The Mysteries of Mystery Snails

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Facts and Myths

By

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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-).

TABLE OF CONTENTS

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My first obligation is to Jamie Delaney, a long-time supporter and protector of the environment and a resident of Three Mile Lake, Muskoka; he first contacted me on June 11, 2019, about their concerns about the Chinese Mystery Snail (CMS) in Three Mile Lake. He had seven exciting questions listed in the preface, and it took me over a week to answer all of them. During that period and subsequent weeks of discussions and searches through peer-reviewed journals, books, chapters in books, and grey literature, I began to realize the extent of information on mystery snails. He also offered several images for the book. But not all of the data was readily available, and I had to rely on some associates and collaborators to "fill in the blanks". I wish to thank the following people for their help in this regard:

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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?

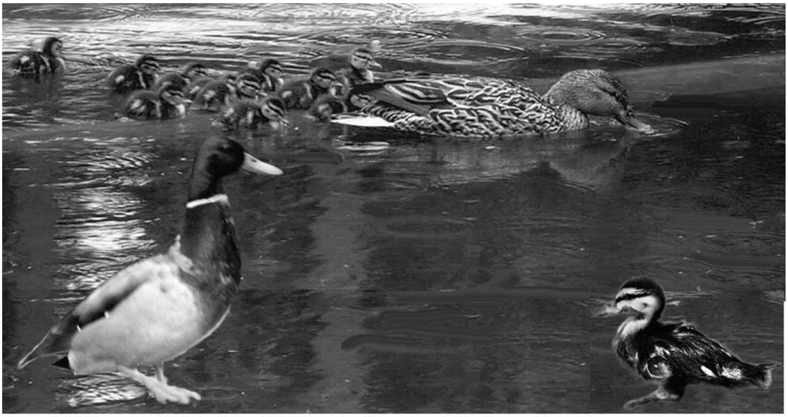

Figure 1. Family of mallards, with 12 ducklings following the mother, with the father in the lower left, and the 13th duckling, Marvin, in the lower right. The ducklings were swimming on the winter blanket of our pool in the spring. Photos taken May 15, 2008, by GLM.

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

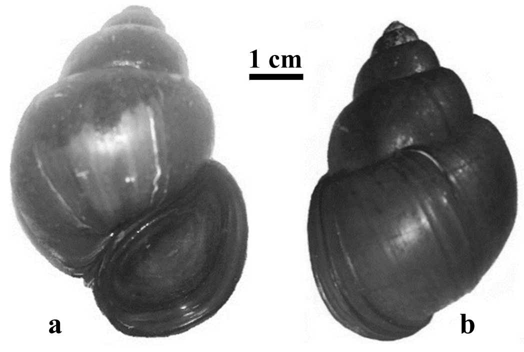

Figure 1-1. Chinese Mystery Snail. (a) Apertural view. (b) Abapertural view. GLM images

(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,

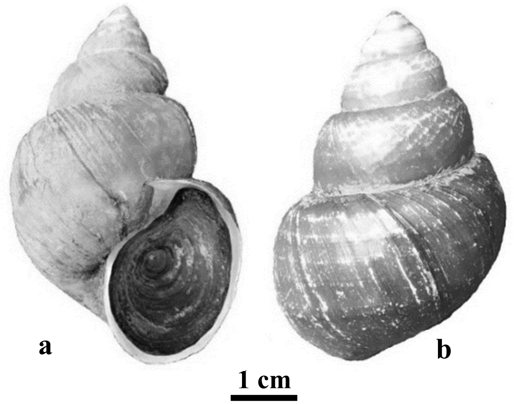

Figure 1-2. Japanese Mystery Snail. (a) Apertural view. (b) Abapertural view. Images are courtesy of Brian Watson.

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
Vivi-paridae	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