
Potamopyrgus antipodarum	CA, US	New Zealand	*Euglesa henslowana*	CA, US	Europe
Radix auricularia	CA, US	Europe, Asia	*Pisidium moitessierianum*	CA, US	Europe
Valvata piscinalis	CA, US	Europe	*Euglesa* (formerly *Pisidium*) *supina*	CA, US	Europe
Viviparus georgianus	CA, US	Eastern US	*Sphaerium corneum*	CA, US	Europe

Impacts of aquatic invasive species can be categorized as ecological, economic, and social. This chapter examines the degree of nuisance or menace of *C. chinensis* and *C. japonica*. There are several interpretations of impacts. An example of extreme menace is that their introduction would cause an alteration of the ecosystem that at least modifies the species composition, especially gastropods, or biodiversity at different trophic levels; these are grouped below under negative impacts. At the lower or lowest level, by contrast, their introduction can be interpreted as beneficial if it enhances local biodiversity, economy, and/or social benefit (e.g., recreation); these are grouped below as beneficial impacts.

An introduced species may only persist if it can pass through environmental and biotic filters. These filters compose the fundamental niche that makes a new habitat suitable for a species to complete its life cycle (e.g., thermal thresholds for growth and reproduction). For example, temperature is a major environmental factor constraining the distribution of organisms (Gunderson and Leal, 2016). Biotic filters include the level and availability of resources, competition, and natural enemies, which define the realized niche. Species that have been able to pass through these filters may not come alone. Numerous examples of parallel invasions have been documented, frequently of species from the same area of origin (see Mills, Leach, Carlton, and Secor 1993). Strayer (2010, 152) predicts “the number of alien species in freshwater ecosystems will increase in the future as new aliens are moved outside of their native ranges by humans, and as established aliens fill their potential ranges.” Because alien species create new ecosystems that have proven difficult to manage, it is prudent to reduce future impacts of invaders by making serious efforts to prevent new invasions and manage existing invaders (Strayer 2010).

B. Negative Impacts

Five negative impacts of *C. chinensis* and *C. japonica* are addressed below: competition, parasitism, ecosystem functioning, social aspects, and economy. Of these, competition, parasitism, and ecosystem functioning have been well addressed in the literature. Some social aspects come from personal conversations with cottagers and comments on the internet. There appear to be no estimates or poor treatment of the impact of mystery snails on the economy, but it is worth discussion because of some false impressions.

1. Competition

David, Thebault, Anneville, Duyck, *et al.* (2017) highlighted five local effects of invaders (in quotes), which are compared to effects of competition between *C. chinensis* and *C. japonica* and native and ex-invasive molluscs discussed in previous sections by me:

(1) "Impacts of invaders on a few interacting species in the recipient ecosystem are more often studied than impacts at the whole food web scale". (This is supported in the discussions in Chapter VI, Ecology. Most of the analyses of effects are from laboratory mesocosm studies or conjectures. Mesocosm studies are of value, but mostly for ranking variables [i.e., no effect, great effect, greatest effect] affecting a specific behavior or trait [e.g., competition, predation, growth, fecundity, etc.], not as definitive evidence of an ecosystem impact; as the maxim states, correlations do not denote cause. Unfortunately, no algorithms exist to guide scaling up from small-scale experiments to the whole-lake, long-term management scale (Stein, Brown, Covich, *et al.* 1998, 53).

(2) "Direct predation underlies the most spectacular impacts, and invasive predators can drive resident species to extinction. (This is not applicable to CMS and JMS, which are herbivores, not predators). "Competition and apparent competition with invasive species lead to declines in resident species but rarely provoke extinctions". (Table 8-1 shows the prevalence of ex-invasive species in North America. There is no definitive evidence of the extinction of native species of freshwater gastropods due to invasive gastropods like CMS and JMS. Links to other trophic levels also have yet to be demonstrated).

(3) "Invaders are often an important new resource benefitting the higher trophic levels in the recipient ecosystems. Still, this positive effect may be opposed or reversed by the decline in local prey due to competition with the invaders". (There is some evidence of higher trophic levels (e.g., mallards) benefiting from CMS and JMS; there is no evidence of native predators such as crayfish being replaced by invasive crayfish preying on CMS or JMS).

(4) "Predation or competition between invaders and residents are often asymmetrical, with more negative impacts of invaders on residents than the reverse". (Yes, some mesocosm studies show impacts of CMS and JMS on native residents, but not in field studies [see Chapter VI. B. Populations Dynamics, c. Competition]). "This situation puts selective pressure on resident species, which often evolve traits to tolerate better or exploit the invasive species". (The

evolution of traits of resident species to tolerate or exploit CMS or JMS has yet to be demonstrated). "For example, mesocosm studies support asymmetrical competition with native species of gastropods, but not the reverse; selective pressures of native or ex-invasive species gastropods to better exploit or tolerate invasive gastropods". (Yes, some mesocosm studies show the impacts of CMS and JMS on native residents [see Chapter VI. B. Populations Dynamics, c. Competition]).

(5) "In favor of invaders over residents, asymmetry in impacts most likely results from a filtering process whereby only introduced species that overall benefit from interactions with residents become successful invaders. Introduced and resident species have no coevolutionary history, resulting in extreme reciprocal impacts one way or the other". (Coevolutionary history is unlikely between CMS and JMS and native and ex-invasive gastropods, given that most ex-invasive species were introduced from countries other than Asia [see Table 8-1]. Asymmetry in impacts of CMS and JMS benefiting from interactions with residents may have already occurred, given their successful invasion throughout North America [except tropical species]; therefore, this is almost impossible to prove for species already firmly established).

As a follow-up to the five local effects of invaders described above by David, Thebault, Anneville, Duyck, *et al.* (2017), Table 8-2 lists several life history traits of invasive species of gastropods and bivalves in North America, the traits of *C. chinensis* and *C. japonica* highlighted in bold. Column 1 shows in parentheses the numbers of states and provinces invaded (e.g., *Elimia virginica* occurs in nine states but has invaded only one state). Column 4 gives the species' sexual state (Hermaph = hermaphroditic, Partheno = parthenogenetic). Column 10 gives the smallest size at sexual maturity, and its maximum size as a percentage, with size ranges, averaged; the remaining columns are explained in the caption. As a surrogate for invasion rate, the rate of spread was calculated by dividing the number of US + Canadian occurrences (given in Column 1 in parentheses) by the interval between 2020 and the year of introduction (e.g., for CMS, the rate used was 39/(2020-1892) = 0.305 invasions$^{/\text{year}}$). A Spearman's rank correlation was performed for each pair of numerical traits, using the average for traits with a range of values, converting development times to days and omitting traits with no data (ND) for some species. The formula used to calculate the correlation coefficient, rho (ρ, or r_s), for tied ranks, was this:

$$\rho = \frac{\sum(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_i(x_i - \bar{x})^2 \sum_i(y_i - \bar{y})^2}}$$

where x and y are the ranks of the variables and $\overline{x}$ and $\overline{y}$ are the mean ranks of the variable.

Table 8-3 gives pairwise correlations of six traits. Only two pairwise metrics were significant at $P \leq 0.05$: maximum size vs. fecundity and maximum size vs. size at maturity. Fecundity is well known to be related to the size of the individual in viviparids (e.g., Ribi and Gebhardt 1986; Therriault and Kott 2002-2003; Jakubik and Lewandowski 2007; David and Cote 2019). The ρ value of 0.662 indicates fecundity increases with the increasing size of the parent. The ρ value, 0.571, for maximum size vs. size at maturity is also positive, showing larger individuals mature at larger sizes. All other pairwise correlations were nonsignificant ($P > 0.05$), implying that co-establishment of ex-invasive species is likely not limited by life history traits. One exception may be fecundity; see Keller *et al.* (2007). Instead, specific habitat factors, which help reduce competition, seem to affect the establishment of ex-invasives. For example, *Biomphalaria glabrata* is a tropical species limited by the need for warm water temperatures (17.0°C to 29.5°C, McCreesh and Booth 2014). *Gillia altilis* has a large, muscular foot that can adhere to rocks by suction and is adapted for inhabiting high-velocity lotic environments (Kipp, Benson, Larson, and Fusaro 2021). Combinations of predators can modify gastropod behavior and shell morphology in aquatic assemblages of different ages and depths. For example, Covich (2010) found a combination of invertebrate and vertebrate predatory impacts led to competitive advantages among individual gastropods with different adaptations: (a) less vulnerable shell morphologies and sizes; (b) predator-avoidance behaviors; and (c) rapid and widespread dispersal with variable life histories, an adaptation supported by the Spearman rank analyses in Table 8-3. Covich (2010) also reported some individuals developed thicker and/or narrow-opening shells or shells with spines and ridges. Some thin-shelled species crawled out of the water or burrowed to lower their risk to shell-breaking or shell-entering predators; some altered their age at first reproduction and grew rapidly into a size refuge. He also speculated that fluctuations in water levels and invasive species introductions could change competitive dominance relationships among gastropods, resulting in major losses of native species.

Table 8-2, next two pages. Life history traits of invasive molluscs (A. Gastropoda; B. Bivalvia) in North America: Column 1 = Species; 2 = year of introduction; 3 = Invasion rate (see text); 4 = Sexuality (hermaphroditic, dioecious, or parthenogenetic); 5 = Fecundity$^{\text{-female}}$; 6 Life span (years); 7 = Maximum size (mm); 8 = Parental care (oviparous or ovoviviparous); 9 = Development time (days, weeks, or months); 10 = Size at sexual maturity (mm, % of maximum size); 11 = Sources of information. ND = No data

A. Invasive Gastropoda

Column # 1	2	3	4	5	6	7	8	9	10	11
Species	**Year Intro**	**Invasion rate**	**Sex**	**Fecund**	**Life span**	**Max size**	**Parent care**	**Develop time**	**Mature**	**Source of information**
Biomphalaria glabrata (1)	1960s	0.017	Hermaph	1419	≤1	6-10	Oviparous	5-6 day	3, 37.5	Dillon (2000) 60
Bithynia tentaculata (15)	1871	0.101	Dioecious	347	1.5-3.3	12-15	Oviparous	3 wk-3 mon	8, 59.3	Jokinen (1982); Mills *et al.* (1993); Kipp *et al.* 2021.
***Cipangopaludina chinensis* (39)**	**1892**	**0.305**	**Dioecious**	**133**	**4-5**	**50-67**	**Ovovivip**	**2 wk**	**25, 29.9**	**Wood (1982); this report**
***Cipangopaludina japonica* (23)**	**1911**	**0.211**	**Dioecious**	**ND**	**4-5**	**50-65**	**Ovovivip**	**ND**	**ND**	**Hannibal (1911)**
Elimia virginica (1)	1860	0.006	Dioecious	ND	5	27-33	Ovovivip	ND	10, 33.3	Kipp *et al.* (2021)
Gillia altilis (2)	1915	0.019	Dioecious	6	>5	6-8	Ovovivip	7-14	3-4, 50.0	Thompson (1984)
Melanoides tuberculata (15)	1950	0.214	Partheno	265-597	2.5-5	36	Ovovivip	100-217 day	8.3-11.5, 27.5	Dudgeon (1986); Pointier *et al.* (1991, 1992); Dillon (2000); Work and Mills (2013)
Potamopyrgus antipodarum (26)	1987	0.788	Dioecious, Partheno	20-120	1	5-10	Ovovivip	90-120 day	3-3.5, 44.0	Zaranko (1997); Mackie (2000); McKenzie *et al.* (2013); Dorlego *et al.* (2014)
Radix auricularia (22)	1901	0.185	Hermaph	50-100	2	35-40	Oviparous	12-30 day	10, 26.7	Salih *et al.* (1881); Adam and Lewis (1992); Mills *et al.* (1993)
Stenophysa marmorata (1)	1978	0.024	Hermaph	12.3-88.3	1-1.2	16.3	Oviparous	7-14 day	8, 49.1	Núñez (2011a, b)
Tarebia granifera (3)	1935	0.035	Dioecious	1000s	3	26-40	Ovovivips	6-12 mon	5.5-7, 24.2	Abbott (1952)
Valvata piscinalis (4)	1897	0.033	Hermaph	150	1.1-1.8	6-7	Oviparous	15-30 day	5, 76.9	Mills *et al.* (1993); Grigorovich *et al.* (2005); Fretter and Graham (1978)
Viviparus georgianus (3)	1906	0.202	Dioecious	4-40	2.3-3.1	21-35	Ovovivips	9-10 mon	15.5, 55.4	Browne (1978); Jokinen (1982)

B. Invasive Bivalvia

Column #1 Species	2 Year Intro	3 Invasion rate	4 Sex	5 Fecund	6 Life span	7 Max size	8 Parental care	9 Develop time	10 Maturity	11 Source of information
Corbicula fluminea (51)	1939	0.630	Dioecious	25,000 - 75,000	6-7	50	Planktonic larvae	2-4 day	15-20, 35.0	Dundee (1969); Eng (1979); Sickel (1979); McMahon and Williams (1986);
Dreissena polymorpha (34)	1986	1.00	Dioecious	~1,000,000	3-5	50	Planktonic larvae	3-5 day	6-9, 15.0	Claudi and Mackie (1994); Chase (1996); Mackie and Claudi (2010)
Dreissena rostriformis bugensis (24)	1991	0.828	Dioecious	~1,000,000	3-5	40	Planktonic larvae	3-5 day	8-10, 22.5	Claudi and Mackie (1994); Chase (1996); Mackie and Claudi (2010)
Lasmigona subviridis (1)	<1959	0.016	Dioecious	>1,000,000	3-4	60-65	Parasitic glocihdia	ND	50-60, 88.0	USFWS (2020); Mills *et al.* (1993); Tremblay *et al.* (2016); Kipp et. al, (2021),
Pisidium amnicum (6)	1897	0.049	Hermaph	12-73	2	9-11	Ovovivip	21-30 day	3-4, 35.0	Fretter and Graham (1978); Mills *et al.* (1993); Grigorovich *et al.* (2005); Mackie (2007)
Pisidium henslowanum (5)	<1916	0.048	Hermaph	25-40	2	4.8-5.2	Ovovivip	ND	2, 40.0	Odhner (1929); Mackie (2007)
Pisidium moitessierianum (3)	1894	0.024	Hermaph	5-10	2	2-2.8	Ovovivip	15-20 day	1.1, 45.8	Grigorovich *et al.* (2005); Mackie (2007)
Pisidium supinum (3)	1959	0.049	Hermaph	?	2	4-5	Ovovivip	ND	ND	Mackie (2007)
Sphaerium corneum (3)	1952	0.044	Hermaph	4-31	1-1.5	9-16	Ovovivip	8 day	3.2, 25.6	Odhner (1929); Mills *et al.* (1993); Mackie (2007)

Table 8-3. Spearman rank correlation values (ρ, r_s) for five life history traits of 22 species of invasive gastropods and bivalves (see Table 8-1 for lists).

	Fecundity	**Life span**	**Maximum size**	**Development time**	**Size at maturity**
Rate	0.312	0.012	0.416	-0.153	0.425
Fecundity	1	-0.143	**0.662***	-0.199	0.435
Life span		1	-0.284	-0.333	-0.001
Maximum size			1	-0.279	**0.571***
Development time				1	-0.35
Size at maturity					1

*Significant at P < 0.05

2. Parasites

The parasites of CMS and JMS were identified and discussed in Chapter VI, C. Parasitism. The most prevalent parasites are trematodes, especially *Aspidogaster conchicola*, a native species that is most commonly found in North American unionids. Trematodes of human health significance are echinostomes, with nine species recorded as parasites of CMS in Taiwan and six species in China. The echinostome parasite *Echinostoma recurvatum* is cosmopolitan in North America, commonly reported from many freshwater molluscs, but has never been reported in Chinese Mystery Snails in North America. No echinostome parasites of CMS in China or Taiwan are known in North America.

Zbikowski and Zbikowska (2009) describe a unique relationship between three native trematode species and the newly-introduced snail host, the New Zealand mud snail *P. antipodarum*. Despite the high invasion intensity, the parasite remains in a long-term relationship with its snail host, successively releasing dispersion forms, mainly cercariae. The parasitic larvae developing in snails were shown to affect various aspects of their host's life, including mortality, condition, reproduction, and behavior. The adverse effect on reproduction of host snails likely caused earlier maturation in the host snail, compensation fecundity, inhibition of gonad activity, or castration. Parasitic castration may result from a disturbed hormonal balance of the host or destruction of the gonad in which the parasite's embryos develop. Limiting or complete prevention of snail reproduction is regarded by many as the reason for the changes in shell growth pattern (shape change, forming additional structures), disrupted calcium metabolism, somatic dwarfishness or gigantism, and also changes in the host's behavior whereby the parasite would manipulate the host to increase its success.

3. Ecosystem Functioning

The nuisance level of CMS and JMS can be rated according to life history traits, the major trait being fecundity. Keller, Drake, and Lodge (2007) showed that nuisance status is positively associated with fecundity. Other aspects of natural history and biogeography did not significantly affect the likelihood of becoming a nuisance. Table 8-2 extracts from Table 2 of Keller, Drake, and Lodge (2007) the fecundities of invasive species in North America from lowest to highest according to the type(s) of impact (economic, environmental) and mode of reproduction. The lowest fecundities are for the ovoviviparous species *C. chinensis* and *C. japonica*. The type of impact for these two species is not identified for a good reason—effects so far have yet to be identified. There is potential for wider distribution of CMS in North America because of their apparent indifference to chemistry. Table 6-4 shows wide ranges for physical variables (e.g., temperature, 0–30°C), Figure 6-21 (e.g., substrates of mud, sand, stone, rocks, water types (permanent ponds, lakes, and rivers), and Table 6-5, trophic levels (e.g., oligotrophic, mesotrophic, and eutrophic). Yet CMS and JMS densities are relatively small (1–40 m^{-2}; see discussion in Chapter VI, B. Population Dynamics, d) Density), mainly because of their low fecundities.

4. Economics

There is no estimate of the cost of impacts caused by either CMS or JMS in North America. However, there are misconceptions of their potential economic impact. The Alberta Invasive Species Council (2018, 2) states, "Economic Impacts: Chinese Mystery Snails would cause costs to municipal water systems by clogging intake pipes and other submerged equipment. Accumulation of dead and decaying shells could have impacts on recreation and tourism." Consider these facts:

- Intake structures are usually constructed of masonry or concrete and provide relatively clean water, free from pollution, sand, and silt. Most intakes are placed well off the shoreline and in deep water and are raised above the bottom to reduce the probability of bottom-dwelling organisms from entering the intake (though it does little to deter planktonic or swimming organisms). A velocity cap is commonly used in open-intake designs to change the direction of water withdrawal from vertical to horizontal. Creating horizontal velocity patterns results in the avoidance of fish and other aquatic organisms. The velocity cap is located at a minimum of 240 m (800 ft) from the shoreline (from 40 CFR § 125.92 (see Appendix A, USA intakes special definitions.

- Thus, specifically addressing intakes for industrial and power-generating cooling water systems in lakes and usually a few kilometers offshore, and in > 9–10 m depth (some > 50 m), consider the following. Industrial and power-generating plants draw cold water (~4°C) from the hypolimnion for secondary cooling and service water systems; few, if any, gastropods live in hypolimnial waters. Most intakes, even near shore, are usually well below freezing depth, below strong surface water currents generated by waves, and light intensity is reduced to the point that growth of plants is inhibited or arrested on intake structures. Both CMS and JMS are herbivores, which means they are most prevalent in littoral and sublittoral zones, in 1 to 3 or 4 m depths. There is no information on how far mystery snails migrate from shore into deep water, but it is highly unlikely for them to move kilometers offshore.
- The fecundities of CMS and JMS are very low (~65 live juveniles per female per year). Such low fecundities are hardly enough to clog industrial or municipal intake pipes or traveling screens, yet some fact sheets consider them threats to intakes (e.g., Kipp, Benson, Larson, and Fusaro 2016; Alberta Environments and Parks 2020; Kipp, Benson, Larson, and Fusaro 2020).

Lastly, mass mortalities of mystery snails would be required to impact recreation and tourism economies. Mass mortalities of CMS and JMS have been reported. They do not have the high densities of zebra or quagga mussels that create taste and odor problems due to mass mortalities (Claudi and Mackie 1994; Mackie and Claudi 2010). Winter kill (Wolfert and Hiltunen 1968) and extreme drought events (Haak, Chaine, Stephen, Wong, *et al.* 2013) can cause mass mortalities of CMS and JMS but are likely accompanied by mass mortalities of other species in the community.

Laverty, Nentwig, Dick, and Lucy (2015) assessed the environmental and economic costs of 49 species of alien aquatics using the Generic Impact Scoring System (GISS) and performed a comparison with other taxa of invaders in Europe. Impacts were scored into six environmental and six socioeconomic categories, with each category containing five impact levels. The six environmental impacts were (1) impacts on plants or vegetation through herbivory, (2) impacts on animals through predation or parasitism, (3) impacts on other species through competition, (4) impacts through the transmission of diseases or parasites to native species, (5) impacts through hybridization, and (6) impacts on ecosystems. Socioeconomic impacts were divided into (1) impacts on agricultural production, (2) impacts on animal production, (3) impacts on forestry production, (4) impacts on human infrastructure and administration, (5) impacts on human health, and (6) impacts on human social life. Of the 49 alien aquatic species investigated, 12 species were molluscs; two of them, *Dreissena polymorpha* (zebra mussel) and *Potamopyrgus antipodarum* (New Zealand mud snail) ranked among the top four; neither the Chinese or Japanese mystery snails were investigated. The additive impacts scores in each category were ranked from 0–80. Based on Figure 2 from Laverty, Nentwig, Dick, and Lucy (2015), the following scores were estimated for each category. For environmental impacts, the rankings were ecosystem (75), predation (51), competition (40), disease (29), herbivory (19), and hybridization (1); for socioeconomic impacts, the rankings were animal productivity (30), infrastructure (30), human health (15), human social life (9); and agriculture and forestry rank (0). Applying these categories to CMS and JMS, herbivory and hybridization within environmental impacts have not been investigated for mystery snails, probably because they do not apply. The same is true for agriculture, forestry production, and animal production of socioeconomic impacts. For infrastructure impacts and costs, Meyerson and Reaser (2003) suggest the effects are not immediate but instead are more subtle and cumulative; impacts on infrastructure would most probably occur as indirect consequences of invasive species introductions. They cite evidence that zebra mussels colonizing and clogging the water intake pipes of power plants, navigational locks, and nuclear power plants have yearly control costs exceeding US$800,000 per plant in the US and Canada. Impacts on infrastructure have been addressed in the text for the Chinese Mystery Snail (e.g., intake structures, condenser tube blockage) but not verified. Human health and human social life have also not been addressed, the latter perhaps relating to swimming and walking among living and broken mystery snail shells.

C. Beneficial Aspects

Beneficial aspects included here are positive impacts derived either directly or indirectly from the presence of CMS and JMS. Direct positive impacts include their nutrition as food, medicinal uses, and the aquarium trade. Indirect positive effects include their contributions to aid and abet in ecosystem functioning.

1. Food

Molluscs are considered a delicacy in many European countries, including France, the Netherlands, Belgium, and Italy (Robert, Sánchez, Pérez-Parallé, Luz, *et al.* 2013), but the major species are marine bivalves. Large viviparids are a food source in Eastern, Southern, and Southeastern Asia and Africa. Snail farming (heliculture or heliciculture) is common and done largely for the consumption of flesh (and of eggs from *Achatina* and *Pomacea* spp.), and for slime for cosmetic purposes. Snail slime contains many of the same ingredients as skin care products.

The use of freshwater molluscs as protein-rich food is very much a habit in several countries, including China, Formosa, India, Mexico, Taiwan, Thailand, and the Philippines (Baby, Hasan, Kabir, and Naser 2010). In China, Li, Wu, Lu, Zhang, *et al.* (2013) attribute its use as food to its rich nutrition with high protein content and low-fat content. Molluscs are used widely for other purposes like poultry feed, fish feed, lime, fisheries, etc. (Baby, Hasan, Kabir, and Naser 2013). Moreover, it is also a medicine used to treat digestive diseases in China (Li, Wu, Lu, Zhang, *et al.* 2013).

Baby, Hasan, Kabir, and Naser (2010) analyzed the nutritional value of the flesh and shells of six species of Bangladesh molluscs. Table 8-4 reports their values for different contents in a closely related species, *B. bengalensis,* of CMS and JMS. The shells of *B. bengalensis* contained (in mg^{-100g}) Calcium, 705.4; phosphorous, 1,680.6; iron, 300.1; sodium, 200.9; potassium, 40.8. They concluded that *B. bengalensis* is an excellent source of some required trace and minor elements needed for human beings' proper growth and development. The snail could be used as high-nutrient supplementary feed for domestic animals, birds, and even fish culture. In one wetland in Bangladesh, *B. bengalensis* are still harvested commercially as fish feed to the shrimp farm of Bagerhat areas. Some other species are also collected and used to feed ducks and local fish farms, including catfish farms and fishponds (Baby, Hasan, Kabir, and Naser 2013).

Engmann, Afoakwah, Darko, and Sefah (2013) analyzed the meat of the African giant snail, *Achatina achatina* for nutritional contents and minerals; their analyses are shown in Table 8-4 for comparison to *B. bengalensis*. They recommended the snails as an excellent source of minerals for growing babies, teenagers, pregnant and lactating women, and people suffering from diabetes and hypertension. In addition, their meat can be used to develop complementary foods for children under five years to prevent rickets, iron deficiency anemia, and protein-energy malnutrition as well as helping prevent postpartum hemorrhage, night blindness, osteoporosis, and hypophosphatemia and to increase high-density lipoprotein.

At least 15 different cultures and states use many snail species with different common and local names. The common viviparids used for food in India are *Filopaludina bengalensis*, *Bellamya dissimilis*, and *Cipangopaludina lecythis*. Mainly tribal people, lower-income groups, and some sections of middle-class people use viviparids as food—the soft fleshy parts are a very prestigious food item in some places. The importance of *C. chinensis* as food in India is well treated by Tripathy and Mukhopadhayay (2015). Ray and Chattopadhyay (1998, 271) describe *B. bengalensis* as a "potent aquacrop of India propagated in freshwater habitat but exposed to the risk of contamination by exposure to methylparathion, an organophosphorus pesticide."

CMS was first introduced as food in San Francisco; its prevalence as a food item in other parts of North America is unknown or is of little consequence as a research topic. It is used in parts of Ontario; Photo 43694172 on iNaturalist, Ontario has this caption: "An Asian family collected about 5, 10L buckets . . . to make a few tasty meals." There are many recipes on the internet. Some key recommendations before cooking them are as follows:

- Remove the operculum with a sharp knife.
- Snails that are at least a week from the water are usually safe, but place them in a bucket of water. If the shells float, discard them.
- To rid the snail of toxic elements, add salt and a touch of vinegar to encourage them to send intestinal contents to waste.
- Take two or three snails in your hands at one time and rub the shells clean of attached algae or debris.
- Discard the water and replace it with fresh, clean water.
- Repeat if necessary.
- Follow your favorite recipe.
- Remove the operculum with a sharp knife.

After meals, the shells are crushed, and the lime is spread on gardens.

Table 8-4. Nutritional and mineral composition of the flesh of *Bellamya* bengalensis and *Achatina achatina*.

Percent composition of nutritional criteria in the flesh of two species of snails

Species	Moisture	Protein	Fat	Ash	Total Carbohydrates	Energy KJ^{-100g}
Flesh						
Bellamya bengalensis	82.1	8.97	0.98	3.64	4.31	NA*
Achatina achatina	6.58	82.96	3.98	3.22	3.26	1613

Minerals in dried meat of two species mg^{-100g}

	Fe	Cu	Zn	Ca	K	P
Bellamya bengalensis	100.7	NA	NA	166.4	40.8	128.8
Achatina achatina	9.8	3.3	39	585.5	331.8	269.2

NA* = Not analyzed

2. Medicinal Uses

As an introduction to the use of snails having medicinal properties, refer to remedies described by Quave, Pieroni, and Bennett (2008) for treating gastritis and warts in Italy; *Arion hortensis*, a slug, is swallowed whole and alive to treat gastritis. To treat dermatitis, inflammations, calluses, and acne, the slug's clear mucus, believed to promote wound healing, is rubbed onto the skin. In one more remedy, "the death of a wart," a special ritual is incorporated in the treatment of warts whereby mucus from a live slug is first rubbed onto the wart, the slug is then hung out in the sunshine to dry and die, at which time it is believed that the wart should be gone. Indeed, how to slug a wart!

Snail slime (mucus) contains mucin, a glycosylate protein, which is composed of hyaluronic acid, glycolic acid, allantoin, and metals (Zn, Cu, Fe, Mn), all of which have benefits for health and skin care (Becker, Bergfeld, Belsito, Klaassen, *et al.* 2010; Papakonstantinou, Roth, and Karakiulakis 2012; Robert, Sánchez, Pérez-Parallé, Ponis, *et al.* 2013; Thomas 2013). In addition, peptide fractions of snail (*Cornu aspersum*) mucus exhibit a predominant antibacterial activity against *Brevibacillus laterosporus*, a spore-bearing bacterium; *Escherichia coli*, an intestinal parasite; *Clostridium perfringens*, a cause of food poisoning in uncooked beef and poultry (Dolashki, Velkova, Daskalova, Zheleva, *et al.* 2020); and *Pseudomonas aeruginosa*, a disease-causing bacterium (Pitt, Hawthornea, Garcia-Mayab, Alexandrovich *et al.* 2019). Similar results were obtained by Kubota, Watanabe, Otsuka, Tamiya, *et al.* (1985), but the peptide fractions lost antibacterial activity when heated at 75°C for five minutes. The primary sources of mucin for skin care products and bacterial diseases are slugs and land snails; viviparid mucus has been used for skin care and cure of antibacterial diseases mainly in Japan. There is a little economic benefit of snail slime in North America due to the synthetic production of hyaluronic acid, glycolic acid, and allantoin in skin care products.

Thomas (2013) describes several other uses of snail slime: treatment of warts; treatment of burns and skin conditions; wound management due to the slime's antioxidant contents; local anesthetics, such as toothaches; soups prepared from the flesh used to cure asthma, arthritis, joint swelling, rheumatism, and quick healing of a wound; and cure of conjunctivitis by immersing cleaned snails in water for few hours and then using the water in drops to the eyes.

The transfer of knowledge from biological phenomena to solve human issues was coined *biomimicry* by Benyus (1998); she describes the term as innovation inspired by nature, supported by numerous examples, many by molluscs. For example, Benyus describes the process the blue mussel, *Mytilus edulis*, uses when attaching its byssus to a surface. First, it cleans or primes the surface (to explain why we prime surfaces before painting them). Then it applies a primer that is waterproof and has cohesive properties (glue molecules sticking to one another) and adds adhesive properties, like the paints humans have now developed. The production of cultured pearls is based on observations made on the production of natural pearls by oysters. Now we can add snail slime as another molluscan example of biomimicry. As described above, the snail's slimy mucus contains mucin, composed of hyaluronic acid, glycolic acid, allantoin, and metals, all of which have been incorporated into the pharmaceutical production of different human health and skin care products.

3. Aquarium Trade

Some people consider mystery snails as beautiful, gentle giants worthy of keeping as aquarium pets. The internet describes the habitat, care, life span, feeding, tank size, etc. for several species (13 on one site), including the Japanese trapdoor snail. Most states and provinces now prohibit the sale of CMS and JMS because of their invasiveness. In addition, it is legal to possess, transport, and introduce by planting or releasing individuals in a free-living state into public waters. However, CMS is widely distributed, easily spotted because of its large size, and some larger ones are taken home and raised in aquaria.

Many people use moss balls in their aquaria for aesthetics, to maintain high oxygen levels, and to reduce nitrates and phosphates' buildups. Some moss balls (e.g., Marimo moss) are algae, consisting mainly of *Cladophora*, a common branching, filamentous green alga; *C. glomerata* is a native species found locally (e.g., Southwestern Ontario) in hard water streams. Marimo moss balls are among the most commonly used in aquaria, at least in British Columbia (British Columbia Government 2021), Alberta (Alberta Government 2021), and Saskatchewan (Saskatchewan Government 2021). Other moss balls consist of mosses (e.g., java moss, *Taxiphyllum barbieri*; flame moss, *Taxiphyllum* sp.; weeping moss, *Vesicularia ferriei*; phoenix moss, *Fissidens fontanus*; Christmas moss, *Vesicularia montagnei*; pellia moss, *Monosolenium tenerum*; crystalwort, *Riccia fluitans*. All are native to Asia, Europe, Africa, or South America and are imported by pet supply retailers. However, recently, zebra mussels have been discovered in some moss balls. There is concern that some people who have become weary of maintaining aquaria pets will dump the contents into nearby lakes, ponds, rivers, etc. Rather than take this risk, jurisdictions (e.g., Fisheries and Oceans Canada) ask owners of moss balls (whether they have zebra mussels or not) to destroy them. (See Chapter IX. Control Options.)

4. Ecosystem Components

While many invasive species are widely regarded as threats to ecosystem structure and function, some species may also benefit ecosystems that have lost former functions to environmental degradation. Twardochleb and Olden (2016) provide evidence that invasive species can alleviate some effects of environmental degradation. They evaluated whether invasive snails provide prey resources or induce trophic cul-de-sacs (divert basal energy away from higher trophic levels) in developed ecosystems where native prey are in decline. They used stable isotopes of 13C, 15N, and 2H to assess whether the Chinese Mystery Snail provides a prey resource to consumers and maintains the integration of benthic resources into food webs of lakes subjected to lakeshore development. They found that, regardless of the snail's presence, consumers in undeveloped lakes were supported primarily by benthic resources, and lakeshore development dramatically reduced consumer reliance on these resources. They attributed this result at least partly due to a reduction in the availability of native snails, a high-quality prey item, to the dominant, molluscivorous pumpkinseed sunfish

(*Lepomis gibbosus*). In developed lakes with non-native snails, the yellow perch (*Perca flavescens*), a generalist, and the largemouth bass (*Micropterus salmoides*), a piscivore, consumed benthic resources in proportions similar to undeveloped lakes, and pumpkinseed sunfish consumed CMS in higher proportions than in undeveloped lakes. Thus, CMS provided a prey substitute in developed lakes where native snail populations were depressed, and CMS's influence extended to higher trophic-level consumers. Twardochleb and Olden (2016) suggested that future research should consider how the effects of invasive species, either positive or negative, may vary across human-modified landscapes.

A benefit for a component of ecosystem functioning was demonstrated by Nakanishi, Takakura, Kanai, Tawa, *et al.* (2014), who showed *C. chinensis* densities in connected paddies positively affected the snail density in each paddy. They used absolute coefficient values (e.g., coefficient of each environmental condition and adjacent densities of snails) in the earth with and without CMS. The most significant value was found in flooded earthen ditches with CMS. They concluded that the spatial structure of paddy fields (i.e., the connectivity of paddies by ditches) was an important factor affecting snail density and environmental conditions in paddies. When the paddies were temporarily dried, the snails could emigrate or immigrate among connected paddies in addition to using the flooded ditches. Because many of the species that inhabit wetlands or ponds exhibited metapopulation dynamics and emigrated or immigrated among patchy habitats, Nakanishi, Takakura, Kanai, Tawa, *et al.* (2014) considered a metapopulation structure effective for biological conservation.

D. Impacts of Mystery Snails Relative to Other Non-Indigenous Species

Impacts of non-indigenous species are related to their dispersal capability or vagility. Chapter VII compared the vagilities of invasive species arising from direct development, as in Chinese and Japanese mystery snails, to those arising from indirect development, as in zebra, quagga, and golden mussels. A pyramid scale of vagility complexity (Figure 7-3) was developed to illustrate the relative magnitude of dispersion along with several geographical scales (e.g., intercontinental, intracontinental interstate, interstate, inter-waterbody, intra-waterbody). Species with indirect development, which results in several larval stages, both swimming and settling, have greater potential for dispersion than those with direct development. This implies that the diversity and magnitude of impacts are also related to development type. Figure 8-1 expands the pyramid scale of vagility complexity to a pyramid scale of ecological and socioeconomic impact complexity. Impact complexity is used here as a relative measure of diversity, degree, and magnitude of negative impacts, including control measures, between indirect developing non-indigenous species (e.g., dreissenid mussels) and direct-developing non-indigenous species (e.g., Chinese and Japanese mystery snails).

The impacted structures or scenarios are based on those described in Mackie and Claudi (2010). Only some components of each scenario are given in Figure 8-1. The width of each arrow reflects the relative cumulative magnitude of impact costs, the magnitude increasing to reflect the level of the ecological and socioeconomic impact associated with non-indigenous species using indirect development species relative to those with direct development. The socioeconomic impact has been well documented for zebra, quagga, and golden mussels but poorly documented for Chinese and Japanese mystery snails and is largely speculative, as indicated by the question marks in Figure 8-1. The total estimated annual cost for dreissenid impact and control was purported to be between US$100 million (Pimentel, Lach, Zuniga, and Morrison 1999; Pimentel, McNair, Janecka, Whitman, *et al.* 2001; Pimentel, Zuniga, and Morrison 2005; Pimentel 2011) and US$4 billion (Morton 1997), but Lovell and Stone (2005) and Ram and Palozzolo (2008) showed these values to be greatly inflated. For example, Ram and Palozzolo (2008) examined annual costs for different industries and utilities over 10-year periods of zebra mussel infestations and estimated mean annual expenditures per facility in 1989–1995 to be US$52,000 per year, decreasing to US$29,000 per year in 1996–2000. Average annual costs per facility since 2000 have fluctuated between US$25,000 and US$35,000. Considering all facilities within the North American range of the zebra mussel and quagga mussel (not including the newly infested sites west of the Continental Divide), the total costs for 1989–2004 were US$267 million (with the 95% confidence interval comprising US$167 million to US$467 million). These estimated costs include facility treatment measures (e.g., intermittent chlorination) and other total costs, such as monitoring, preventative measures before infestation, lost production and revenues, etc.

One scenario not included in the costs is the impact on ecosystems, for which estimates are difficult to calculate. However, the impact on ecosystems, particularly the Great Lakes, is well documented (US EPA 2021 and references therein). Notable are the declines in population densities of unionids with dreissenids inculpated in the endangerment of many species (e.g., COSEWIC 2003a, b; 2013a, b). Changes in food web structure, mobilization of ammonia and phosphorous from sediments, increased contaminant burdens in sediments, and taste and odor problems are impacts of zebra mussel impacts that are difficult to quantify in terms of economic costs. CMS has been in North America for more than 130 years, yet no such ecological or socioeconomic impacts have been estimated and therefore not demonstrated.

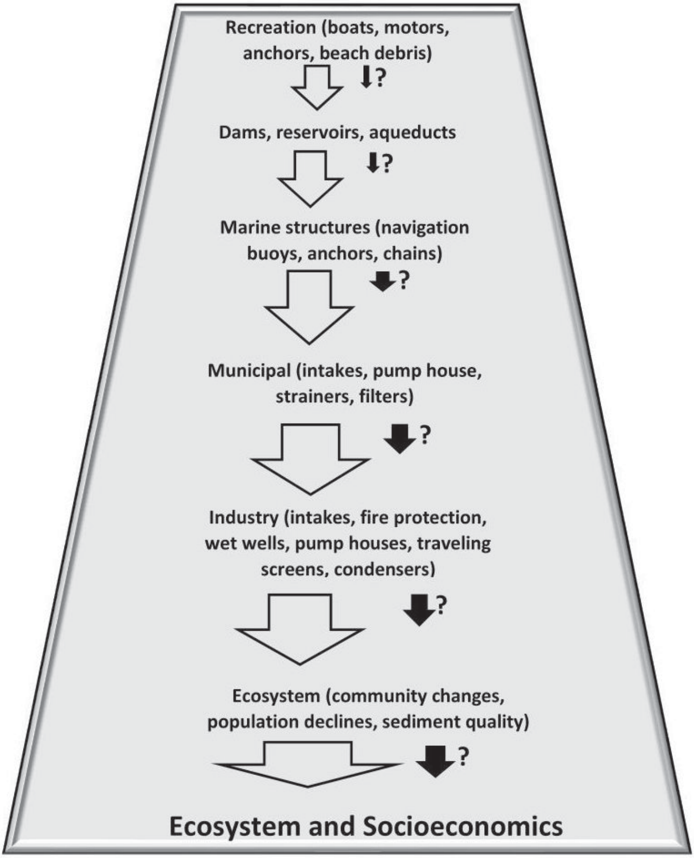


Figure 8-1. Pyramid scale of impact complexity, illustrating the increasing diversity of impacted structures and ultimate impacts on ecosystem and socioeconomics based on indirect development (open arrows) and direct development (solid arrows). See text.

E. Risk Assessment

Cottage associations can make risk assessments for their lakes or watersheds to determine the potential for the introduction of a non-native species and its ability to impact the target ecosystem and its species, habitat, and resources. The protocols of risk assessment depend on the species (e.g., dreissenids by Snyder, Mandrak, Niblock, and Cudmore 2012; golden mussel by Mackie and Brinsmead 2017; Chinese Mystery Snail by Collas, Breedveld, Matthews, van der Velde, *et al*. 2017; Matthews, Collas, Hoop, van der Velde, *et al.* 2017), dispersal vector (e.g., ballast water by Casas-Monroy, Linley, Adams, Chan, *et al*. 2013; aquaculture by Kohler 1992), jurisdiction (e.g., Canada by Mandrak et al. 2011; Canadian Arctic by Chan, Brnnenhuber, Bradie, Howland, *et al.* 2011), and waterways and watersheds (e.g., European waterways by Panov, Alexandrov, Arbaciauskas, Binimelis, *et al.* 2008; Great Lakes by Grippo, Hlohowskyj, Fox, Herman, *et al*. 2017). Perhaps the list is somewhat excessive, but it does demonstrate that models and protocols can be quite different. However, there are some common themes among them.

Risk assessments often contain three levels—screening level, rapid, and detailed—the assessment levels using increasing amounts of information and taking increasing amounts of time. Species assessed as low risk with moderate or lower uncertainty at a given level may need not be assessed any further at a higher tier, whereas species considered at moderate risk or higher—or high uncertainty—should be further screened at a higher level (Snyder, Mandrak, Niblock, and Cudmore 2012). According to Snyder, Mandrak, Niblock, and Cudmore (2012), there are four commonly used types of risk assessment protocols: scoring systems, decision tree systems, combination scoring-decision tree systems, and probabilistic systems. Scoring systems prioritize the risk or threat posed by nuisance invading species. The scores are assigned based on answers to a series of questions about the species. The questions include the species' biology and ecology; potential to arrive, establish, and spread in an area; and its potential impact on the invaded ecosystem. The decision tree is designed to screen species in or out of the class of invasive species in a systematic manner, usually using a dichotomous tree structure. Scoring and decision tree approaches can be combined, typically with the scoring system embedded within a decision tree framework. Probabilistic systems use prior knowledge of species biology and invasion history elsewhere to form invasion probabilities for the assessment area in question and incorporate quantitative uncertainty and variation. Details of each system are given in Snyder, Mandrak, Niblock, and Cudmore (2012) and need not be repeated here.

Usually, many people contribute to the assessment by answering several questions and rating the risk probability. In general, the smaller the scope (e.g., lake vs. watershed vs. district vs. province vs. nation), the easier it is to make a risk assessment. For example, cottage associations will probably find the following:

- Fewer dispersal mechanisms and invasion pathways
- Fewer available dispersal mechanisms
- Smaller ranges of water quality features (e.g., levels of pH. calcium, alkalinity, conductivity)
- Similar colonization potentials are similar for connecting lakes within their watershed
- Similar survival characteristics (e.g., habitat suitability, climate, water temperatures, etc.)
- Similar establishment criteria (e.g., minimum and maximum temperatures for reproduction)
- Similar environmental effects (e.g., competition, predation, parasitism) because species assemblages are similar
- Similar economic and social effects

One example of a risk assessment tool comes from the Alberta Invasive Alien Species Working Group (Alberta IASWG 2008). Their calculation of overall risk is the sum of environmental risk + economic risk + social risk; each is calculated as a product of exposure (e.g., environmental risk = exposure x environmental effect). Exposure = (present status + introduction) x (survival) + (establishment) + (dispersal ability). They developed criteria 1.1 to 1.22 (defined below), where:

[Present Status + Introduction] = ∑ [(1.1–1.3) + 1.4–1.8)]

[Survival] = [∑1.9–1.12]

[Establishment] = [∑1.13–1.19]

[Dispersal Ability] = [1.20–1.22]

Exposure Score = ∑ [(1.1–1.3) + (1.4–1.8)] x ∑ [1.9–1.12)] + ∑ [1.13–1.19] + ∑ [1.20–1.22].

Then they summed all scores from effects:

Environmental Effect = ∑ (2.1–2.13)

Economic Effect = ∑ (3.1–3.14)

Social Effect = ∑ (4.1–4.9)

Now, to explain their criteria and scores for 1.1–1.22, 2.1–2.13, 3.1–3.14, and 4.1–4.9 (without explaining each one): For present status (Is it here?), they give a rationale for the criterion, pose questions, and provide their scoring system:

1.1 Is the species present in the assessment area?

0 = Not present
3 = likely not present
6 = Likely present
9 = Confirmed
9 = Unknown

1.2 What is the abundance of the species in the assessment area?

0 = No abundance
1 = Rare/trace
2 = Occasional
3 = Scattered
4 = Abundant
4 = Unknown

Guidance is provided for each score (e.g., rare/trace = sporadic numbers; occasional = low or occasional numbers; scattered = moderate or scattered numbers; abundant = dense or high numbers). The decision is made on knowledge of the species' maximum abundance; for CMS, go to Chapter VI. Ecology, which states the maximum density would be > 40 m^{-2}. Rare would then be arbitrarily selected, for example, rare 5%, occasional 5–10%, scattered 10–25%, abundant > 25%. Unknowns are scored as maximum numbers.

For environmental criteria, including competition, predators, and parasites, these questions are asked:

2.1 Is the species known to compete for resources with desired non-native species?

0 = No effect
1 = Mild effect
2 = Moderate effect
3 = Severe effect
3 = Unknown

2.4 Is the species a predator or parasite of a desired non-native species?

0 = No effect
1 = Mild effect
2 = Moderate effect
3 = Severe effect
3 = Unknown

2.7 Is the species a host or vector for known diseases, parasites, or pests that will cause harm to desired non-native species?

0 = No effect
1 = Mild effect
2 = Moderate effect

3 = Severe effect
3 = Unknown

For CMS and JMS, refer to Chapter VI. Parasites, which states they are hosts to native parasites with no known effects. Guidance might include mortality rates, if any.

The economic effects (3.1–3.13) given in Alberta's tool include industry, agriculture, and aquaculture, but cottagers might include property value and recreational impacts (public beach costs). Scores could be as follows:

0 = No effect
1 = Mild effect
2 = Moderate effect
3 = Severe effect
3 = Unknown

Guidance might include devaluations of properties since the arrival of the snails and loss of revenues at beaches, restaurants, accommodations, etc.

Some social effects (4.1–4.9) described in the Alberta tool might be expected for CMS and JMS:

4.1 What will be the expected effects on human health and well-being?

0 = No effect
1 = Mild effect
2 = Moderate effect
3 = Severe effect
3 = Unknown

4.7 To what extent will the species lead to reduced or lost food supplies (including fish and game) traditionally available from the assessment area?

0 = No effect
1 = Mild effect
2 = Moderate effect
3 = Severe effect
3 = Unknown

Guidance would include documented evidence of human diseases caused by parasites hosted by CMS and JMS. Some parasites hosted by molluscs affect fish and waterfowl; any Chinese or Japanese mystery snails acting as intermediate hosts of fish parasites would be considered here.

After the questionnaire is completed and scores assigned, the calculations of risk for each effect (environmental, economic, social) can be made using the formulae given earlier. Summing all three will give the overall risk.

Before summarizing this chapter, it is prudent to remind ourselves of the precautionary principle and two types of false alarms enunciated by Hansen and Tickner (2013, 17) in risk analyses: (1) "false negatives — instances where early warnings existed but no preventive actions were taken. In debates surrounding the precautionary principle it is often claimed that widespread application of the principle will lead to a large number of regulatory false positives — over-regulation of minor risks and regulation of non-existent risks, often due to unwarranted public 'fears." (2) "false positives, where government regulation was undertaken based on precaution but later turned out to be unnecessary." They identified 88 cases to be alleged false positives, but their detailed analysis showed most of them to be either real risks, or cases where "the jury is still out, or unregulated alarms, or risk-risk trade-offs, rather than false positives" (Hansen and Tickner 2013, 17). For CMS and JMS, many of the impacts can be categorized as the jury is still out.

F. Chapter VIII Summary

The chapter begins with defining native, resident, invasive, exotic, and introduced species. Native species have been present since prehuman time (i.e., they have a pre-Pleistocene geological record). Resident species include ex-invasive species that have become established locally and have potential competitive significance. Invasive species are any non-resident species that are intentionally or accidentally introduced that can maintain, spread, and reproduce in the new habitat. Exotic species are those that have been introduced to a place or have otherwise become established because of human activities but have not dispersed much beyond the watershed in which they were introduced. Exotic species could be embraced by introduced species, which are any intentionally introduced non-resident species that can maintain, spread, and reproduce in the new habitat. Introduced species should apply only to those intentionally introduced, like brown trout and rainbow smelts. The Chinese and Japanese mystery snails are categorized as invasive species to compare them to ex-invasive species, like the faucet snail, New Zealand mud snail, red-rimmed melania, and bivalves like the zebra and quagga mussels and the Asian clam.

Both negative and positive impacts are addressed. Among the negative impacts addressed are the following: (1) Competition with native and ex-invasive species; this has not been demonstrated to result in the extinction of native species, at least based on life history metrics, tolerances and requirements, and habitat selection by *C. chinensis* and *C. japonica*. (2) Parasitism is a significant issue in Asian mystery snails but not in North America. The main parasites are *Aspidogaster conchicola* and *Echinostoma recurvatum*, both native to and parasitize native and ex-invasive molluscs well established in North America. The cosmopolitan *E. recurvatum*, while commonly reported from freshwater molluscs of North America, has never been found in Chinese Mystery Snails. *Aspidogaster conchiola* does use CMS as a host. (3) Ecosystem functioning is balanced by differences in life history traits and habitat selection by native, ex-invasive, and invasive Chinese and Japanese mystery snails. (4) Misconceptions or lack of studies provide basic estimates of Chinese or Japanese mystery snail's socioeconomic impacts.

Perhaps the most misunderstood of all impacts is competition. Mesocosm studies are needed to analyze competitive interactions between and among snail species, both pulmonates and operculates, the former because they are grazers of algae and the latter because they also filter feed. However, mesocosm studies can accommodate only a limited number of variables, a tiny fraction of those operating in the natural environment, including temporal and spatial variations, including immigrating and emigrating snails and predators, species of other taxa (e.g., insects, crustaceans, fish) with similar functional feeding behaviors, depth preferences (e.g., sediment vs. water vs. sediment-water interface), etc. The literature is quite clear that invasive species are not known to extirpate native species through competition, at least within the same functional feeding group(s) in the scope of herbivorous and/or filter-feeding snails). Still, changes in species assemblages have been demonstrated after the arrival of some of the most impactful species (e.g., the zebra mussel). Parasites and predators can also eliminate species, especially those with specific host preferences. From my perspective, vis-á-vis mystery snails, impacts in nature purported to be due to competition take a back seat to those caused by parasitism, predation, and socioeconomics.

Several beneficial impacts are presented, including their nutritional value as food, medicinal uses, like snail slime used to eliminate warts and treat burns, skin conditions, and wounds due to the slime's antioxidant contents. These uses are good molluscan examples of biomimicry, or innovation inspired by nature. The slimy mucus of snails contains mucin, composed of hyaluronic acid, glycolic acid, allantoin, and metals, all of which have been incorporated into the pharmaceutical production of different human health and skin care products.

Despite state and provincial prohibitions to buy, sell, transport, or introduce by planting or releasing individuals in a free-living state into public waters, the Chinese and Japanese mystery snails are popular aquarium pets. Evidence is presented to indicate that some species may benefit ecosystems that have lost former functions to environmental degradation. However, the most potential concern is the bioaccumulation of metals from sediments by mystery snails to levels that may be toxic to humans.

Finally, risk assessments are discussed, and one example is provided to help explain the risk assessment process. The risk assessment includes calculations for environmental, economic, and social risks. Some example criteria and their scoring systems are given to help demonstrate its use for cottagers.

CHAPTER IX

CONTROL OPTIONS

A. Introduction

Categorizing a species as invasive conjures up immediately zebra and quagga mussels, arguably the two most invasive and nuisance of all freshwater species introduced to North America. However, when discussing control options, those of the zebra mussel seem to set the agenda for evaluating the most effective to the least effective. Claudi and Mackie (1994) and Mackie and Claudi (2010) review the impacts, summarized in Table 9-1, and the control options and evaluate the efficacies of the several physical, chemical, and biological options for mitigating the impacts of zebra and quagga mussels. Nalepa (2014), basing his experience in the Laurentian Great Lakes relative to Swedish lakes, recommended assessments of invader potential by conducting a thorough assessment of invaders relative to potential vectors of introduction; this advice would apply to all newly invaded lakes. In addition, he recommended an assessment of long-term monitoring programs to provide baseline information of the ecosystem and track ecosystem responses if indeed an invader becomes established.

Before engaging in offering control options for the Chinese and Japanese mystery snails, it is necessary to examine the purported impacts of mystery snails and the need for control options. Fortunately, the life history tactics of the zebra mussel and quagga mussel are much different than those for CMS and JMS (see Table 8-2). In particular, the planktonic larval stages of the zebra and quagga mussels add to their enhanced dispersibility over the brooding habit of the mystery snails, which immediately excludes control options for preventing larval settlement and byssal attachment, including coatings on intake trash racks and walls of pump wells. In addition, millions of planktonic larvae can be distributed much more widely by water currents (e.g., advection, Langmuir circulation, surface and internal seiches, Coriolis forces, etc.), than tens of purely benthic-destinated embryos. Add to this the depth limitations of CMS and JMS to primarily 3–4-m depths. Any structures much deeper than 3–4 m generally need not be considered for control options. Densities of settled zebra mussels are orders of magnitude greater than those of CMS and JMS. The numbers and kinds of control options depend on the severity and impacts of human activities, navigation and fishing buoys, industrial and municipal facilities, and repair and remediation costs. Because zebra and quagga mussels are strongly attached to surfaces by byssal threads, the animals must be blasted (e.g., with water jets) or scraped off their attachment base. On the other hand, mystery snails merely need to be touched; the snail withdraws its head and foot (thereby losing its attachment) and covers its aperture with its operculum to prevent desiccation.

Based on Table 9-1, CMS and JMS lag far behind in published confirmed impacts and control options. Among the impacts purported in many published articles (many are fact sheets) are the large densities of CMS and JMS; for example, "fishermen often made seine hauls containing two tons of snails" (*C. japonica*). (Wolfert and Hiltunen 1968, 32). They were a nuisance to fishermen, which prompted Wolfert and Hiltunen (1968) to perform surveys of Sandusky Bay in Lake Erie. They surveyed 34 stations with a 16-ft (4.9-m) semi-balloon otter trawl fixed with a heavy chain attached to the footrope of the trawl to help ensure the collection of specimens that were partially buried in the sediment. Each tow covered about 0.1 hectares of the bottom. A total of 3,787 specimens of *C. japonica* were collected from the bay; the largest number collected in one haul (0.1 hectares, 1,000 m^{-2}) was 783 specimens on the north shore of Lower Bay. Or, to express this largest number in density m^{-2}, 783/1,000 = 0.78 m^{-2}, a small density, considering the average density of CMS is 1–8 m^{-2}, the highest reported being 40 m^{-2} (see Chapter VI. Ecology, B. Population Dynamics, 2. Density). Even 40 m^{-2} is small compared to many native snails, like *Physella gyrina* (168–1,928 m-^{2}), *Gyraulus deflectus* (2,686–15,378 m^{-2}), and *Valvata humeralis* (82–7,686 m^{-2}), all reported by Gillespie (1969). Other invasive snails, like the New Zealand mud snail for which Kerans, Dybdahl, Gangloff, and Jannot (2005) reported as high as 299,000 m^{-2}, and for *V. georgianus*, 215 m^{-2} by Browne (1978), comparable to 258 m^{-2} reported by Jokinen, Guerette, and Kortmann (1982).

Under the heading "Natural Mortality," Wolfert and Hiltunen (1968) reported many decomposing Japanese snails floating in Saginaw Bay, Lake Erie, suggesting the mortality probably resulted from winter kill, old age, or both. Mortality due to senescence (aging) is natural, but winter kill is death due to low-oxygen stress. Likewise, the mortality observed by Wolfert and Hiltunen (1968, 37) in the marshes bordering the bay during the summer, when "many snails were stranded on hard, sunbaked mud, and clay," is mortality due to thermal and/or desiccation stress. There is no control for mortality due to senescence (or natural predation, competition, etc.), but there are for anoxia and thermal stresses. The controls for anoxia can be the reduction of nutrient inputs that cause eutrophication in the bay or the use of artificial oxygenation of waters in areas of high socioeconomic value (e.g., fisheries). Dredging of organic sediments with high internal loadings of phosphorous can also reduce anoxia. However, eutrophication is a long-term process, and so are the remedies. So are the remedies for the impacts of climate change on the water cycle; the most evident are the effects on evaporation and precipitation, causing more severe droughts and floods and more severe weather events.

Table 9-1. Impacts of zebra (ZM) and quagga (QM) mussels compared to Chinese (CMS) and Japanese (JMS) mystery snails. O = not addressed in the literature; P = purported in the literature; R = confirmed in the literature; RC = confirmed with control options.

Impacted Systems	ZM, QM	CMS, JMS
Industrial Structures		
Navigation, fishing buoys	RC	O
Fishing gear, nets	RC	P
Water intake cribs	RC	P
Water intake trash bars	RC	O
Penstock, intake tunnels	RC	O
Forebays	RC	O
Traveling screens	RC	O
Pump wells and houses	RC	O
Instrumentation	RC	O
Condenser cooling systems	RC	P
Safety, fire protection systems	RC	O
Dams, impoundments, holding ponds	RC	O
Locks and canals	RC	R
Human Recreational Systems	RC	
Aquaria	RC	R
Golf course sprinkler systems	RC	O
Shell windrows on beaches	RC	P
Boats, motors, trailers, anchors	RC	R
Ecosystems	RC	
Competition with native species	RC	P
Infestations on molluscs	RC	O
Plankton removal	RC	O
Food webs	RC	P

Such impacts are of global cause, like climate change and acid precipitation. The massive accumulations of shells that result in offensive odors due to their putrefaction is a result of human neglect at the personal and jurisdictional levels; included in jurisdictions are authorities from the top down: countries, states/provinces, municipalities, and individuals. Control of impact must be efforts by the different jurisdictions. The mass mortalities of invasive species are not directly due to the species themselves but neglect of causes in the deterioration of water quality (e.g., eutrophication, acid precipitation, pollution) and quantity (e.g., climate change, reservoir management).

Human health due to parasites is often, and justifiably, cited as an impact of the introductions of CMS and JMS. Fortunately, the impacts caused by the mystery snails acting as intermediate hosts of human or wildlife parasites have not yet been confirmed in North America. There is concern that the two mystery snails carried with them some of the Asian parasites when they were introduced. However, CMS and JMS have been in North America for over 130 years. There has yet to be any report of the Asian parasites among the most concern to human health. The parasites include the high-impact human intestinal trematodes, *Echinostoma cinetorchis*, *Echinoparyphium recurvatum*, *Echinostoma cinetorchis*, *Echinostoma macrorchis*, and *Euparyphium ilocanum*, all of which infect *C. chinensis*, and *E. macrorchis* in *C. japonica* (Chung and Jung 1999; Sohn, Chai, Na, Yong, *et al.* 2013). None of these species occurs in North America. The rat lungworm, *Angiostrongylus cantonensis*, was incriminated in a case of eosinophilic meningitis arising in an eight-year-old by Chang, Cross, and Chen (1968). Nevertheless, there continues to be a perpetuation of the fear of Asian parasites in the two North American mystery snails, perhaps impending but not of current concern.

There are other published reasons for the need to control *C. chinensis.* Seng and White (2003) reported shells of large exotic snails clogging intake screens at two power generating plants in Marion County, Indiana. Apparently, "the large conically shaped shell creates a troublesome problem for the plant maintenance, as the shells clog the cooling water condenser tubes (Seng and White 2003, 15)." If the snails clog intake screens, how did they get to the condenser tubes? What were the sizes and densities of snails on the screens and in the condenser tubes? What depth and how far from shore is the intake? Zebra and quagga mussels are known to clog screens and condenser tubes (Claudi and Mackie 1994), but their densities are three to four orders of magnitude higher than that of the Chinese Mystery Snail; were any zebra or quagga mussels associated with the purported mystery snail? These questions need to be addressed before confirming the mystery snail as a problem with water intake and before offering control options.

Sax, Stachowicz, Brown, Bruno, *et al.* (2007) contend that much of the world is becoming dominated by ecosystems composed of species that do not share a long evolutionary history. As globalization and global climate change continue to occur, a greater number of ecosystems will be made up of exotic species assembled from multiple sources. These contentions imply that invasive (or ex-invasive, introduced, exotic) species will outcompete native species. The impact of CMS on native gastropods as competitors and altering ecosystem structure has been exhaustively addressed in Chapter VI. B. Population Dynamics, 8. Competition, but culminating in contradictory scenarios. Perhaps we are in a transitional stage of exotic species dominating snail assemblages in current ecosystem structures, or mesocosm studies do not definitively validate impacts, such as changes in algal biomass, algal species composition, and increases in N: P ratios (Johnson, Olden, Solomon, and Vander Zanden 2009). But then, there is a lack of or weak evidence of impacts on alterations in native snail assemblages reported by some (e.g., Solomon, Olden, Johnson, Dillon, *et al.* 2010; Ellman 2019). Invasive predators reported to have greater impacts on native snail assemblages than the invasive CMS (Johnson, Olden, Solomon, and Vander Zanden 2009; Olden, Larson, and Mims 2009) may not be definitive evidence either. A lake ecosystem study by Olden, Larson, and Mims (2013) showed that high densities of CMS might influence microbial communities either directly by using bacteria as a food source or indirectly by producing sufficiently large quantities of fecal and pseudofecal material. These waste materials affect bacterial activity and growth, suggesting such impacts may be large and should be further investigated to understand better its potential role in coupling benthic and pelagic food webs in lake ecosystems.

Options for eliminating or reducing competition between established invasive and native species assemblages in an ecosystem are limited or are likely not to succeed definitively. It is too late once exotics become established. The best option is prevention; to repeat Franklin D. Roosevelt's axiom, "An ounce of prevention is worth a pound of cure," and this applies to invasive species (Leung, Lodge, Finnoff, Shogren, *et al.* 2002; Simberloff 2012). Kolar and Lodge (2001) and Brönmark and Hansson (2012) suggest that efficient control of invading species may require a more integrated approach where characteristics of both the invader and the invaded community are included.

Indeed, not all jurisdictions agree on the level of control. The Chinese Mystery Snail is a regulated invasive species in Minnesota; it is legal to possess, sell, buy, and transport and may not be introduced into a free-living state. They may not be released or planted in public waters (MN Administrative Rules, 6216.0260 Regulated). It is a restricted species in Wisconsin (NR40.05: Restricted) (Wisconsin DNR 2017). In Ontario, the Invasive Species Act sets out rules to prevent and control the spread of invasive species. It is illegal to import, possess, deposit, release, transport, breed/grow, buy, sell, lease, or trade them for prohibited invasive species. It is illegal to import, deposit, release, breed/grow, buy, sell, lease, or trade restricted invasive species. The Chinese Mystery Snail is not on either list yet. Alberta has restrictions on fishing-related activities licenses: invasive species: 11.01(1). “A person shall not place or keep an invasive organism in or allow an invasive organism to enter the water of any kind” (Government of Alberta 2016, 11); 11.02(1) regards possession of invasive species; and 11.03(1) regards importation of invasive species.

Once invasive species acts are enacted, several nonprofit organizations produce fact sheets to help control the spread of invasive species (e.g., Alberta Invasive Species Council 2020; Severn Sound Environmental Association 2020). Common recommendations for prevention/control are given below, with some comments:

- Vegetation that is attached to boats to be moved from one lake to another must be removed.
- Inspect all aquatic recreational and fishing equipment (bait buckets) after use and ensure they are cleaned, drained, and cleared of all mud and plant material, including anchors with mud and debris attached.
- Drain bilge pumps (not needed if the pumps have screens to prevent the entry of smallest juveniles; adults are too large to gain entry even without screens; they do not have planktonic larvae like zebra mussels; snails cannot swim).
- Motors should be drained, and the live well and bait well plugs pulled. But remember, snails cannot swim or jump at any stage in their life history. Chinese and Japanese mystery snails are not like zebra mussels, which produce free-swimming larvae; instead, they have live young at about 5 mm minimum dimension. In outboard motors, water is drawn into the water pump through a grate-like inlet on the lower unit just above the propeller, entering the water pump itself. Some may have a plastic screen over the inlet. These can become clogged up with debris (unlikely containing snails of any species) fairly quickly, especially if the lower leg of the engine does not come out of the water completely when the boat is not in use. If it does appear clogged, remove the screen, if possible, or use a small scraper or pick to clean the area. Once the water passes

through the engine, it exits through a "squirter" on the lower side at rear of the engine. The flow from the squirter should be steady and strong. If the flow is weak or stopped, clear the squirter with a wire. If steady and strong flow does not come back after running the engine, the problem is most likely the water pump impeller. As impellers age, the rubber blades lose their strength and cannot push the water as easily as new. The damaged impeller will reduce the pressure and volume one sees exiting from the squirt nozzle. Get the impeller fixed before it fails. All this preamble indicates that Chinese or Japanese mystery snails cannot enter the water pump or even reach the squirter. If zebra mussels are in your lake, drain the motor before moving the boat. As for live and bait wells that are filled by a water pump with an entry through the hull of the boat, the entry port is too small for mystery snails to enter, but they (or any snail species) may be plugging the port; merely remove them from the port. The drains of the wells also exit through the hull of the boat. The exit port may also have snails covering the port, and these need to be removed.

- Waterfowl hunting equipment (decoys, waders, etc.) should be thoroughly washed and left in the sun to dry for several days. Snails of any species may be embedded in mud, which should be carefully searched and washed.
- Clearing water intake pipes is possible for cottage intakes near the bottom of shallow lakes. Many intakes have a foot valve that prevents water from draining back into the lake. Most foot valves have a screen or slots to prevent debris from entering the valve. Check the foot valve for any debris, snails, or other aquatic life that may be clogging the openings.
- Do not purchase or keep Chinese or Japanese mystery snails.

Some options for controlling the spread and nuisance aspects of Chinese and Japanese mystery snails have been offered in the literature. Unfortunately, the options are few, likely because they have garnered no socioeconomic interest. Only when the economics of an impact becomes high or whenever a threshold cost is attained do funds seem to become available to support studies for control options. The options are divided here into physical and chemical control options, with some comments.

B. Physical Control Options

Four physical control options have been addressed in the literature: temperature, water velocity, air exposure, and desiccation, the latter two being somewhat related.

1. Temperature

Van der Schalie and Berry (1973) examined the effects of temperature on optimal growth and reproduction and the lethal thresholds of several species of freshwater gastropods. They found sensitivity to temperature surprisingly narrow, especially for reproduction. Gonad development was arrested at even slight increases in temperature (e.g., 5ºC). However, they examined only one prosobranch (*Amnicola limosa*). They recommended using the "plop test" to determine the effects of temperature on operculates, such as viviparids. The plop test subjects animals to sudden changes of temperature in tanks, from room temperature. While flop tests may provide upper lethal threshold values for temperature, chronic effects on life history traits, like fecundity, would also be valuable.

The optimal water temperature for *C. chinensis* to grow and develop is between 20–28ºC; it hibernates while the water temperature is lower than 10–15ºC or higher than 30ºC (Li, Wu, Lu, Zhang, *et al.* 2013). The Chinese Mystery Snail has a wide temperature tolerance, with adults surviving acute heating to approximately 45ºC and freezing water temperatures for > 24 hours (Haak (2015). Haak (2015) also observed no reproduction at water temperatures ≤ 12ºC. Collas, Breedveld, Matthews, van der Velde, *et al.* (2017) gives 0–30ºC as a range for the establishment of CMS in North America.

The use of high temperature (> 40ºC) as a control option for CMS is perhaps viable in industrial settings, specifically, hydrogenating plants with thermal backflush capabilities. But the issue is still the likelihood of CMS to plug condenser tubes. In some fact sheets, there are parenthetic remarks that "shells of large exotic snails have been clogging intake screens" (USFWS 2018, 6); was the species in fact CMS? Apparently, the large conically shaped shells of snails also create a troublesome problem for the plant maintenance, as the shells clog the cooling water condenser tubes. These incidental remarks need to be expanded upon to explain whether the large conically-shaped snail densities are high enough that a control option is required and to explain how the snails get from the lake intake to the pump well. The intakes are often a few kilometers offshore, in deep water, and largely inaccessible to CMS. If they reach the pump well, they will likely settle lifelessly to its floor (they cannot swim) or be shredded by the turbines before reaching the condenser tubes.

2. Water Velocity

Rivera (2008) found that current velocities ranging from 2.2–22 km^{-hr} in culverts can prevent the *C. chinensis* from going upstream. The snails were not as abundant as expected in his creek site, and they do not express a preference for upstream or downstream migration. He suggested using a culvert or any other means of accelerating the water current as a management tool for an invading population of *C. chinensis*. However, CMS is a quiet-water species, preferring standing waters with minimal flows, and are rarely found in fast-flowing waters, which likely explains its absence in Rivera's creek site. The need for culverts as a control option, therefore, becomes redundant. Placing a culvert in an area with CMS may result in migrations of snails into the culvert to avoid predators. If the culvert is easily removable, it may be a method for capturing large numbers of CMS and then disposing them.

3. Air Exposure

Havel (2011) found the resistance of CMS to air exposure robust and dependent on ranges of temperature and relative humidity. Using field studies, he found the LT_{50} for medium-sized shells was > 28 days at temperatures ranging from 8–30°C and relative humidity from 37–100%. Using small shells in lab bioassays at temperatures ranging from 19–22°C and relative humidity ranging from 33–42%, the LT50 was > 3 days. These results indicate that individuals can survive exposure to air for at least four weeks, and larger juveniles were more resistant than smaller juveniles. His 2014 studies better simulated boater transport by placing snails individually in mesh bags, hung outdoors and allowing exposure to both sun and rain while recording temperature, precipitation, and humidity. CMS survived nine weeks and released viable young after 54 days of exposure, clearly allowing long-term transport overland. It may be a control option to prevent spreading if it takes more than four to nine weeks to travel from one lake to another. Still, the distances involved are likely from East to the West Coast or from the most northern latitude to the most southern latitude in North America and back again.

Unstad, Uden, Allen, Chaine, *et al.* (2013) also tested the ability of individual *B. chinensis* to survive prolonged periods of air exposure, but due to impoundment drawdowns, using laboratory bioassays. They found survival in air exposure up to > nine weeks with survivorship greater among adults 41–56 mm high than juveniles < 40 mm high. Thus, they recommend that drawdowns alone may not be an effective means of eliminating *C. chinensis* from impoundments.

4. Desiccation

Strachan, Chester, and Robson (2015) define desiccation tolerance as the ability to dry to equilibrium in air (< 0.1 g H_2Og^{-1}) that is moderate to extremely dry and then to regain normal function after rehydration. The highest post-desiccation survival rates occur after slow drying that gives individuals sufficient time to adjust their metabolism. Hibernation occurs in habitats that freeze in the winter with no free water, common in high latitudes. During this period, there is slowed metabolism. In lower latitudes, desiccation is associated with long periods of drought and induces aestivation, a period of slowed metabolism during a hot and dry period.

Invertebrates survive adverse conditions by using physiological adaptations and/or behavioral responses, including strategies defined as resistance traits or strategies because they allow individuals to resist the drying of water bodies (Strachan, Chester, and Robson 2015). Viviparids respond to dormancy by quiescence, a period of inactivity, regardless of its physical or metabolic state. The driving force for dormancy is temperature-related, hot leading to aestivation, cold to hibernation. The physiological response to aestivation is a hidden state called cryptobiosis; if it is in a dehydrated state, it is called anhydrobiosis.

Kew (1893) was among the earliest to report the ability of viviparids to survive long periods of desiccation. He reported a specimen of *Paludina vivipara* that was “accidentally ‘ejected’ from an aquarium and allowed to remain for more than three weeks on the ground in a field; on being restored to its fellows seemed to have taken no harm” (Kew 1893, 28). On the other hand, Haak, Chaine, Stephen, Wong, *et al.* (2013) observed a massive die-off of CMS in a reservoir during three months of an extreme drought event, coincident with abnormally hot and dry weather. Haak (2015) demonstrated in laboratory bioassays that adult CMS could survive a nine-week desiccation period. Desiccation may also be a control option to prevent spreading if it takes four to nine weeks of travel time from one lake to another, which is unlikely to happen, as explained for air exposure.

C. Chemical Control Options

1. Dissolved Oxygen

For DO, the occurrence of the *C. chinensis* ranges from 7.0–11 mg^{-L} in Connecticut waters (Jokinen 1982a). Harman (1974) lists 1–8 mg^{-L} as the range for the occurrence of *V. georgianus* in US waters. Haak (2015) examined the effect of temperature on the oxygen consumption rate (mg O_2^{-Kg-Hr}) of CMS adults > 22.4 mm, the highest rate being 187.9 mg O_2^{-Kg-Hr} at 20^{o}C and the lowest being 74.0 mg O_2^{-Kg-Hr} at 27^{o}C. Snails were still active at 12^{o}C and 173.2 mg O_2^{-Kg-Hr}. He did not test the rates at temperatures lower than 12^{o}C. As a reminder, the availability of DO to aquatic life is better expressed as percentage of saturation, not the absolute value in mg^{-L}, because the solubility of oxygen is inversely related to temperature; the lower the temperature, the more soluble the DO. Further, 100% DO occurs at several temperatures, for example at 1^{o}C, 100% occurs with 14.2 mg^{-L}; 4^{o}C, 13.1 mg^{-L}; 8^{o}C, 11.8 mg^{-L}; 14^{o}C, 10.3 mg^{-L}; 20^{o}C, 9.1 mg^{-L}; 26^{o}C, 8.1 mg^{-L}. Using the ranges in values of DO given above, 8 mg^{-L} could be 100% saturation at 26^{o}C, but only 56.3% saturation at 1^{o}C. 1 mg^{-L} is only 10% saturation at 26^{o}C and 7% saturation at 1^{o}C. Pulmonates, which have lungs and can respire atmospheric oxygen, are generally more tolerant of low DO than are prosobranchs. However, *V. georgianus* has been collected at a low surface value of 0.4 mg^{-L} (Harman 1974). However, from personal experience, *C. chinensis* cannot survive anoxia under the ice (~0^{o}C) for more than one to two months; see discussion under Chapter VI. G. Tolerance and Toxicity, b) Dissolved Oxygen.

2. Metals

There appear to be no bioassays showing the toxicities of various metals. Two studies examined the bioaccumulation of metals in *C. chinensis*. Tornimbeni, Galvez, Triffault-Bouchet, Dassylva, *et al.* (2013) estimated concentrations of heavy metals to describe their relationship to values of metals in rice paddy field sediments. The overall common trend in the heavy metal concentrations (mg^{-Kg} dry tissue) was: Fe > Mn > Zn > Cu > Ni > Pb > Cd > Cr, or 224.3 > 68.8 > 56.9 > 10.8 > 1.05 > 1.0 > 0.6 > 0.3, respectively. However, their analyses showed that *C. chinensis* could not be used as a bioindicator of heavy metal pollution because of the lack of correlations between body content and sediment content. This lack of correlation between tissue levels in CMS from rice-paddy fields was also reported by Kurihara and Suzuki (1987a, b). Still, the trends were almost identical to those of Tornimbeni, Galvez, Triffault-Bouchet, Dassylva, *et al.* (2013). In short, metals are not a control option until the acute toxic levels of metals to CMS are known.

3. Pesticides

Studies on the effects of pesticides on mystery snails are limited. However, Haak, Stephen, Kill, Smeenk, *et al.* (2014) tested the efficacy of copper sulfate and rotenone as potential control chemicals to eliminate adult CMS using laboratory bioassays. All snails survived exposure to 1.25 mg^{-L} copper sulfate solution, 90% survived exposure to 2.50 mg^{-L} copper sulfate solution, and 80% survived exposure to 5.0 mg^{-L} copper sulfate solution.

Copper sulfate is a well-known control agent for invasive species (Mackie and Claudi 2010). However, it is difficult to obtain a certificate of approval for its use in natural settings. It could be considered in closed systems if and when CMS has been shown to impact such systems.

Haak, Stephen, Kill, Smeenk, *et al.* (2014), tested rotenone as a control agent and found 100% survival of *C. chinensis* after 72-hour exposure to rotenone-treated lake water and 96% survival after 72-hour exposure to pre-determined rotenone concentrations of 0.25, 2.5, and 25.0 mg^{-L}. All snails survived in the control aquarium, the 0.25 mg^{-L} aquarium, and the 2.5 mg^{-L} aquaria. Nine of the ten snails that survived in the 25.0 mg^{-L} aquaria survived. Rotenone and copper sulfate are unlikely to be successful unless they penetrate the operculum or the shell at higher concentrations than were tested.

D. Dispersal Control Options

The most likely dispersal vectors of *C. chinensis* and *C. japonica* are birds (gulls), waterfowl, and humans; overland transport of the snails by trailered boats is possible but not probable, as discussed further below. Chapter VII has already described the potential of birds as dispersal vectors of the two species, which is highly likely. Humans are also probable dispersal agents, especially considering the snail species seem to be associated in some way with human activities, a relationship considered synanthropic because they live in close association with people and benefit from their surroundings and activities. As discussed in Chapter VII, both CMS and JMS likely qualify as synanthropic, based on two anthropogenic vectors, disposal of aquarium pets, and arguably overland transport of trailered boats.

Disposing of aquarium invasive plants and animals into wild habitat (e.g., ponds, lakes, rivers, etc.) is a well-known unintentional (or occasionally intentional) mechanism for spreading invasive species, especially fish (Courtney and Taylor 1986; Courtney and Stauffer 1990; Courtney 1999; Rixon, Duggan, Bergeron, Ricciardi, *et al.* 2005), but also *C. chinensis* and *C. japonica* (Schmeck 1942; La Rocque 1948). The recent introduction of zebra mussels attached to moss balls in the United States and Canada has resulted in many pronouncements for immediate protocols for controlling the moss with invasive invertebrates. Very quickly, instructions have been developed by state and provincial jurisdictions for people who have moss balls in their aquaria to carefully decontaminate them, destroying any zebra mussels and larvae they contain using one of several methods. Each jurisdiction has its own protocols for destroying the moss balls. First, remove the pets (fish, snails, etc.) and put them temporarily in clean containers. Then, treat the water and moss (e.g., by freezing them for at least 24 hours, raising the water temperature to 50°C for one to two minutes, add diluted chlorine bleach or salt (sodium chloride), or submerge them in undiluted white vinegar for at least 20 minutes. Then, dispose of the moss balls and water. These decontamination instructions have been developed by the US Fish and Wildlife Service, the USGS, representatives of the pet industry, and federal (e.g., Department of Fisheries and Oceans) and provincial (e.g., Alberta, British Columbia, Ontario, Québec) authorities.

Duggan (2010) examined a variety of methods for the disposal of aquarium water. Of the 55 tanks he recorded,

- 19 disposed of their washings on the garden (16 of 43 owners),
- 27 put their washings exclusively down the sink (19 owners),
- 5 tanks had their washings either poured on the garden or poured down the sink (4 owners),
- 2 tanks never had water removed; one was a new tank, and the other owner did not feel the need to remove the water, even after having the tank for two years,
- 1 aquarium was disposed of in an external fishpond, and
- 1 was emptied into a stormwater drain accessible outside the window from the aquarium.

Duggan, Champion, and MacIsaac (2018) recommend chemical treatment for removal of invertebrates from macrophytes at or pre-border and from tanks containing plants at culture and retail facilities. UV light treatment was the final treatment step, which led to the death of individual invertebrates. Disposal in ornamental fishponds could act as a stepping-stone for species into natural waters via, for example, waterfowl. Given the large numbers of individuals modeled to be released from tanks, Duggan (2010) recommend that aquarium owners be educated on the potential risk of incidental fauna in their tanks and tip-washings on their lawns or gardens a best practice for disposal.

Courtenay and Robins (1975) and Courtenay and Taylor (1986) recognized the projected future growth of aquaculture and the aquarium industry and its continued use of exotic species. They found other animal escapes from these sources inevitable. To reduce risks from such escapes, fish and game agencies must regulate what can be imported. Operators should be required to make their facilities as escape-proof as deemed appropriate for the facility's geographic location and its proximity to open water (Courtenay and Taylor 1986). Such regulations must have a biological rationale, such as a lack of wisdom in prohibiting or restricting exotic species or require breeders or growers to have escape-proof facilities in areas where escapees could not overwinter in the wild. Courtenay and Robins (1975) stated that most incoming lots of fish are destined for shipment to wholesalers, retailers, and fish farms for cultural purposes. The vast majority of exotic species, now established in our waters, were released from this last source. Courtenay and Robins (1975) cited specific recommendations to solve the problem of accidental introductions of aquarium species, such as the enforcement of existing jurisdictional laws to eliminate purposeful introductions from the aquarium industry. They suggested that the home aquarist appears to play only a minor role in introductions. Labeling the plastic bags with warnings against the release of exotic species into natural waters aids the education process immensely. Aquarium societies should make the home aquarist aware of the undesirability of releasing unwanted stock, which is considered under several severe first-degree misdemeanors under some state laws and is illegal in most states and provinces. It is generally agreed that public education may be the best method to slow these introductions, although it is likely they never will be eliminated (Courtenay and Robins 1975; Courtenay and Taylor 1986; Courtenay and Stauffer 1990; Courtenay 1999).

Finally, and I leave this to the last for reasons that will become apparent, one of the anthropogenic pathways for spreading *C. chinensis* and *C. japonica* is deemed to be by overland transport of trailered boats from infected to uninfected lakes. I maintain this may happen, but it is not a probable pathway. Looking at the reasons from a process point of view as a boat is pulled out of an infected lake with a trailer and then transported, I offer these observations:

- Trailers sit for a long time on dry land and then are pushed into the water at a boat launch with either a concrete base or just lake substrate.
- The trailer is usually in the water for a very short time (e.g., 5-15 min).
- Snails in the immediate area creep, crawl, slither, and possibly (but highly unlikely) attach to the trailer in the short term while the trailer is in the water.
- If any snails attach with their foot, they detach as the trailer is pulled from the water because they retract their head and foot into the shell, sealing the aperture with the operculum, thereby losing their attachment and falling off.
- Some snails may be crushed by the wheels of the trailer while being pulled from the water.
- However, if the trailer pulls through a bed of submerged vegetation harboring snails or the wheel rims carry mud with snails, the snails remain protected by their operculum and may be transported overland.
- Careful inspection of the trailer for attached vegetation and mud and their removal will decrease the likelihood of the trailer as a vector for snail dispersal (i.e., a control option).

The boat is also a potential vector for dispersal of the mystery snails, but similar arguments as those for trailers and control options are presented here:

- Many boats may have been in the water for a long time (e.g., months), and snails could attach to the hull and motor, especially if the bow is sitting onshore or among vegetation.
- As explained earlier, it is unlikely snails will enter the water intake, the water pump and impeller, or via pumps to the live and bait wells, but if any end up in the wells (e.g., with vegetation), the plants and snails (even juveniles) are easily spotted and removed.
- Only snails attached to the hull and motor shaft could be transported overland. However, as with the trailer, as soon as the boat is pulled out of the water, the snails withdraw their head and foot, dropping off as they lose their attachment.
- In addition, any snails attached to the hull in the areas the boat slides over the felted rails of the trailer will be crushed.
- As with the trailer, any vegetation attached to the boat and motor needs to be removed and discarded, with any snails among the leaves.

- One other control recommendation: there are not many crevices or channels that could protect juveniles that could remain on the boat when it is removed; if there are, check them closely and discard any snails found (and there may be more than one species).

An often-ignored refuge for snails is muddy anchors, especially when fishing by jigging in a hot spot for a few hours. Snails can crawl through the mud and settle on the anchor during the fishing event. Some mud and/or vegetation is often left on the anchors when retrieved and placed in the boat where operculate snails can survive long periods (four to nine weeks) in the drying mud. The anchors need to be flushed clean of the mud and vegetation in lake water before placing it in the boat, especially if it is trailered to another lake.

E. Chapter IX Summary

The zebra and quagga mussels seem to have set the agenda for evaluating impacts and the most to the least efficacious control options. These are compared to what has been published in the literature for *C. chinensis* and *C. japonica*. The purported impacts of mystery snails and the need for control options are briefly reviewed. The main factor is the different life history tactics between zebra and quagga mussels and those for the Chinese and Japanese mystery snails. The mode of attachment is also a factor—the strong byssal attachment of zebra and quagga mussels needs much more aggressive control options, such as hydroblasting or hydrolasing (e.g., use of ultrahigh water pressure) or scraping off zebra and quagga mussels, compared to a mere touch to induce snails to withdraw their organ of attachment, the foot.

Among the impacts purported in the literature are the large densities of CMS and JMS; for example, “fishermen often made seine hauls containing two tons of snails” (Wolfert and Hiltunen 1968, 32). A review of the densities of the Japanese Mystery Snails in Saginaw Bay, Lake Erie, from which the fish hauls were made, showed the density was 0.78 m^{-2}, a small density, considering the highest reported in the literature is 40 m^{-2}. Even 40 m^{-2} is small compared to many native snails, some as large as 7,686 m^{-2}, or other invasive snails, like the New Zealand mud snail with densities as high as 299,000 m^{-2}.

Some impacts are of global cause, like climate change and acid precipitation. The massive accumulations of shells resulted in offensive odors due to their putrefaction, a result of human neglect at several jurisdictional levels, including the top country leadership, states/provinces, municipalities, and individuals. Control of these impacts must be efforts by the different jurisdictions. The mass mortalities of invasive species are not due entirely to the species themselves but to neglect of causes in the deterioration of water quality (e.g., eutrophication, acid precipitation, pollution), and quantity (e.g., climate change, reservoir management).

Impacts of the two mystery snails on industrial and municipal water intakes have been reported but not to the extent that control options appear to be required. For example, there are no reports of human recreational facilities, such as golf course sprinkler systems, blocked by mystery snails or outboard motor intakes plugged by the mystery snails.

The impacts caused by mystery snails acting as intermediate hosts of human or wildlife parasites have yet to be confirmed in North America. It should be recognized that the Chinese and Japanese mystery snails have been in North America for more than 130 years without any report of parasites that are of concern to human health in Asia. This likely explains the little concern for actions to control even endemic parasites in ex-invasive species at this time. The parasites considered as high-impact human intestinal parasites are the trematodes *Echinostoma cinetorchis*, *Echinoparyphium recurvatum*, and *Echinostoma cinetorchis* and the nematode the rat lungworm, *Angiostrongylus cantonensis*.

Some parasites infect wildlife, such as the trematode *Sphaeridiotrema pseudoglobulus*. Harried, Fischer, Perez, and Sandland (2015) did successfully infect CMS, but the parasites were often found encased in the shells of the snails in a non-viable state. *Sphaeridiotrema pseudoglobulus* was implicated in waterfowl die-offs, but Harried, Fischer, Perez, and Sandland (2015), using experimental exposures, found that CMS infection levels were very low.

Modification of native snail assemblages have been reported in mesocosm studies, but extirpations of species have not been reported. Eliminations or reductions in abundances of native molluscs by competition from established invasive species have also been reported, but such impacts have not warranted control studies. If control options are offered, they are likely not to succeed in all scenarios. Once exotic species become established, they are almost impossible to control in large water bodies. The best option is prevention; to repeat Franklin D. Roosevelt's axiom, "An ounce of prevention is worth a pound of cure," which applies to invasive species. The findings so far suggest that the best approach to find an efficient control of invading species is to take a more integrated approach that includes characteristics of both the invader and the invaded community.

Some control options are evaluated for controlling mystery snails, including physical (e.g., temperature, water velocity, air exposure, desiccation) and chemical (DO, metals, pesticides), but none are of promise.

The chapter ends with a challenge of the overland dispersal by boats and trailers as a major pathway for the spread of mystery snails. The challenge is based on the long-term (> nine weeks) resistance to desiccation of both the Chinese and Japanese mystery snails by withdrawing their foot and head into their shells and sealing off the soft tissues with their operculum. In addition, the opportunity for mystery snails to attach to boat trailers is slim at best. If any attach, they will drop off immediately upon removal of the trailer from water. Finally, arguments are made that juvenile mystery snails cannot on their own enter water pump ports or cooling systems. Also, any snails attached to the boat hull or outboard transom will fall off for the same reason as trailers.

CHAPTER X

MYSTERIES ADDRESSED, MYTHS, CONCLUSIONS, AND RECOMMENDATIONS

A. Introduction

The answers to the 12 questions posed in the Preface are addressed first. Of the 12 responses, many agree with the hypotheses, some hypotheses are myths based on innuendoes, and some are still mysteries until definitive evidence is provided. Moreover, as stated in the Preface, hypotheses are usually tested with statistical methods, which are not provided herein. Still, the verdicts rely on published evidence to either accept or reject each hypothesis, designated in bold as **$H1_0$** to **$H12_0$**.

The myths are addressed after answering the 12 hypotheses. The myths arise from equating the invasive and nuisance traits of *C. chinensis* and *C. japonica* with those of zebra and quagga mussels. The single most obvious difference—and ignored attribute—between the mystery snails and zebra and quagga mussels are the benthic mystery snails directly developing embryos versus the planktotrophic development through larval stages before assuming a benthic existence. In other words, the zebra and quagga mussels have swimming stages, whereas the mystery snails do not. This single characteristic explains the differences in impacts and control options for the two types of development. Figure 10-1 is an overview of vectors, impacts, and controls resulting from the two types of development. The left panels show the scenarios documented in the text for indirect (planktotrophic) development using the zebra mussel. The panels on the right show the scenarios documented for direct (lecithotrophic) development using the Chinese Mystery Snail. The middle habitat panels show the lake scenarios. The dispersal vectors for the zebra mussel are much more diverse than for CMS. They have numerous propagules, or larvae in several stages (D-form, veliconcha, umbonal, pediveliger, plantigrades) settling out of the water column, while the adults spew more eggs sperm to perpetuate the life cycle. The numbers of planktonic forms range from 100,000 to 1,000,000 m^{-3}, and the adult density ranges from 10,000 to > 100,000 m^{-2}. This life cycle results in numerous kinds of impacts with documented costs of control options. The stark difference between indirect and direct development is the lack of swimming forms in the plankton for CMS, which cause fewer impacts, and, so far, no control options have been documented. The adult densities range from 10-100 m^{-2}, three to four orders of magnitude less than the zebra mussel.

After providing rationales for accepting or rejecting the hypotheses, a few remain mysteries, depending on one's choice of acceptance or rejection, both having some support. One mystery particularly relates to the question of the origin of the common name, "mystery snail," which applies to the entire family. But the Chinese and Japanese mystery snails have a unique history, dating back to Marco Polo, which is proffered in Chapter III and again below.

The conclusion focuses on the degree of invasiveness and nuisance of the two mystery snails. There can be little doubt that the main criterion for assessing the nuisance extent of an invasive species is controlling impacts, which makes the degree of impact a key variable. The higher the cost of diminishing or eliminating impacts, the greater the cost for a nuisance appraisal.

Finally, some recommendations for future research are provided. All are based on the lack of information for CMS and JMS to date.

B. Mysteries (Null Hypotheses, H_0) Addressed

1. $H1_0$: The two species are not nuisance species.

Nuisance is defined on p. 274 as a potential threat to native species through the economy, predation, grazing, competition, parasitism, disease, hybridization, or habitat alteration. Compared to the zebra and quagga mussels, the Chinese and Japanese mystery snails should be exempt from such a dubious distinction as a nuisance until substantial research proves definitively that they have impacts on (1) industrial and municipal structures and facilities and navigational and fishing equipment; (2) human recreational systems (e.g., golf courses); and 3) ecosystem structure and functioning assessed by such criteria as abundance, assemblages, parasitism, and predation; 4) and that the impacts justify control measures that affect society and economics at several jurisdictional levels (e.g., state, province, municipality, individuals). Costs at the federal government level will likely be the driver to promote the Chinese and Japanese mystery snails to a nuisance species.

Verdict: $H1_0$ is accepted at present.

Indirect Development

Impacts

Documented controls established

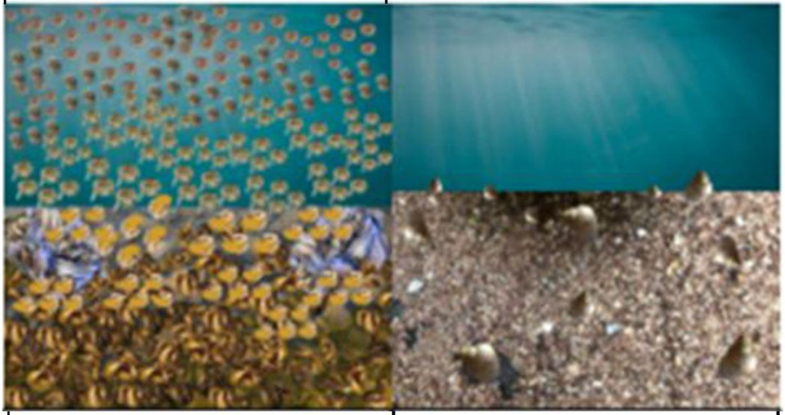
Industries & Utilities:
Intake trash racks, tunnels.
Forebays, wet wells.
Travelling screens.
Pumps.
Condenser tubres.
Service water systems.
Fire safety systems.
Emergency service water systems.
Navigational aids
Ecological:
Mussel species at risk.
Food web alterations.
Benthic community structure.
Recreational:
Beach shell debris.
Scuba diving activities.
Socio-Economic:
Costs for repairs & controls

Direct Development

Impacts

No established controls

Ecological:
Perhaps competition.
Recreational:
Beach shell debris.



Dispersal Vectors

Natural: Waterfowl, fish, currents.

Anthropogenic: Ships, commercial fishing boats, overland boat transport, aquarium releases, canals, commercial products (e.g. moss balls, plants), navigational aids, fishing equipment, accidenatl/intentional human dispersal.

Dispersal Vectors

Natural: Waterfowl.

Anthropogenic: Commercial fishing boats, aquarium releases, canals, accidental/ intentional human dispersal.

Figure 10-1. Overview of the effect of differences between indirect (left panels) and direct (right panels) development on their impacts and controls in industries, utilities (e.g., water treatment and hydrogenating plants), navigational aids (e.g., buoys), recreation, and economy.

2. $H2_0$: They do not compete and displace native species.

There is evidence that competition occurs with native species of gastropods. Still, the evidence is based on mesocosm studies that examine correlations between exotic and native species' responses, correlations that often do not translate into cause–effect relations. Moreover, responses based on mesocosm studies usually cannot be extrapolated to the natural habitat where myriad life history strategies exist. Behaviors, species abundances and assemblages, transient temporal factors (temperature, DO, water currents, etc.), and spatial factors (proximities of food, shelter, predators, etc.) occur naturally. They are not manipulated as in the mesocosms, as discussed in detail on pp. 310-316. In conclusion, as Lodge, Stein, Brown, Covich, *et al.* (1998, 53) professed, "unfortunately, no algorithms exist to guide scaling up from small-scale experiments to the whole-lake, long-term management scale."

Verdict: $H2_0$ rejected, likely with marginal significance.

3. $H3_0$: They do not eat eggs of fish, especially sport fish.

Yes, there is evidence that other viviparids (Banded Mystery Snail) will prey on fish eggs (e.g., largemouth bass), as reported on p. 309. However, there is no record of either *C. chinensis* or *C. japonica* feeding on eggs of any fish species. Mystery snails are herbivores, not predators. It is clear from the studies reported above that CMS and JMS are benthic feeders, grazing on attached algae on other snails and deposit feeding on algal and organic elements, living or dying, in the sediments. The preference of epiphytic algae over planktonic algae suggests that CMS relies more on grazing and deposit feeding than on food filtration. Neither CMS nor JMS have been reported to feed on fish eggs. If the snails are seen on clusters of fish eggs, it is likely random movement or snails feeding on attached algae, causing collateral damage to the eggs.

Verdict: $H3_0$ is accepted.

4. $H4_0$: They do not cause or abet blue algae blooms.

Based on mesocosm experiments, there is evidence that N:P ratios increase in the presence of *C. chinensis*, probably because of a low P-excretion rate relative to native snail species. Coincident with the rise in N:P ratios is a reduction in periphyton biomass (measured as mesocosm wall and sediment algae), suggesting CMS either does not affect algal biomass production, or there is an inverse effect relative to the N:P ratio, as discussed on pp. 310-311; the inverse relationship between low P-excretion rate and reduced periphyton biomass suggests CMS either did not affect algae biomass production or an inverse effect relative to the N:P ratio. Moreover, pp. 310-311, CMS reduced phytoplankton biomass, the loss in weight being mostly by toxic cyanobacteria and flagellates, whereas those with positive weight were mostly colonial green algae. Among the toxic cyanobacteria taxa that increased most strongly were *Cryptomonas ovata*, *Microcystis flos-aquae*, *Merismopedia tenuissima*, and *Microcystis viridis*, and the floating green alga, *Scenedesmus acuminatus*. *Merismopedia tenuissima* produces sheets or mats. *Microcystis viridis* is a harmful, bloom-forming alga that can produce neurotoxins and hepatotoxins, such as microcystin, and forms large surface blooms through rapid division and buoyancy in the production of gas-filled vesicles. *Scenedesmus* is a colonial, green alga that forms small chains of four cells and is often found floating on the water and not attached to bottom rocks.

Verdict: $H4_0$ is accepted.

5. $H5_0$: They are not tolerant of anoxia or contribute to anoxia.

Unfortunately, no data shows the tolerance of *C. chinensis* or *C. japonica* to different DO concentrations. The desired unit for oxygen tolerance is percentage of saturation because of the inverse effect of temperature on the solubility of oxygen, as expounded on pp. 357, 452. However, from personal experience, mortality of *C. chinensis* in a fishpond was due to anoxia for one to two months at 0°C. From published accounts of significant winter kills of *C. japonica* (see pp. 305, 443), both species are sensitive to anoxia, especially winter kills. There is no evidence that either species contributes to anoxia, which happens only during mass mortality events. Mass mortality usually occurs for more than one species, especially due to anoxia. Until bioassays determine the lower threshold tolerances of DO to the two mystery snail species, the evidence so far indicates neither is tolerant of anoxia.

Verdict: $H5_0$ is accepted.

6. $H6_0$: They do not carry infectious diseases and/or parasites unique to them.

In this age of pandemics, one of the greatest concerns of the introduction of *C. chinensis* and *C. japonica* is the co-introduction of human health parasites. Epizootics, outbreaks of disease affecting many animals, especially humans, are becoming commonplace. The parasites of these two snails of most concern are trematodes and nematodes. Of the trematodes, there are two classes, Monogenea and Digenea. Monogeneans are ectoparasitic flatworms found on the skin, gills or fins of fish. They are hermaphrodites, have a direct life cycle, and do not require an intermediate host. Only one species of *Aspidogaster conchicola* occurs in freshwater molluscs, including *C. chinensis*, but mostly freshwater bivalves of North America. It is of little economic or medical importance to humans. See Figure 6-14 for its life cycle.

Digeneans have an alternation of generations between sexually reproducing adult and asexually reproducing larval stages and have a definitive vertebrate host and at least a mollusc first intermediate host; additional hosts may be involved. The most infectious parasites to humans are in a group called echinostomes, many species of which cause echinostomiasis. Clinical symptoms of echinostomiasis include abdominal pain, violent watery diarrhea, and anorexia. Clinical symptoms are related to parasite load: light to moderate infections cause anemia, headache, dizziness, stomachache, gastric pain, and loose stools; heavy infections are associated with abdominal pain, profuse watery diarrhea, anemia, edema, and anorexia; damage to the intestinal mucosa can cause extensive intestinal and duodenal erosions and inflammation of airway passages. Up to 15 species of echinostomes have been reported in *C. chinensis*, six in Taiwan and nine in China. Several species of echinostomes are parasitic to humans. None of the echinostome species has ever been reported from a North American population of *C. chinensis*. Even the cosmopolitan *E. recurvatum*, commonly reported from freshwater molluscs of North America, has never been found in Chinese Mystery Snails in the New World, and not for a lack of studies, as described on pp. 326-327 and Figure 6-17. Almost all cases of echinostomiasis resulted from eating uncooked or improperly cooked snails and fish.

Another dangerous parasite to humans is the rat lungworm, *Angiostrongylus cantonensis*, which also uses *C. chinensis* as an intermediate host. Reports of angiostrongyliasis are from northern, western and southern Africa, but none in North America. People get infected by ingesting the worm’s larvae, either by eating infected snails or in mucus trails left by infected snails on salad material; they penetrate the central nervous system, resulting in eosinophilic meningitis.

As discussed on p. 329, epizootics may occur after the introduction of exotic species due either to “parasite spillover” (exotic parasites infecting novel hosts in invaded areas) or “parasite spillback” an increase of the native parasites' impact because of their amplification in an exotic host), neither of which has been demonstrated for CMS or JMS.

Verdict: $H6_o$ is accepted.

7. $H7_0$: They cannot tolerate a wide range in water chemistry (e.g., acidic to alkaline waters; near to complete anoxia).

Both *C. chinensis* and *C. japonica* are found in a wide range of physical and chemical habitat conditions (except anoxia), making it difficult to restrict their ranges to a narrow set of habitat variables. However, there is a need to examine the upper thermal tolerances of both species; both live (hibernate) at 0°C and avoid freezing by emigrating to deeper water in the fall and immigrating back to the shallows in the spring. They prefer quiet waters, with some water circulation but not persistent turbulence; typical water bodies include shallow and deep ponds, small and large lakes, slow depositional areas of streams, large rivers, swamps, underground aquifers, and springs. Their choice of substrates varies from rocks, gravel, sand, mud, and silt, usually with submersed vegetation, often in turbid water from wind action over soft sediments. In other words, you will likely find either species in a wide variety of habitats. The full range in chemical and physical habitat conditions is described in Table 6-7.

Verdict: $H7_o$ is rejected.

8. $H8_0$: They are intolerable of degraded habitat conditions.

The only habitat in which neither species will be found is ephemeral, including periodically drying ditches and shallow forest ponds. They occur in the shallows of eutrophic (organically enriched) waters. They do not occur in the hypolimnia of deep oligotrophic or eutrophic waters. They cannot tolerate organically (e.g., pesticides) or inorganically (e.g., metals) polluted waters. All mystery snails have an operculum that closes the aperture during dry periods, such as drought or reservoir drawdowns. The most extended period of dormancy recorded for *C. chinensis* is nine weeks;

9–10 weeks is a criterion for the duration of dry periods in ephemeral habitats, including some temporary ponds. See pp. 367, 450-451.

Verdict: $H8_o$ is accepted.

9. $H9_0$: They do not disperse themselves but are introduced by people, either intentionally or unintentionally.

Chapter VII is entirely devoted to *C. chinensis* and *C. japonica*'s dispersal mechanisms and the myriad factors that determine a species' success in its newly found environment. Included among the myriad factors are life history traits, biotic, both natural; passive (e.g., water currents) and active (e.g., birds) mechanisms; and anthropogenic mechanisms (dispersal agents), including intentional, unintentional, or accidental releases. Table 7-2 lists all potential mechanisms available for short-range and long-range dispersal and their likelihood of success for *C. chinensis* and *C. japonica*. The two most likely and confirmed mechanisms are intentional introductions for food and the aquarium trade. Other possible dispersible mechanisms include natural transport on attachment to claws of feet and to feathers of birds and stream currents carrying logs, debris, etc. with snails; possible but not probable intentional anthropogenic mechanisms include overland transport of boats and trailers with attached submerged vegetation and mud; fishing equipment (e.g., bait buckets, muddy waders); unintentional spread may occur on purchased commercial products (e.g., fishpond plants, moss balls). There is ample evidence that humans are responsible for many introductions, either intentionally or unintentionally. Boater movements have been suggested as vectors in some reports. Still, these are challenged based on the snail's inability to swim at any life stage or remain attached to the hull of the boat and frame of the trailer and the unlikelihood of even small snails entering bait and wet wells (see pp. 396-394, 456-457).

Verdict: $H9_o$ is accepted.

10. $H10_0$: They are not edible.

Both mystery snails are edible; they were introduced to North America as Chinese immigrants in 1892. But they do bioaccumulate heavy metals to toxic levels if consumed in quantities, the quantity depending on the biomass consumed (see pp. 364-365, 452). Otherwise, they are nutritious and contain many essential elements for humans such as iron, zinc, and manganese in addition to calcium and magnesium needed for bone formation and phosphorous, nitrogen, and sulfur for protein synthesis (see Table 8-4). The Chinese and Japanese mystery snails and slugs produce mucus (snail slime) over their body surface, especially the foot. Snail slime has several medicinal uses. It has been used to clear warts and cure antibacterial diseases. In addition, snail slime contains skin care value compounds, including hyaluronic acid, glycolic acid, allantoin, and metals. Its skin care value is an example of biomimicry, whereby skin care products manufactured today contain many of the components of snail slime (see pp. 434-435).

Verdict: $H10_o$ is rejected if obtained from unpolluted sources.

11. $H11_0$: They are not so invasive that they need a risk assessment for each jurisdiction (province, state, etc.).

Many terms are used in the literature for native species, invasive species, nuisance species, ex-invasive species, exotic species, and introduced species. Native species are identified here as those that have been present since prehuman time (i.e., they have a pre-Pleistocene geological fossil record, mostly from the Palaeozoic and Precambrian eras); resident species include ex-invasive species that have become established locally and have potential competitive significance; invasive species are any non-resident species, intentionally or accidentally introduced, that is able to maintain, spread, and reproduce in the new habitat; nuisance is defined here as a potential threat to native species through economy, predation, grazing, competition, parasitism, disease, hybridization, or habitat alteration, the key being economical costs; exotic species are those that have been introduced to a place or have otherwise become established there because of human activities but have not dispersed much (to be defined) beyond the watershed in which they were introduced; introduced species are any non-resident species that are intentionally introduced (i.e., unintentional introduction is not included) and are able to maintain, spread, and reproduce in the new habitat. The main issue with an assessment of nuisance species is that the term nuisance is ambiguous in most literature to date. If an assessment of a nuisance species is based on perpetuating hearsay, unproven impacts or of other assessment criteria, the assessment would be meaningless, if not embarrassing. Based on the previous responses, which is why this hypothesis is the last to address, a risk assessment needs to be postponed until more convincing evidence of impacts has been demonstrated. See pp. 435-439.

Verdict: $H11_o$ is accepted until proof of nuisance level is provided.

12. Why are they called mystery snails?

The internet has a few reasons for the name “mystery snails”; some are rather flippant, but one sounds reasonable: “Because you start with one, then mysteriously have dozens,” which applies to all mystery snails. Still, the genus name of the Chinese and Japanese mystery snail is *Cipangopaludina*. Cipango is derived from a poetic name used by Marco Polo for Japan, who called an island east of Asia “Zipangu.” The poet incorporated the name Cipango in his poem, “Les Conquérants,” which tells the story of the search for gold (fabulous metal) at Cipango. The poem consists of two quatrain stanzas followed by two tercet stanzas; Table 3-1 translates the first two quatrain and tercet stanzas into English. The pertinent part of the poem is the second quatrain stanza:

> They were going to conquer the fabulous metal,
> As *Cipango* matures in its distant mines
> And the trade winds tilted their antennas, at the *mysterious* edges of the Western world.
> This is my vote, and I am sticking to it or suffer the slings and arrows of outrageous fortune!

C. Myths

A few myths are circulating in the literature, especially in fact sheets. The essence of the myths appears to arise from consigning the same attributes of zebra and quagga mussels to those of *C. chinensis* and *C. japonica*, which have entirely different life histories, habitats, dispersal capabilities, and history in North America. The Chinese Mystery Snail has been here (i.e., North America) for at least 130 years, perhaps longer, yet there is no consensus of impact or proclamation of it being a nuisance species. Below are my provenances of some myths:

- Predation by CMS and JMS on fish eggs is primarily a myth, considering the snails are filter feeders and sediment deposit feeders of fine organic material. If the eggs are covered with algae, the mystery snails and any freshwater mollusc herbivore damage the egg membrane as collateral damage, but there is no evidence that CMS or JMS hunt, as a predator, for fish eggs. The mystery snails are prey, not predators.
- CMS and JMS have little or no powers of self-dispersal or passive dispersal mechanisms (e.g., water currents, etc.) over long distances within watersheds or among watersheds using overland

translocations vectors, like trailered boats; the latter especially is primarily a myth. This allusion no doubt arises from equating the dispersal prowess of zebra mussels to those of the two mystery snails. As desperately described in Chapter IX, mystery snails have direct development and bear living young, not planktonic development as with zebra mussels, and they cannot hide in small crevices or cavities in boats and trailers. Moreover, the snails attach to surfaces by their large foot but withdraw the foot as soon as it is disturbed; even a mere touch of the shell will cause the snail to detach and fall off. The only concealed habitat for snails on boats and trailers are mud and submersed vegetation, but as soon as the mud and plants dry or are removed before transport, the snails lose their concealment and fall off.

- The Chinese and Japanese mystery snails have been here for at least 130 years, and not a single Asian epizootic of humans has been recorded in North America. Therefore, it should seem obvious that they are not the source of lethal alien parasites, another myth. If and when any epizootic is found in CMS or JMS, it most likely was introduced by another vector, at which time the two mystery snails can become intermediate hosts.
- The innuendo that CMS and JMS cause or abet blue algae blooms is a myth. Based on current evidence, CMS has a low P-excretion rate relative to native snail species, suggesting CMS either has no effect on algal biomass production or has an inverse effect relative to the N:P ratio. Thus, the more likely scenario would be a reduction in periphyton biomass, especially toxic cyanobacteria (see 4. $H4_0$).
- The implication that the *C. chinensis* and *C. japonica* are a nuisance is not supported by their life history attributes and inuendoes of impacts to humans, native species, environment, and industries. The innuendo that they are invasive and nuisance species is arguable; they have invaded over 75% of the United States and Canada jurisdictions, but it has taken them 130 years or more to achieve that feat; at best, they are slowly invasive. As for being nuisance species, the jury is still out; perhaps it will take another 100 years to certify its nuisance impacts to humans, native species, environment, industries, and economy. Most of the evidence to date is based on mesocosm studies that found correlations between the densities of CMS and impacts on native species. However, correlations do not necessarily denote cause–effect relationships. Moreover, mesocosm studies can examine

relationships among a limited number of variables relative to the myriad present in nature.

- There are no data (e.g., numbers, sizes, species of snails) to show that CMS or JMS clog industrial cooling water condenser tubes or intake screens.
- The CMS has been inculpated as leading the charge as in invasive species in the Great Lakes. One report in 1974 (e.g. p. 310) states, "man has characteristically complicated historic patterns by introducing foreign species into the Great Lakes (e.g., *Viviparus malleatus*, a Japanese gastropod; and *Bithynia tentaculata*, a north European snail)". This particular study was reported after one early record in 1942 of CMS in the Niagara River, which flows from Lake Erie into Lake Ontario, and another in Lake Ontario along the shoreline in 1965. The meagre reported occurrences of mystery snails in the Great Lakes between 1942 and 1974 raises the question of why *V. malleatus* was inculpated as an example of complicity of the "historic patterns" of invasive species in the Great Lakes. Little did the authors know the extent of this aggrandizement when compared to the Zebra Mussel's historic pattern after its introduction into Lake Erie in 1986.
- So far, the evidence indicates that the Chinese and Japanese mystery snails are gentle giants, possibly as benign as many other freshwater molluscs cited in the text.

D. Conclusions

Most studies to date have demonstrated there is no correlation between the occurrences of CMS and JMS and the physical or chemical conditions of the water bodies, with the possible exception of water body surface area. But the densities of the snails in the areas occupied have not been examined. The presence of boat launches was a significant predictor of *C. chinensis* and other aquatic invasive species in Wisconsin lakes; the boat launches are also likely for aquarium dumping because of their ease of access. A study of several northern Wisconsin lakes with snails found *C. chinensis* to be present in half of them and were more likely to occur at sites near boat launches than at sites more distant from launches. However, arguments were presented to show that dispersal overland by trailered boats is an unlikely major dispersal mechanism. Unlike zebra and quagga mussels, which produce planktonic larvae, fully developed juveniles of mystery snails are unlikely to remain attached when boats and trailers are removed from the water. Only when plants and mud are not removed from boats and trailers could the mystery snails be transported overland by trailered boats. The extent of dispersal of the mystery snails in plants and mud has not been assessed any nuisance status.

What is clear is the distributions of the Chinese and Japanese mystery snails are associated with human activities. This synanthropic relationship between undomesticated organisms and closely associated people apparently benefits from their surroundings and activities. Thus, both CMS and JMS qualify as synanthropic, especially based on humans being an anthropogenic vector. The main human-related activities are the snail's value as aquarium pets (the aquaria often being released into nearby water bodies when the snails are no longer valued as pets) and as food. Added to these associations are proximities of boat launches and the potential for snails to disperse in plants and mud attached to trailers and boats. To date, this synanthropic relationship has not been demonstrated as a nuisance.

What is not clear is how the two mystery snails establish themselves in very remote ponds, marshes, and wetlands in North America. The only vector that explains these disjunct populations is birds, especially waterfowl. Evidence is presented to show that mallards are predators of CMS and JMS and probable dispersal agents. This mechanism is suggested to be abetted by the periostracal hairs on young snails, which perform as Velcro strips meshing with the barbs and barbules on the birds' feathers.

For two nuisance invasive species of gastropods that have been in North America for more than 130 years, it is disappointing to learn how meager information is available on ecological impact (experimentally, demonstrably) in the literature. There is a perpetuation of impacts based on hearsay and innuendos, for example, "Did I tell you about the nuisance of a large conical snail at a power generating plant where my friend works?" or "Fishermen often made seine hauls containing 2 tons of snails (assumed to be entirely of *C. japonica*) that were a nuisance to them." The latter implies that the entire haul consisted of only mystery snails—no mud, no fish, no debris, and no names of other snails. These remarks are perpetuated in many fact sheets.

The take-home message from the information presented here will depend on one's motives and interest in this extensive review of the Chinese and Japanese mystery snails. Are they gentle giants that have yet to be exploited for their benefits, or have the giants slipped between the cracks and will take more time to unleash their defilement? Lowe, Browne, Boudjelas, and De Poorter (2000) condemn 100 species to the World's Worst invasive alien species, the zebra mussel being among them, mystery snails are not. While the full impact of an alien species is often not immediately apparent, 130 years of invasion by the CMS has not fomented outcries of impacts on the biological diversity and/or human activities in North America, nor, apparently in other continents.

On the rewarding side is the discovery and perhaps the escalation of the realized benefits of *C. chinensis* and *C. japonica* to society, not only as well-known sources of food and pet appreciation but in their contributions to medicinal cures and health care used in their countries of origin.

Did You Know?

- The heart (auricle) of mystery snails is a urine filter, that is, uses auricular urination.
- Viviparid sperm heads are screw or cork-screw shaped, giving a whole new meaning to “getting corked” or “getting screwed”.
- The screw-shaped sperm are accompanied by nurse sperm to provide energy for fertilization.
- Some people swallow slugs (*Arion hortensis*, recommended) whole and alive to treat gastritis.
- Snail slime has the same ingredients as skin care products.
- Snail (especially slug) slime will remove warts.
- There is poetic justice to the common name of mystery snail.
- The Chinese Mystery Snail can survive nine weeks out of the water, long enough to pull a boat and trailer overland from coast to coast (~4,210 km, or 3,500 mi) in North America, with snails lodged among any attached aquatic vegetation and mud, and back again (at 12 days return, using the longest route). The snails would survive the trip, but the plants and mud would dry up and release the snails somewhere along the way.
- Mystery snails undergo a complete torsion of their bodies and shell through 180° from back to front during their development.
- Mystery snails have a radula, a ribbon of teeth used as a rake to scour up microscopic algae.
- The teeth of mystery snails grow throughout their life, generating up to five rows per day.
- You can age a mystery snail, approximately, by the number of rings on its trap door.
- Mystery snails grow throughout their lives.
- Female mystery snails live longer than males.
- Mystery snails are migratory.
- Some leeches prey exclusively on snails.

- Mystery snails are synanthropic, undomesticated organisms living closely with people, apparently benefiting from their surroundings and activities.
- The Chinese Mystery Snail has been in North America now (2022) for more than 130 years (since 1892), the second oldest introduced freshwater mollusc species from Eurasia, the oldest being the Faucet Snail, *Bithynia tentaculata*, introduced in 1870. There is a possibility that *C. chinensis* has been here earlier, having been reported in Hawaii in the 1800s.

E. Recommendations

There is much information about *C. chinensis* and *C. japonica* presented here, more on the former than the latter, but there is so much more to learn about both species. Therefore, some studies are suggested below.

1. Japanese Mystery Snail studies recommended:

- Life-history traits, including fecundity, natality, embryo development time, size and age at sexual maturity (i.e., basic knowledge of any invasive species)
- Growth rates of males and females under different physical, chemical habitat conditions (to determine nuisance levels of population sizes and temporal variations)
- Genetics (e.g., chromosome number) because little is known
- Desiccation resistance vs. temperature, humidity (to help determine the distance of transport overland)
- Shell sexual dimorphism (as an added trait to tentacle dimorphism)

2. Both *C. chinensis* and *C. japonica* studies recommended:

- Nuisance traits and level of impact to establish mitigation strategies, if possible
- Mortality due to predation to determine top predators on snail sizes of each species
- Effect of the monogenean trematode *Aspidogaster conchicola* as a limiting factor in population size, mortality, reproductive effort, etc.
- Tolerances to silt loading and turbidity as a limiting factor in establishment and population size

- Lower threshold tolerance to DO as a possible population mortality factor and perhaps as a control option
- Use as a food item in North America (how common, the source(s), nationality, etc.)
- Upper thermal threshold tolerances as a possible population mortality factor and perhaps as a control option
- Competitiveness with native species of molluscs, with and without predators, under natural field conditions if possible—competition with deposit feeders (e.g., bivalves), herbivores (e.g., pulmonates and prosobranchs), and filter feeders (e.g., bivalves, other viviparids)
- Socioeconomic impacts (costs of impacts and control options)
- Definitive evidence that periostracal hairs are an adaptation for dispersal by birds, especially waterfowl
- The importance of overland transport by boat and trailer as a vector for dispersion. For trailers, determine:
    - Time of submersion of trailers vs. rate of snail attachment
    - Numbers of snails attached to different areas of the trailer
    - Densities of snails in different launching sites and the amount and type of vegetation and the substrate type at launching sites (e.g., concrete runway vs. natural beach substrate)
    - Numbers of snails detaching after the trailer is removed from the water
    - Rate of detachment while trailer stands at different air temperatures and humidity
    - Methods and time to remove any snails attached; include clumps of attached vegetation and numbers of snails and their sizes in the clumps
    - Leave some snails attached to determine how far they remain attached when transported overland over different distances; record air temperature and humidity

  For boats, determine:
    - Numbers of snails attached and their locations vs. depth and time anchored onshore
    - Numbers of snails that remain attached to the boat after removal from water
    - Methods and time to remove the snails from the boat, including those among attached plants
    - Leave some snails attached to determine how far they remain attached when transported overland over different distances;

record air temperature and humidity—trailers can be examined on the same occasions

3. Socio-economic concerns

- For any industrial or municipal intake impacts of nuisance CMS or JMS snails, determine where they are a nuisance (e.g., intake, travelling screen, pump house, condenser tubes, safety systems, etc.), their nuisance density, how long they have been a nuisance (days, weeks, months, years), sizes of snails living or dead, and costs, if any, to control them
- For commercial fishermen who find snails a nuisance, confirm species, density, and biomass of snails in each seine haul; composition of the net's contents (e.g., mud, plants, fish, other invertebrates); area of bottom trawled; frequency of seine hauls; and where the net's contents are dumped; it may be possible that commercial fishermen are controlling the population densities of mystery snails in lakes. What costs are associated with the nuisance snails caught as bycatch, e.g., their disposal?
- Where in North America are CMS and JMS used as food? Determine the value of any snails sold in markets. Are any ponds devoted to raising the snails for sales to markets or personal consumption; if so, what are the costs of raising the snails and what is their retail value?

APPENDICES

Appendix A

Websites for molluscs, maps, and information for different countries that are described in the text. The countries are listed alphabetically.

Country	URL	Access date
Denmark	https://www.iNaturalist.org/observations?place_id=8051&subview=Table&taxon_id=83795	July 28, 2020.
USA canals	North American Canals	December 2, 2021
USA, hydrologic unit codes	https://nas.er.usgs.gov/hucs.aspx	July 8, 2020
USA, intakes, special definitions	https://www.law.cornell.edu/cfr/text/40/125.92	December 16, 2020.

Appendix B

Websites for Species Discussed in the Text with Species Listed Alphabetically

Species' Name	**URL**	**Access Date**
Black Snail	Chinese Mystery Snail - NS Invasive Species Council	December 3, 2021
Great blue heron	https://iNaturalist.ca/photos/86443417?size=large	April 14, 2021
Mystery snail?	https://www.fishlore.com/aquariumfishforum/threads/why-the-name-mystery-snail.83533/	April 13, 2020
Mystery snail legend	https://web-japan.org/nipponia/nipponia45/en/feature/feature01.html,	May 1, 2020
Mystery snail, Zipangu	https://fr.wiktionary.org/wiki/Cipango	May 1, 2020
Ringed-bill gull	https://iNaturalist.ca/observations/68189258	April 14, 2021
Trapdoor snail	Zack DeAngelis: 6 Reasons Why Trapdoor Snails Are Good For Your Pond – Pest Pointers: Tips for at home pest control	September 28, 2021
Viviparus georgianus	https://www.fwgna.org/maps/FWGO-Viviparus.jpg	July 8, 2020
Viviparus intertextus	https://www.fwgna.org/maps/viin-vige-visu.pdf	July 10, 2010
(a) *Viviparus subpurpureus*	https://www.fwgna.org/maps/viin-vige-visu.pdf,	July 10, 2020
(b) *Viviparus subpurpureus*	https://www.fwgna.org/FWGTN/Viviparus_Campeloma-tn.pdf	July 10, 2020
(c) *Viviparus subpurpureus*	https://www.fwgna.org/maps/FWGO-Viviparus.jpg	July 10, 2020

Appendix C

Sources for Photos Cited in Text, Listed Numerically. All with Permission by Creative Common License BY or CC BY (https://creativecommons.org/licenses/by/4.0/, accessed April 14, 2021)

Photo #	Owner	URL	Access Date	Text Figures
2734482	Hyun-tae Kim	https://iNaturalist.ca/photos/2734482?size=large	April 14, 2021	Fig. 6-7
2734482	Hyun-tae Kim,	https://iNaturalist.ca/photos/2734482?size=large	March 12, 2020	Fig. 6-7
2764764	Hyun-tae Kim	https://iNaturalist.ca/photos/2764764?size=large	April 15, 2021	Fig. 5-4
2764764	Hyun-tae Kim	https://iNaturalist.ca/photos/2764764?size=large	March 12, 2020	Fig. 5-13
5663472	Hyun-tae Kim	https://iNaturalist.ca/photos/5663472?size=large	April 15, 2021	Fig. 5-6
5663472	Hyun-tae Kim	https://iNaturalist.ca/photos/5663472?size=large	April 14, 2021	Fig. 5-7
5663950	Hyun-tae Kim	https://iNaturalist.ca/photos/5663950	March 12, 2020	Fig. 5-17
7266575	Judy Gallagher	https://www.iNaturalist.org/photos/7266575	April 14, 2021	Fig. 5-11
7888513	Hyun-tae Kim	https://www.inaturalist.org/photos/37888513?size=large	April 14, 2021	Fig. 6-21
17466617	Robert T. Jackson	https://iNaturalist.ca/photos/17466617	April 14, 2021	Fig. 5-7
30220864	David McCorquodale	https://iNaturalist.ca/photos/30220864?size=original	March 12, 2020	Fig. 5-13
33156571	Mathew	https://iNaturalist.ca/photos/33156571	April 15, 2021	Fig. 5-6
33329610	Quinten Wiegersma	https://iNaturalist.ca/photos/33329610	March 12, 2020	Fig. 5-13
38659436	Hyun-tae Kim	https://www.inaturalist.org/photos/38659436?size=large	April 14, 2021	Fig. 6-21
41028439	Marcus Rosten	https://iNaturalist.ca/photos/41028439?size=original	March 12, 2020	Fig. 5-14
41028454	Marcus Rosten	https://iNaturalist.ca/photos/41028454	April 15, 2021	Fig. 5-6
41028454	Marcus Rosten	https://iNaturalist.ca/photos/41028454	March 12, 2020	Fig. 5-13
43624667	Rod	https://www.inaturalist.org/photos/43624667?size=large	April 14, 2021	Fig. 6-21

47691926	Steven Bodzin	https://www.iNaturalist.org/photos/47691926	April 14, 2021	Fig. 5-12
49557225	Alexis Williams	https://www.iNaturalist.org/photos/49557225	April 14, 2021	Fig. 5-7
64525033	Threelark	https://iNaturalist.ca/photos/64525033?size=large	April 15, 2021	Fig. 5-6
70953936	Tia Offner	https://www.inaturalist.org/photos/70953936?size=large	April 14, 2021	Fig. 6-21
86443417	Sandy Wolkenberg	https://iNaturalist.ca/photos/86443417?size=large	April 17, 2021	Fig. 6-18
87226688	Oceanicadventures	https://www.inaturalist.org/photos/87226688	April 18. 2021	Fig. 6-9
88941454	Elissa Totin	https://iNaturalist.ca/photos/88941454?size=large	April 15, 2021	Fig. 5-6
91446580	Andrew Sebastian	https://iNaturalist.ca/photos/91446580	April 15, 2021	Fig. 5-6
92302990	Andrew Sebastian	https://iNaturalist.ca/photos/92302990	April 14, 2021	Fig. 5-10
92618707	Andrew Sebastian	https://iNaturalist.ca/photos/92618707?size=large	April 15, 2021	Fig. 5-6
92633223	Elliot Greiner	https://iNaturalist.ca/photos/92633223?size=large	April 15, 2021	Fig. 5-6
99554948	Erik Erbes	https://www.inaturalist.org/photos/99554948?size=large	April 14, 2021	Fig. 6-21

GLOSSARY

Acute	Forming an angle of less than 90°.
Acute toxicity	The adverse effects of a compound that results from a single exposure in a short period (usually <24 hours). For the toxicity to be termed acute, the adverse effects should occur within 14 days of the administration of the substance.
Adult.	Any individual that is more than half-grown and can reproduce.
Allee effect	A positive relationship between any component of individual fitness and either numbers or density of conspecifics.
Alveoli	The divided adhesive depressions on the opisthaptor of monogenean parasites formed by muscular septa; also termed loculi.
Anastomosing	The joining of connecting channels, or interconnecting channels, as of blood vessels and urinary channels.
Anemochory	Dispersal by the wind.
Angulate	Forming an angle; not rounded.
Annulate	Ringed; surrounded by a ring of a different colour; formed in ring-like segments.
Annulation	Formation of ring-like parts or subdivision of a segment; also applies to rest marks and rings.
Annulus	A ring or division that usually corresponds to an annual growth ring.
Anoxia	Lacking oxygen, usually a result of hypoxia. Extended periods can cause taste and odour problems from the buildup of hydrogen sulphide and methane gas.
Anterior	In the direction of the head; the opposite of posterior. In bivalve shells, the end with the foot is usually the narrower end; in gastropods, the aperture end.

Anthropochory	Dispersal by human activities.
Aortic bulb	The slightly bulbous extended initial part of the ascending aorta of some prosobranch hearts. Also called bulbus aorta.
Apertural view	View of a gastropod shell with the aperture facing you.
Aperture	Opening usually referring to the opening of a snail shell. The view needed to differentiate sinistral and dextral shells.
Apex	The tip or top of a snail shell.
Apical	Toward the tip of a structure or appendage.
Apical angle	The angle of the top of the spire, including the nuclear whorl and the penultimate whorl.
Apical view	View of a snail looking down at the apex.
Apyrene	The vermiform or worm-like forms of spermatozoa of prosobranch snails.
Aragonite	A crystalline form of calcium carbonate; most molluscs shells consist of aragonite.
Arch	A curved structure.
Archaeogastropoda	An order of the class, Gastropoda; snails having a streptoneurous nervous system with ganglia gathered together, such as the pleural and pedal ganglia, which lie close to each other in the anterior region of the body.
Architaenioglossa	A higher taxon of Gastropoda, a clade of Caenogastropoda.
Asymmetrical	Lacking in symmetry and not capable of being divided into equal or corresponding parts.
Basal	At or about the base or point of attachment.
Base	The lowest part of a body or structure; the portion upon which a structure rests; the broadest portion of a cone-shaped structure.
Behavioural drift	In the context herein, it is the drift of benthic organisms that actively enter the drift because of cues, like light, current, avoidance of predators, etc.
Benthic	Of, or about, the bottom of a body of water or the organisms living at the bottom.

Bifid	Cleft, or divided into two parts; or two-pronged.
Bifurcate	Divided partly or forked into two.
Bioaccumulation	Accumulation of contaminants (e.g. metals, pesticides) in an organism's tissues.
Bioassay	Laboratory or field experiment designed to determine the toxic level of a contaminant, often expressed as LC_{50} or EC_{50}.
Biomass	Weight often preferred over dimensions because differences in animal sizes often have similar biomasses.
Biomimicry	The science of applying nature-inspired designs (e.g. oyster pearls) in a human invention (e.g. manufacturing cultured pearls) to solve human issues.
Bipectinate	Having two margins toothed like a comb, as in ctenidia of prosobranchs.
Bivalved	Having a shell consisting of two valves or valve-like parts, as in mussels.
Bivalvia	A class of molluscs with two valves, like mussels and clams.
Bivoltine.	Producing two litters or broods each year.
Blood colourless	In most freshwater molluscs, blood is a clear fluid containing haemocyanin.
Blood red	In some pulmonates, and blood is red colour due to haemoglobin.
Body whorl	The last and largest whorl of a snail shell.
Brood size	The number of embryos or larvae surviving within the uterus; in mystery snails, each embryo is contained in a brood sac.
Buccal apparatus	Components in the mouth of gastropods; includes the radula and odontophore with all their muscles, and the salivary glands.
Bulbous aortae	The initial extended bulbous part of the ascending aorta of some prosobranch hearts. Also called the aortic bulb.
Byssus	Threads produced in the posterior portion of the foot for anchoring the mollusc to the substratum, as in zebra and quagga mussels.
Calcareous	Containing calcium carbonate.

Carina	An elevated ridge or keel.
Catastrophic drift	Results from erosion of sediments with its organisms due to ice scour, log scour, large spring spate events, or floodwaters
Cephalic retractor muscle	The muscle involved in bringing about torsion in gastropods. A right-sided cephalic retractor rotation with a left-sided pedal retractor causes the two to cross one another more or less at right angles, bringing about 180° rotation to complete the torsion process.
Cephalic sinus	A haemocoel in the anterior end of the snail's body; blood passes from the sinus.
Cephalic tentacles	Two tentacles on the head of mystery snails.
Cercariae	A free-swimming parasitic larval stage of a trematode that passes from an intermediate host, to another intermediate host or a final vertebrate host.
Cerebral	Related to the head, like cerebral ganglia and commissures.
Chevron-shaped	Shaped like a wide-angled V, typically positioned or inverted.
Chitin	A naturally occurring polysaccharide made from chains of modified glucose and is created by the organism. After cellulose, it is the next most plentiful biopolymer in the world. Chitin makes up the radulae of gastropods.
Cilia	Fringes; series of medium or thin hairs.
Clade	A grouping of organisms based on their presumed evolutionary history; it consists of a common ancestor and all of its descendants. See monophyletic.
Cleft	Split, partly divided longitudinally.
Component Allee effect	An Allee effect manifested by a component of fitness
Compressed.	Flattened laterally.
Concave	Having a curved, depressed surface.
Concentric	A series of circles or ellipses having a common centre.
Conchiolin	An insoluble protein secreted by molluscs; it forms the organic matrix of the shell binding the calcium

	carbonate crystals that make up the nacre. It is a primary component of the periostracum.
Conical	Cone-shaped.
Constant drift	Drift constantly occurring at low flows; represented by most benthic taxa (e.g. mayflies, stoneflies, caddisflies, and occasionally molluscs, such as limpets.
Contaminant	A polluting or poisonous substance that affects the well being of an organism**.** It includes heavy metals, herbicides, insecticides, molluscicides, piscicides, bactericides, insect repellents, and fungicides, to mention a few.
Contiguous	Adjacent to; in contact with; adjoining.
Convex	Having a curved rounded exterior, like that of a sphere.
Copulatory bursa	A sac of the female into which the male inserts its penis and fills it with sperm.
Copulatory tentacle	The penis of prosobranch gastropods. The tentacle is modified as a copulatory organ.
Corneous	Hardened proteinaceous layer.
Crystalline style	A rod containing digestive enzymes in the stomach of bivalves and some gastropods
Ctenidium	A gill that functions in both respiration and feeding
Demographic Allee effect	A positive relationship between any measurable constituent of individual fitness and population size.
Deposit feeding	Ingestion of organic detritus and micro-organisms in the top few centimetres (5-15 cm) of sedimentary deposits. The particles are captured by cilia in a pallial food groove or on the mucous of the foot.
Depressed	Flattened so that the body is low and wide; having a low height/width ratio; the opposite of compressed.
Desiccation resistance	An adaptive life-history trait of an organism to reduce water loss. In mystery snails, the operculum, or trap door, seals the aperture and prevents or restricts the loss of body water.

Detritus	Fine, loose material; rock fragments and organic material; can be suspended in the water column or the sediments.
Dextral	To the right of the median line, or coiled to the right.
Differentiated	Modified and specialized for the performance of specific functions.
Diffuse	Spread out; not localized.
Digenea	Refers to the alternation of generations between sexually -reproducing adult and asexually-reproducing larval stages. A subclass within the Platyhelminthes consisting of parasitic flatworms (flukes), usually with two suckers, one ventral and one oral.
Dioecious	Separate sexes, with some individuals being male and others female.
Direct development	Non-planktotrophic development proceeds without an external food source and uses the yolk of the egg or some other nutrient provided by the female. The egg undergoes typical spiral determinate cleavage resulting in embryos that are born live. Often referred to as lecithotrophy.
Discoidal	Disk-shaped; shaped like a round plate.
Dispersal vector	An agent (biotic or abiotic) that moves a dispersal unit, or organism, away from its birth population to another location or population in which it can establish itself.
Distal	Near or toward the free end of any appendage. The part farthest from the body.
Divergent	Spreading out from a common base.
Dorsal	Toward the upper surface when the body is in normal walking position; the opposite of ventral.
Dorsal margin	The upper edge of the shell.
Ductule	A small duct, usually branching off a larger duct.
EC_{50}	Effective concentration; the concentration of a toxicant induces a response halfway between the baseline and maximum after a specified exposure

	time (e.g. 24 hr, 48 hr, 96 hr); often referred to as median exposure concentration.
Ectozoochory	Dispersal on the outside of animals, as in or on the feathers of birds.
Elliptical	Shaped like an ellipse, with an oval body, rounded at both ends.
Elongate	Lengthened; slender; longer than wide.
Emarginate	Having the margin notched or indented.
Embryo.	The stages of marsupial development up to and including gastrulation.
Encapsulated	Encased in a cyst or closed capsule.
Encysted	Enclosed in a sac, capsule, or cyst.
Endozoochory	Dispersal inside an animal's body, the propagule remaining viable during transport.
Ephemeral	Lasting a very short time; short-lived; transitory, as in temporary ponds.
Epicardium	The innermost layer of the pericardium and the outer surface of the heart.
Epipodium	A lateral lobe of a gastropod foot.
Eupyrene	A kind of flagellated spermatozoa that provides an ordinary amount of nuclear material to fertilize the eggs of female gastropods.
Eutrophic	Enriched with nutrients, typically an oversupply of soluble phosphorous.
Ex-invasive Species	Species that have become established locally relative to a particular time and the invader.
Exotic Species	Those species that have been introduced to a place or have otherwise become established there because of human activities have not dispersed much beyond the watershed in which they were introduced.
Expanded	To open outwards or spread.
Exposed	Open to view; not shielded or protected.
Fecundity	The maximum potential reproductive output of a female over a specified period. It can be estimated by counting the number of eggs produced and developing but not yet hatched or born.
Filament	A leaf-like structure on the gill or ctenidium. Several filaments make up a gill lamella.

Fingernail clam	Common or vernacular name for members of the genera *Sphaerium* and *Musculium*.
Foot	Single in molluscs. It has creeping, crawling or burrowing function.
Frontal	Of, or about, the anterior portion of the body or a part.
Gastric shield	A chitinous plate secreted by epithelial cells of the stomach wall of some bivalves, gastropods, and other molluscs; the crystalline style rotates against it and mixes enzymes from the style with food from the oesophagus.
Gill	A structure especially adapted for the exchange of dissolved gases with water in the mantle cavity. Compare to the ctenidium.
Globose	Approaching the shape of a sphere.
Globule	A small spherical body.
Glochidium	A larval stage of unionacean clams/mussels. Most are parasitic on fish, some on amphibians. The plural is glochidia.
Gravid.	Carrying embryos or larvae.
Grooved	Having a narrow channel or elongate depression.
Growth lines	The fine ridges left on the periostracum in a direction parallel to a shell's direction of whorl growth; not to be confused with spiral striae.
Hatchet-shaped.	Having an axe shape. The bivalve foot is hatchet-shaped.
Height.	The greatest distance from the ventral edge of the shell to the top of the apex.
Height/Width (or H/W) ratio.	The number or quotient obtained by dividing the greatest height of a shell by its greatest width.
Hermaphrodite	Has both male and female sexual organs in the same individual. Same as monoecious.
Hinge teeth	Any of various ridges or thickenings on the dorsal side of the interior of a bivalve shell that aid in holding the two halves of the shell together.
Hirsute	Hairy; surface with numerous cilia or hairs
Holostomatous	Having an entire aperture.
Hydrochory	Dispersal by water currents

Hypobranchial gland	Means "under gill". The gland is a single highly glandular area of the epidermal lining of the mantle roof. Its principal function appears to be the secretion of mucin.
Hypoxia	Below a normal level of oxygen.
Impoundment	A body of water created by installing a dam. Also referred to as a reservoir.
Incised	Notched or deeply cut into.
Incision	The impressed line marking the juncture of two segments.
Inclined	To have a bend or slant.
Indirect Development	Planktotrophy, meaning "feeding on plankton" refers to development via a larva that must feed in the plankton to develop to metamorphosis.
Inflated	In a snail shell, it refers to swollen as if the whorls had been pumped full of air. A bivalve refers to laterally expanded, as opposed to compressed.
Introduced species	Any species that are non-resident, intentionally introduced, can maintain, spread, and reproduce in the new habitat.
Invasive species	Any non-resident species, intentionally or accidentally introduced, can maintain, spread, and reproduce in the new habitat.
Irregular	Not uniform; not conforming to the usual pattern.
Iteroparous.	Producing more than one litter or brood in the life span of an individual or the average life span of a cohort.
Juveniles.	The born young are less than half-grown and unable to reproduce.
Keel	An elevated ridge; a carina.
Lacuna	A blank space, pit, hollow cavity, or a gap. The plural is lacunae.
Lamella	A sheet or thin plate in ctenidia and gills composed of an inner and outer lamella. Plural - lamellae.
Larvae	The stages of direct development where the shell is largely absent; often is planktonic and swims.
Lateral	Toward the side of the body; the opposite of mesial.

LC_{50}	The concentration of a toxicant that induces 50% mortality of a sample population after a specified exposure time (e.g. 24hr, 48hr, 96hr).
Lecithotrophy	Means, "feeding on yolk"; it refers to development with a non-feeding larva, which depends on the egg's yolk reserve supplied by the mother. Same as direct development.
Length.	The greatest distance from the anterior end of the shell to the posterior end.
Lentic	Of, or about, standing water.
Life span	Age, life expectancy, estimated from birth (egg hatch, parturition of embryos, or settled stage of larvae) to death.
Limnetic	About organisms inhabiting open waters of ponds, lakes and inland seas.
Litter size.	Same as brood size, the number of embryos or larvae.
Longitudinal	Lengthwise; extending along the long axis.
Lotic	Of, or about, flowing water.
LT_{50}	The time (period of exposure) required for a compound or toxicant to induce 50% mortality of a sample population; often called median lethal time. LT_{50} can be used in conjunction with EC_{50}.
Macro-	Being large, thick, or exceptionally prominent; of, involving, or intended for use with relatively large quantities or on a large scale.
Malleated	Having small flattened areas as if having been tapped with a hammer.
Mantle	In molluscs, a thin layer of tissue that secretes the shell and lines the shell's interior. The thin epithelial layer hangs down like a skirt around the entire soft parts of the animal.
Mantle collar	See mantle edge.
Mantle cavity	The cavity formed by the mantle wall has a double layer, the inner and outer epithelium between a water space. The cavity contains the mollusc's gills, hypobranchial gland, osphradium, nephridiopores, gonopores, and anus. The mantle cavity functions as a respiratory chamber and contains the brood sac in mystery snails.

Mantle edge.	The growing edge of the mantle usually bears three folds; the inner fold is large and muscular, the outer fold is elongate and secrets the periostracum and part of the shell, and the middle fold is elongate and sensory; helps to mould or form the growing edge of the shell. Also called mantle fold, mantle collar.
Mantle fold	See mantle edge.
Medial	Lying in the midline of the body.
Mesial	About the middle; toward the middle; the opposite of lateral.
Mesogastropoda	A former Order of the Subclass, Prosobranchia, but because it was not a one taxon origin, the taxon was considered invalid and is no longer used in modern classifications.
Mesopodium	Middle part of a gastropod foot.
Mesotrophic	Having a moderate amount of dissolved nutrients, particularly phosphorous.
Metacercariae	An encysted larval stage of a trematode occurs only when there are three intermediate hosts in a life cycle and are usually found in or on the intermediate host.
Metapodium	Posterior part of a gastropod foot.
Miracidia	A larval trematode stage that hatches from eggs either in the environment or in the intermediate host. They lack a mouth, cannot eat, and therefore need to find a host quickly. They develop into sporocysts. Singular is miracidium.
Molariform	Molar-like; heavy teeth found in fish, like Freshwater Drum, Round Gobi, and Pumpkinseed Sunfish that feed on thick-shelled molluscs.
Monoecious	Has both male and female sexual organs in the same individual. Same as hermaphrodite.
Monogenea	A group of ectoparasitic flatworms found on the skin, gills or fins of fish. They have a direct lifecycle and do not require an intermediate host; however, one species of *Aspidogaster conchicola*, occurs in freshwater molluscs, including the Chinese Mystery Snail.

Monopectinate	A type of ctenidium consisting of flattened filaments arranged on only one side of the ctenidial axis.
Monophyletic	A group (clade) of organisms composed only of a common ancestor and all of its lineal descendants.
Mucocytes	Mucous cells, which are transformed from epidermal cells.
Multispiral	Having numerous spirals, as on the operculum of Valvatidae
Multivoltine.	Producing more than two litters or broods each year.
Nacre	The pearly white or coloured material covering the inside of a shell. Typically made of aragonite. The colourful, thick, iridescent layer in freshwater mussels, thinner and usually whitish in mystery snails.
Naiad	Common name for unionid shell.
Natality	The number of surviving, viable eggs.
Native species	Species that have been present since prehuman time (i.e. they have a pre-Pleistocene geological record, mostly from the Paleozoic and Precambrian eras).
Nematode	Often called roundworm, any worm of the phylum Nematoda; are not closely related to true worms. They can occur as parasites in animals and plants or as free-living forms.
Nephridial gland	A wedge-shaped thickening of the pericardial wall of gastropods; its ciliated surface bears a series of slit-like openings into narrow branching tubular evaginations of the kidney lumen
Nephrostome	A funnel-shaped opening in a kidney through which waste leaves a nephridium. In the Chinese Mystery Snail, it is a round, small pore located in the centre lower region of the ventral surface of the kidney.
Newborn.	Both plural and singular noun refer to those newly born individuals and have not added shell material since birth.

Niche	A specific habitat with sufficient factors necessary for the existence of an organism or species.
Non-resident species	A species that is not a resident of a particular jurisdiction but is a resident elsewhere.
Nuchal Lobe	Lobes projected anteriorly over the foot. They are prolongations of the mantle on the left and right side of the foot and are innervated by nerves from the pleural ganglia. In prosobranchs, water enters through the left nuchal lobe, or the siphon, and exits through the right siphon due to muscle contraction and relaxation in the mantle and lobes.
Nuclear whorl	The first whorl on the apex of a snail shell; also called the protoconch.
Nuisance Species	Species that are a potential threat to native species through economy, predation, grazing, competition, parasitism, disease, hybridization, or habitat alteration
Obliquely	At or from an angle.
Obtuse	Forming an angle exceeding 90^{o}.
Odontoblasts	Cells in the posterior part of the radular membrane that secrete new teeth.
Oligopyrene	A type of spermatozoa with little nuclear material.
Oligotrophic	Poor or low in nutrients, especially phosphorous.
Ommatophore	A tentacle or movable peduncle bearing an eye; in the Chinese and Japanese mystery snails, it is fused to the outer base of each cephalic tentacle.
Operculate	Having an operculum.
Operculum	A lid or cover. Present on the foot of all prosobranch snails. Often referred to as a trap door.
Opisthaptor	The large, ventral attachment organ of the monogenean, parasitic Platyhelminthes
Opisthobranchia	Means “gills behind the heart”, usually on its right side. It was considered a subclass but now is an informal taxon for a large and diverse group of gastropods in the subclass Heterobranchia.
Organic	About, consisting of or related to organs, originates in, or derived from, living organisms; about compounds that contain carbon.

Osphradium	A pigmented patch of sensory epithelium in the body wall, near the base of each ctenidium. In viviparids, its main function is thought to test incoming water for silt and possible food particles. See also Spengel's organ.
Ovate	Somewhat oval.
Oviparity	A reproductive condition in which animals lay their eggs with little or no other embryonic development within the mother. See oviparous.
Oviparous	Producing eggs that develop and hatch outside the body of the parent. In gastropods, fertilization of the egg occurs internally, and development occurs externally.
Ovoid	See ovate.
Ovoviviparity	A type of reproduction in which embryos develop inside eggs that are retained within the parent's body until they are ready to hatch.
Ovoviviparous	Producing young using eggs that are hatched within the body of the parent.
Palaeogeography	The historical geography of the earth's surface; may also include the study of human or cultural environments.
Paleozoic Era	Or Palaeozoic Era. The Era is divided into the Cambrian, Ordovician, Silurian, Devonian, and Carboniferous periods, each with characteristic groups of fossils. It began with the Cambrian period about 541 million years ago and ended about 252 million years ago. Molluscs appeared in the Cambrian Period.
Pallial	Relating to the mantle.
Papilla	A small projecting body part; a protuberance often with a terminal opening, as in renal papilla, anal papilla, genital papilla.
Parent.	Any gravid individual or individual that is or was gravid.
Parietal lip	The outer lip of the part of the body whorl that adjoins the aperture (called the parietal wall).
Patelliform	Limpet-shaped.

Paucispiral	Marked by a spiral with few turns, as on the operculum of hydrobiid snails.
Pectinibranchia	An order of Gastropoda and subclass Streptoneura that have a single kidney, usually a single ctenidium, which resembles a comb traditionally attached to the mantle throughout its length, and has a heart with only one auricle.
Pedal	Relating to the foot, as in pedal ganglion that supplies nerves to the foot in viviparids.
Pedicel	The word is derived from the Latin pediculus, meaning "little foot". In gastropods, they are interdigitating feet on a basement membrane in the walls of the auricle that communicate with podocytes in the ultrafiltration of urine.
Pericardium	The membrane enclosing the heart.
Periostracal hairs	Hairs on the periostracum, usually in one to three rows around the whorls; most apparent on young shells. The hairs can be thick, dense, and clumped, or thin and single.
Periostracum	The coloured, proteinaceous layer that covers the outside of mollusc shells. It originates in the mantle edge in a groove between its outer and middle folds. The conchiolin undergoes sclerotization or tanning to harden the proteins by cross-linking them.
Peripheral	Of, towards, or constituting an external surface or boundary; away from a centre; towards the surface.
Pharyngeal jaws	Consist of thick pharyngeal teeth on hard, movable plates used to crush shells or the exoskeletons of prey.
Planktonic	Of, or about, aquatic organisms of fresh, brackish, or seawater which float passively or exhibit limited locomotor activity.
Planktotrophy	Means "feeding on plankton". Refers to the development of larvae, usually of several stages, that must feed among the plankton to develop and metamorphose into juveniles, and then adults.

Podocyte	An epithelial cell of the visceral layer of the kidney; bears several footlike, radiating pedicels on a basement membrane. See also pedicel.
Polyphyletic	A group characterized by convergent features or habits that are lacking an inherited common ancestor.
Posterior	In the direction away from the head; the opposite of anterior.
Precambrian Era	The period extending from about 4.6 billion years ago, when the earth began to form, to the beginning of the Cambrian period, 541 million years ago.
Process	An elongation of the surface, or a margin, or an appendage. Any prominent part of the body not otherwise definable.
Prohaptor	The anterior structure located at the anterior part of the monogenean parasites. It is the chief adhesive organ of the monogeneans.
Propagule	A reproductive stage released by an organism that may develop into another stage, or a new individual.
Propodium	Anterior end of the foot of a mollusc.
Prosobranch	Means “gills in front of the heart”. Includes a group of snails that has an operculum, respires with gills, and are generally dioecious.
Protoconch	The first whorl on the apex of a snail shell; also called the nuclear whorl.
Proximal	Away from the tip of a structure or appendage; the opposite of distal. Nearest, the beaks of the shell in an anterior-posterior axis.
Pseudofeces	Particulate, indigestible material from the incurrent water and enveloped and contained within mucous balls in the mantle cavity, and then expelled through the incurrent siphon without passing through the digestive system.
Pulmonate	Having lungs, as in Physidae, Lymnaeidae, Planorbidae, and Ancylidae
Pustule	A large projection lump.

Rachidian tooth	The central tooth of a taenioglossid radula; usually has a large, blunt central cusp and one or smaller lateral cusps, the shapes and numbers of which aid in species identification.
Rachiglossa	A division of Stenoglossa of the order Pectinibranchia. Comprised mostly of carnivorous marine gastropods with a radula consisting of three or more longitudinal series of teeth, a long retractile proboscis, and a distinct siphon.
Radula	The ribbon of horny teeth found in the mouths of all molluscs except the bivalves. It consists of a protrusible odontophore with the ribbon of teeth (denticles) used for rasping food particles from a surface in Viviparidae.
Recess	A depression, fossa, cleft, or cavity.
Recurved	Bent backwards.
Rediae	A larval stage of parasitic trematodes that is produced from cells within a sporocyst then liberated from the latter and develop in the tissues of a host snail as an elongated, sac-like organism with a mouth and gut.
Reduced	Diminished in size, amount, or number.
Renopericardial canal	A short and muscular duct, folded upon itself and forming a loop, connected proximally by a ciliated renopericardial funnel with the base of the pericardial cavity; at the distal end, the canal connects to the kidney reservoir or bladder at a papilla.
Reservoir	See impoundment.
Resident species	All species that were established before the arrival of an invasive species.
Respiratory	Of, or about, the interchange of gases between an organism and its environment.
Rest mark.	A darker or thicker concentric part of the shell formed during a rest period in growth.
Reticulate	Covered with a network of lines.
Retractile	Capable of being drawn in or back.
Ridge	A crest or elevation.
Robust	Strongly formed or constructed; sturdy.

Rudimentary	Of, or about, an organ or structure that is just beginning to develop or one in which development has been arrested. Describes a vestige or the remains of a functional structure in an earlier stage of evolutionary development.
Secrete	To produce a substance discharged through a duct from a gland.
Sedentary	Permanently attached to the substratum; not free-moving; remaining in the same place; not migratory.
Segmentation	The state of being divided into segments or parts which are marked off or separated from adjacent parts.
Semelparity	A reproductive strategy characterized by a single reproductive episode in its lifetime.
Semelparous	Producing only one litter or brood in the life span of an individual or the average life span of a cohort.
Seminal receptacle	A sperm storage structure in females. Same as spermatheca.
Seminal vesicle	A gland that secretes fluid containing sperm.
Serrate	Saw-like, with notched edges.
Serrated.	Notched on the edge, like a saw blade.
Serrulate	Finely serrate; bearing minute teeth.
Sessile	Attached by the base; without stem or stalk.
Seta(e)	Slender, hairlike appendage.
Setiferous	Bearing setae or cilia.
Setose	Furnished or covered with setae or stiff hairs.
Shallow	Lacking in depth.
Sigmoid	S-shaped, curved in two directions.
Simple	Unmodified, not branched.
Sinistral	To the left of the median line, or for snails, coiled to the left; opposite to dextral.
Sinuous	Curving in and out.
Sinus	A cavity, hollow, recess, channel, or space.
Siphon	A tube or tube-like structure for drawing in or expelling fluids, like that in bivalve molluscs.
Slender	Small or narrow in circumference.
Solitary	Existing singly or alone.
Sparse	Not thickly grown; scattered.
Spatulate	Broad and rounded at the tip, spoon-shaped.

Spengel's organ	Pioneering studies by French biologists of pallial organs first described the osphradium as l'organe de Spengel.
Spermatocytes	Cells derived from immature germ cells, called spermatogonia, in the testis. There are two types, primary spermatocytes that are diploid (2N chromosome), and haploid secondary spermatocytes (N chromosomes).
Spherical	Having the form of a sphere or globe.
Spinous	With many spines.
Spiral	Winding in a continuous and gradually broadening curve; can occur around a central point on a flat plane, as in the opercula of valvatid snails, or about an axis to form a cone, as in the spire of snails.
Spire	The entire snail shell, excepting the body whorl.
Sporocyst	An elongated sac that produces either more sporocysts or rediae in the trematode life cycle.
Statocyst	An organ of equilibrium found in the foot of a mollusc. It contains a round statolith that rests amongst hairlike projections of sensory cells; a change in orientation of the animal moves the statolith against a receptor, sending an impulse along the statocyst nerve to the cerebral ganglion.
Stenoglossa	A suborder of Pectinibranchia containing many common marine snails (e.g. cone shells, olive shells, whelks), which have a concentrated nervous system. The suborder has been renamed, Neogastropoda.
Striae	Concentric raised striations or lines on the exterior surface of the shell. They may vary from very fine to very coarse, the latter often called ribs or rest marks. Singular is stria.
Striate	Having striae or lines.
Sub-	Prefix, more-or-less.
Subcentral.	Not quite central in an anterior-posterior axis; off centre.
Submersed	Covered with water; growing or adapted to grow underwater.

Subtropical	Refers to zone, region, and climate; located to the north and south of the tropical zone, or latitudes between ~23°26′ and ~35° in the northern hemisphere and the southern hemisphere.
Succeeding	Coming next to one another in position; following in order.
Suture	A seam or impressed line indicating the division of the distinct parts of the body wall, on a snail shell, separating the whorls.
Symmetrical	The quality of being composed of exactly similar parts facing each other or around an axis. Exact correspondence.
Synanthrope	An undomesticated organism living in close association with people, apparently benefiting from their surroundings and activities.
Taenioglossa	A suborder of Pectinibranchia comprising marine and freshwater gastropod molluscs distinguished by a long and narrow odontophore usually bearing a radula with seven teeth in each transverse row.
Tapered	Becoming progressively smaller at one end.
Teeth	The opposing lamellae on the hinge that serve to stabilize the two valves against shearing forces. The rasping structures on the radula of snails.
Teleconch	Adult shell.
Temperate	Refers to zone, region, and climate; the part of the globe lying between the tropic of Cancer (~23°3N) and the Arctic Circle (~66.5°) in the Northern Hemisphere or between the tropic of Capricorn (23.5°S) and the Antarctic Circle (66.5°S) in the Southern Hemisphere; characterized by having a warm summer climate, cold winter, and moderate in the spring and fall.
Terminal	About, placed at, or forming an end or extremity; being the last of a series; located at the end of a body or structure.
Terminate	To come to, or form, a terminus or end.
Tetrahedron	A triangular pyramid composed of four triangular faces, six straight edges, and four vertex corners.
Transverse	At right angles to the long axis of the body.

Trematode	A class of flatworms of the phylum, Platyhelminthes; distinguished by the presence of two suckers, one close to the mouth and the other on the underside of the animal, also called flukes.
Tropical	Refers to zone, region, and climate; the part of the globe between the Tropic of Cancer (~23°3N) and the Tropic of Capricorn (23.5°S); characterized by a hot climate.
Truncate	With a shortened end; often squarish; Having the end cut off more or less squarely.
Tubercle	A small bump or pimple-like structure; a nodule or small eminence occurring on the surface of the shell or part of the shell.
Tubercular.	The shape of a raised eminence or elevation that has a rounded top and vertical sides.
Tuberculate.	Covered with tubercles or rounded knobs.
Tubular	Having the shape of a hollow cylindrical structure; composed of, or possessing tubes.
Tubule	A small, elongate tube-like structure.
Tuft	A small cluster of flexible structures, like hairs, feathers, or blades of grass, closely associated at their bases but with free ends spread apart.
Typhlosole	An internal fold of the intestine inner wall. Its function is to increase intestine surface area for absorption of digestible products.
Umbilicus	The small opening present in some snail shells behind the base of the aperture.
Unequal	Of different sizes or proportions.
Uniform	Presenting an unvaried appearance of surface, pattern, or colour.
Univoltine.	Producing only one litter or brood each year.
Vacuole	A small space or vesicle within cell tissue, enclosed by a membrane and typically containing fluid.
Vagility	Degree to which organisms can or do move or spread within their common environment. It is a function of the distance that their viable propagules are carried from the source and of the frequency of such transports.

Vas deferens	The tube attached to the penis and the prostate and aids in the movement of sperm from the prostate to the penis.
Vector	An agent of biological dispersal that moves an organism away from its source population to another location or population in which the individual can establish itself.
Veliger	A larval stage of dreissenid and corbiculid bivalves.
Ventral	Toward the lower surface when the body is in normal walking position; the opposite of dorsal.
Ventral flexion	A ventral bending of all organs contained in the visceral hump that takes place in the course of torsion.
Vertical	Of, or about, the highest point, summit or apex; upright; perpendicular to the horizontal plane; lengthwise, or in the direction of the longest axis.
Vestigial	Small or degenerate.
Visceral	Related to the viscera.
Viviparous	Bringing forth live young that have developed inside the parent's body and deriving nourishment from the body of the parent via a placental cord.
Watershed	A dividing ridge between drainage areas; demarked by the highest elevations of headwater streams.
Weakly	Not strongly; not overly pronounced.
Whorl	One 360° turn of the spiral of a snail shell.
Width.	The greatest distance from one side of the shell to the other.
Width/Length (or W/L) ratio.	The number or quotient obtained by dividing the greatest width of a mollusc shell by its greatest length.
Zoochory	Dispersal by animals.

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