

Chapter 1

A Brief History of the Lymnaeid Research



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Abstract The history of the lymnaeid research, from the mid-sixteenth century to the present, is briefly outlined, with a special emphasis on the development of the systematics of this family and the studies of parasitological significance of the pond snails. An index to the lymnaeid literature published during the last 120 years, which includes references to the most important publications, is also provided.

It appears that the lymnaeid gastropods (the pond snails is the English vernacular name for these animals) have been totally overlooked by the ancient and medieval naturalists. Aristotle, “the father of zoology,” did not mention them, as well as many of the natural historians who lived prior to the mid-sixteenth century (Vinarski 2015). Ulisse Aldrovandi (1522–1605), a scientist of the Late Renaissance Italy, was, most probably, the first naturalist to mention a lymnaeid snail in his book, and to illustrate its shell. Aldrovandi (1606) published an image of the shell of *Lymnaea stagnalis* (Linnaeus, 1758), the great pond snail, and named it “Turbo levis item in stagnis degens” (i.e., “Turbo with smooth shell, living in stagnant waters”). Though one cannot find a scientific description of this mollusc in Aldrovandi’s book, but in that epoch the very Latin name (non-binomial, i.e., consisting of more than two words) served as a brief account of an animal and contained some information helping to identify it. It is not surprising that the shell in Aldrovandi’s picture

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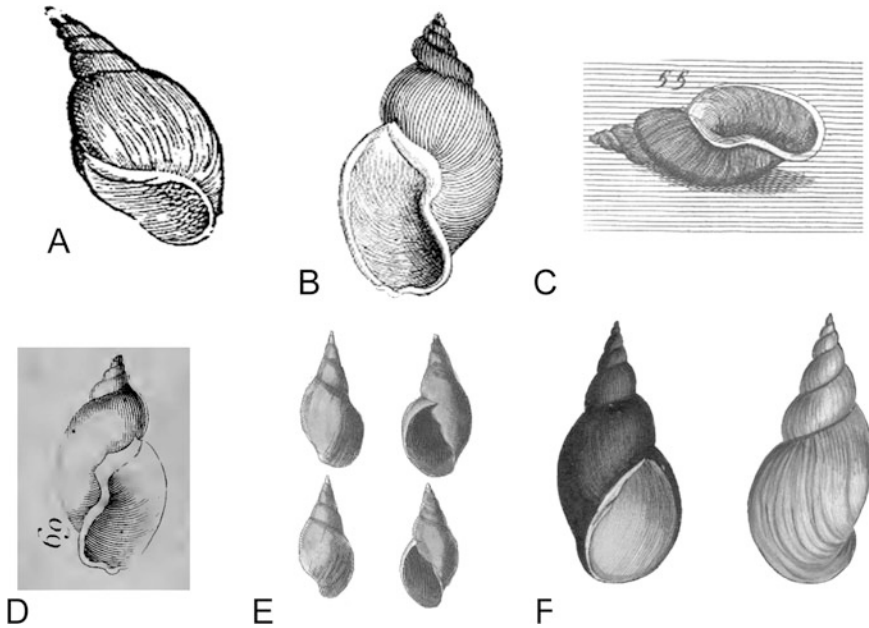


Fig. 1.1 Evolution of accuracy in illustrations of *Lymnaea stagnalis* shells made by naturalists of the seventeenth–eighteenth centuries. (a) Ulisse Aldrovandi (1606). (b) Martin Lister (1678). (c) Filippo Bonanni (1709). (d) Jacob Theodor Klein (1753). (e) Albert Seba (1758). (f) Johann Samuel Schröter (1779)

(Fig. 1.1) is sinistral (pond snails have normally dextral, or right-coiled, shells). The usual technique of engraving in the sixteenth and seventeenth centuries demanded that the plate must be a mirror image of the object to be illustrated. The printers usually were “not preparing a reversed engraving (on wood or copper), but carving the image [of a shell] as it appeared, which would produce a reversed image when printed” (Allmon 2007, p. 175).

Only 70 years later, a book authored by Martin Lister (1639–1712) was published in England, which contained much more detailed accounts on *L. stagnalis* and some other species of freshwater snails. Martin Lister was an English physician and naturalist, vice-president of the Royal Society from 1685 to 1686. Being a devoted conchologist, he wrote the first European treatises on molluscs (*Historiae Conchyliorum*, 1685; *Conchyliorum Bivalvium*, 1696). O.F. Müller (1774, p. xiii) called him “Conchyliologorum princeps» (head of conchologists), which is a clear analogy with Linnaeus’ informal title “Princeps botanicorum.”

In Lister’s *Historiae animalium Angliae tres tractatus* (Lister 1678), one may find a detailed account of *L. stagnalis* that follows much higher standards of zoological descriptions compared with Aldrovandi’s. This text contains not only the polynomial name (= short diagnosis) for this species, but also a relatively long two-page sketch of the great pond snail’s bionomics. Lister provides a lengthy general description of its external morphology (including the pattern of mantle

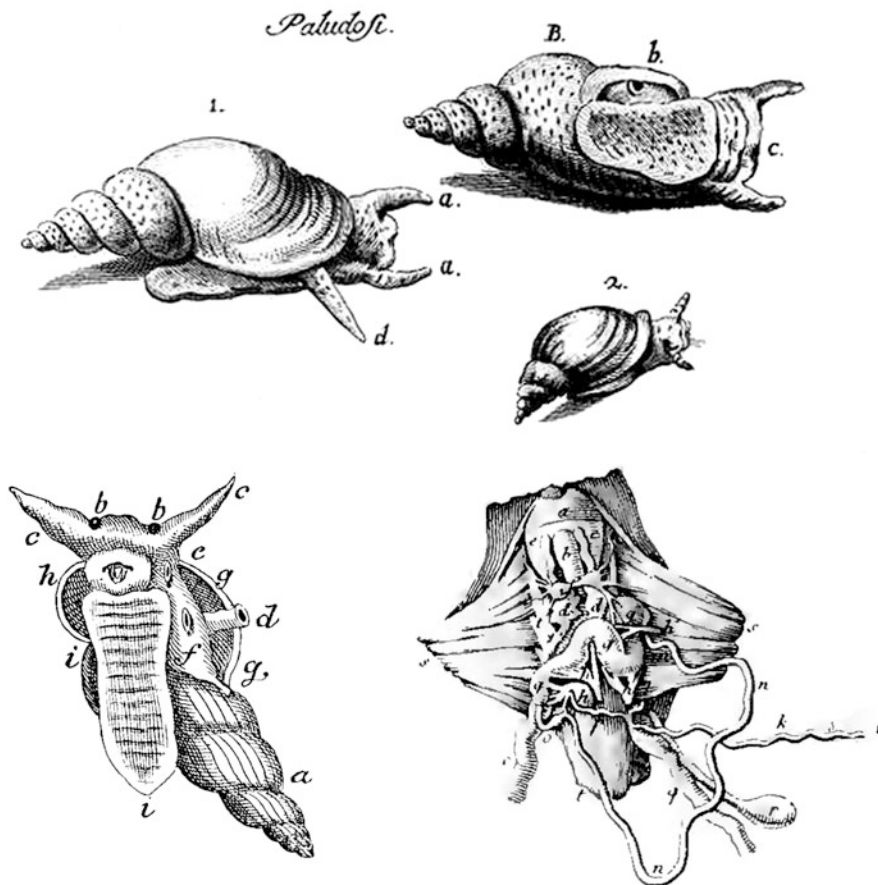


Fig. 1.2 Early illustrations demonstrating some details of the external and internal anatomy of *L. stagnalis*. Upper row – from Ginanni (1757), lower row left – after Swammerdam (1738), lower row right – after Cuvier (1817)

pigmentation), the shape of its excrements, the mode of copulation, the structure of egg-masses alongside a list of aquatic plants being its food. Some localities of *L. stagnalis* in England were also mentioned. Lister’s species’ account was almost 100 years ahead of its time. This high standard of publication of malacological data was not established until the end of the eighteenth/early nineteenth centuries, when comparable works of naturalists appeared (Müller 1774; Draparnaud 1805). Lister’s account looks more detailed and inclusive than the account of the same species published a century later by Da Costa (1778)!

Later on, Lister (1695) published a very detailed report of the *L. stagnalis* internal structure, accompanied by engravings. Trained as a *medicus*, Lister was a brilliant anatomist aiming to dissect molluscs belonging to different taxa, both terrestrial and aquatic. Another perfect anatomist of the age, the Dutch Jan Swammerdam

(1637–1680), was also interested in freshwater molluscs (Fig. 1.2), and his study of the *L. stagnalis* anatomy was published posthumously in the author's prominent book *Bybel der natuure* (Swammerdam 1738). However, in both cases, the advance of anatomical research did not enhance the progress in taxonomy. Systematists of the seventeenth and eighteenth centuries typically did not use anatomical information in their works, and the classification of molluscs long remained purely conchological (Vinarski 2014).

In addition to *L. stagnalis*, Lister (1678) described two other lymnaeids, which may be tentatively identified with *Ampullaceana balthica* (Linnaeus, 1758) and *Radix auricularia* (Linnaeus, 1758). However, their descriptions are less detailed as compared with that of *L. stagnalis*.

The story of taxonomic investigation of the Lymnaeidae starts in 1753, when Jacob Theodor Klein separated lymnaeid snails into a taxon of their own—the genus *Auricula* with three species included (Klein 1753). Before Linnaeus' seminal work (Linnaeus 1758), Klein already explicitly used binomial nomenclature and introduced the first two-part name for the great pond snail—*Auricula stagnorum*. This name has a formal priority before the Linnaeus' *Helix stagnalis* but, being published before 1758, it is not available for taxonomic and nomenclatorial purposes.

Two other members of Klein's genus *Auricula* are more difficult to identify. His *Auricula pellucida*, is, perhaps, identical to *A. balthica*, whereas the third species, *Auricula exigua*, is of exotic origin (“Javana”) and one is unable to identify it.

The basis for the subsequent taxonomic work on the family was laid within the 50 years after publication of the tenth edition of Linnaeus' *Systema Naturae*. During these years, several European naturalists and conchologists published descriptions of around 20 lymnaeid species, ten of which are accepted valid today (Box 1.1). It covered nearly one half of the overall diversity of this group in Western and Central Europe. The scope and quality of these descriptions ranged from short (1–2 phrases) and not illustrated diagnoses (Linnaeus 1758; Gmelin 1791) to more or less comprehensive accounts which included various data on species' morphology and ecology (Müller 1774; Draparnaud 1805). Toward the end of the eighteenth century, the minuteness of illustrations of the lymnaeid shells increased greatly and almost reached the modern standards (see Fig. 1.1).

All lymnaeid species described during the first 50 years of the post-Linnean taxonomy (i.e., since 1758) were placed within large and heterogeneous genera *Helix* and *Buccinum*, which included marine, terrestrial as well as true freshwater forms. Only in 1799 a new genus *Lymnaea* was erected by Lamarck, followed by other lymnaeid genera like *Galba* Schrank, 1803, *Radix* Montfort, 1810, and *Omphiscola* Rafinesque, 1819.

In the first half of the nineteenth century, the lymnaeid snails of the non-European (including exotic) countries were discovered. In North America, Thomas Say, “the father of American Conchology” (F.C. Baker 1911, p. 117), explored the Nearctic fauna of continental molluscs (Say 1817, 1821). He is the discoverer of many lymnaeid species accepted today as valid (*Bulimnea megasoma*, *Ladislavella catascopium*, *Pseudosuccinea columella*, and others). Travelers brought to Europe collections of freshwater molluscs of tropical countries. Lamarck (1822), Michelin

(1831), Krauss (1848), and some other workers contributed to the taxonomy of lymnaeids of India, East Asia, Africa. In Russia, Middendorff (1851) published a description of the pond snails of Siberia, a country whose invertebrate fauna was then almost unknown to zoologists.

This descriptive activity culminated in the mid-nineteenth century, when the first catalog of all known lymnaeid species appeared (Küster 1862). Küster's book was an annotated enumeration of almost 90 species from all continents, with descriptions and illustrations of their shells. This tradition was continued by illustrated catalogs authored by G.B. Sowerby II (1872) and Clessin (1882–1886). Westerlund (1885) compiled an annotated (but not illustrated) list of all species and varieties of lymnaeids occurring in the Palearctic region.

The volume of the family Lymnaeidae and its type genus, *Lymnaea*, had changed drastically during the last 100–150 years. In the nineteenth century, most workers treated Lymnaeidae as a family embracing almost all freshwater pulmonate snails, i.e. not only lymnaeids but also physids, planorbids, and some other groups (see, for example, Forbes and Hanley 1852–1853; Clessin 1882–1886; Locard 1893). Since the early twentieth century, the volume of the family became narrower. F.C. Baker (1911), Thiele (1931), Hubendick (1951) accepted it in an almost modern sense. Władysław Dybowski (1838–1910) who worked in Poland (then—a part of the Russian Empire) proposed the most radical system. This zoologist split the Lymnaeidae into three families of smaller volume: Limnaeidae, Lymnophysidae, and Amphipeplidae (W. Dybowski 1903). All his contemporaries, except Władysław's own brother Benedykt (B. Dybowski 1913), ignored these novelties.

The genus *Lymnaea* (alternatively spelled as *Limnaea*, *Limnaeus*, *Lymnaeus*, *Limnea*) had long served as a mega-genus to embrace almost all diversity of the pond snails, except of some conchologically peculiar forms like *Lanx* and *Myxas*. Typically, the genus *Lymnaea* s. lato had been divided into series of subdivisions (*Galba*, *Radix*, *Stagnicola*, and some others), which are ranked as separate genera in the present-day taxonomy. This “broad” concept of this genus dominated in the twentieth century (see review by Vinarski 2013), however most of the modern systematists arrange the family into numerous genera (Burch 1989; Ponder and Waterhouse 1997; Glöer 2002, 2019; Vinarski 2013; Aksenova et al. 2018; Vinarski et al. 2019, 2020).

Typically, the nineteenth century European malacologists accepted a relatively small number of lymnaeid species, albeit they used ad libitum the category of “varietas” (variety) in order to arrange the enormous intraspecific variation in lymnaeid shell size and proportions. The number of intraspecific entities delineated within some widespread and variable species might have been gargantuan; more than 80 “varieties” of *L. stagnalis* were proposed by taxonomists of the nineteenth and the first half of the twentieth century (Vinarski 2015). In most cases such varieties were based on relatively slight morphological deviations from the “type,” i.e. in size, shell shape and proportions, shell surface coloration, etc. Not rarely, juvenile and aberrant individuals were used to establish a new “variety” or a new “morph.” The extreme of such a splitting approach to taxonomy was observed in the nineteenth century France, where some malacologists created, on the basis of slight

shell modifications, not “varieties” but “full” species. For example, Arnould Locard (1841–1904) delineated not less than 130 (sic!) species of Lymnaeidae in France alone (Locard 1893). One reason for it was that he considered the species category as arbitrary, non-objective. Locard wrote “L’espece malacologique est une notion purement arbitraire, indispensable aux naturalistes pour le besoin de la connaissance et de la classification des êtres” (“the malacological species is a purely arbitrary notion demanded by naturalists for the sake of knowledge and classification of [living] beings”) (Locard 1893, p. 136).

It should be noted, however, that all abovementioned works were purely conchological and did not contain descriptions of anatomical characters. Until the early twentieth century, the shell characters remained virtually the only basis for genera and species delineation within the family.

At the same time, the anatomical studies on the Lymnaeidae, initiated in the late seventeenth century by Lister and Swammerdam, were continued by the great French zoologist and anatomist Georges Cuvier (1769–1832). In 1817, his “memoir” on morphology of *L. stagnalis* appeared (Cuvier 1817), in which the author described the external structure of the animal as well as the structure of its respiratory, digestive, nervous, and reproductive systems (see Fig. 1.2c). Some data on morphology of two other lymnaeid species were provided in the same paper. However, the anatomical studies had long remained detached from the taxonomic ones. Though the attempts to use the anatomical data for the purpose of lymnaeid classification were undertaken several times during the nineteenth century (van Beneden 1838; Troschel 1839; Klotz 1889), their impact on the practical taxonomy was almost negligible.

Let us, for example, consider a system of the Lymnaeidae proposed in 1905 by William H. Dall (1845–1927), a prominent American malacologist, in his monograph on Alaskan freshwater Mollusca (Dall 1905). This system was praised by F.C. Baker (1911, p. 118) as “the first attempt to place the classification of this group . . . on a modern basis.” A closer look at Dall’s system reveals that the diagnoses of genera and subgenera published by this author include only conchological characters, and Dall apparently did not dissect studied snails.

The system created by Frank C. Baker (1867–1942) himself constituted an important step toward the use of both conchological and anatomical data as the basis for classification of the pond snails. It was built by combining the traits of shell, radula, and genital anatomy (F.C. Baker 1911, 1915). In Europe, malacologists also started to describe the anatomical differences between lymnaeid species, with the strongest emphasis on reproductive organs, considered a very valuable source of taxonomic signal (Roszkowski 1914a, 1914b, 1925, 1929; J. Wagner 1927; de Larambergue 1928). Roszkowski (1914b) was among the first authors to apply anatomical data to clarification of the true taxonomic identity of some peculiar varieties and local races of lymnaeids described on the basis of shell characters. The jaw and radula structure were decided to be of rather low taxonomic value due mainly to its great intraspecific variation (Roszkowski 1929).

A new standard in lymnaeid taxonomy was set in the works of the Swedish malacologist Benigt Hubendick (1916–2012), perhaps the most influential researcher

of the Lymnaeidae of the last century. Contrary to F.C. Baker's (1911, 1915) opinion, he believed that conchological differences are of lesser importance for lymnaeid taxonomy, and only qualitative structural distinctions in the reproductive anatomy may constitute a good basis for classification. During his extensive anatomical work, Hubendick (1951) could recognize only two *Bauplans* of the reproductive system within Lymnaeidae, and therefore sorted all pond snails into two genera: *Lymnaea* Lamarck, 1799 and *Lanx* Clessin, 1882. The latter genus is of North American distribution and includes lymnaeids with limpet-like shells and very peculiar anatomy (H.B. Baker 1925). The internal structure of *Lanx* is so unusual as compared to the rest of Lymnaeidae that this genus has often been placed in a separate family Lancidae Hannibal, 1914 (H.B. Baker 1925; Taylor and Sohl 1962; Starobogatov 1967; but see Walter 1969). All other species of lymnaeids from all continents proved to be too uniform in their anatomical structure even to delimit subgenera within the genus *Lymnaea* (Hubendick 1951). Hubendick demonstrated this amazing uniformity of the internal structures of the pond snails does not correspond to morphological diversity of their shells. Hubendick believed that conchological differences among taxa should be neglected if these are not accompanied by qualitative and stable differences in anatomical structures. He adhered to a very broad species concept and, as a result, he reduced a huge amount of 1150 species and varieties of lymnaeids, proposed prior to 1951, to a totality of nearly 40 species. Some of these species were conchologically polymorphic and characterized by very wide ranges. The quantitative anatomical differences between forms were almost ignored by Hubendick (1951).

However, as soon as 8 years later, Maria Jackiewicz (1920–2018) in Poland has shown that there are really more “good” species of pond snails even in the European waterbodies than it was accepted by Hubendick (Jackiewicz 1959). She reported clear anatomical differences among Eastern European species of the (sub-)genus *Stagnicola* Leach in Jeffreys, 1830 and described a new species, *Galba occulta* Jackiewicz, 1959. Since 1959, a new stage of description of novel species of pond snails has started. The classical approach to classification of the pond snails, based primarily on study of their shell characters and internal morphology, was accepted in the former USSR by Yaroslav I. Starobogatov (1932–2004) and Nikolay D. Kruglov (1939–2010). Working together, these authors developed an original system of the family and described several tens of new species as well as new supraspecific taxa (summarized in Kruglov 2005). In total, Kruglov and Starobogatov (1993a, 1993b) distinguished more than 140 species of Lymnaeidae in the fauna of Europe and Northern Asia, which far exceeded the species richness estimates made by the Western European malacologists. Their approach, however, met strong criticism and no malacologist working beyond the former USSR agreed with the lymnaeid classification proposed by Kruglov and Starobogatov (1993a, 1993b), though usually no serious analysis of their arguments was provided. For instance, Jackiewicz (1998, p. 3) stated that “opinions of Russian malacologists on the lymnaeid taxonomy <...> raised great doubts and <...> have not been taken into consideration.” The reasons of these “great doubts” were, however, not explained by Jackiewicz. It is worth to note, however, that some species and genera delineated by Kruglov and

Starobogatov have recently received a molecular support (Vinarski et al. 2011, 2012, 2016; Aksenova et al. 2018).

An alternative morphology-based version of the Lymnaeidae system was published in 1997 by Ponder and Waterhouse (1997). Essentially, it was the last example of a “traditional” classification, since from 1997 onwards the DNA taxonomy starts to gain a foothold in the field (Bargues and Mas-Coma 1997; Remigio and Blair 1997a, 1997b; Bargues et al. 2001, 2003; Remigio 2002).

The limits of the strictly morphological approach to lymnaeid classification were obvious to everyone who is familiar with the high degree of shell and anatomical variability of these snails, both at the intra- and interspecific level. In the second half of the twentieth century, there were numerous attempts to expand the set of taxonomic methods and to apply new sources of information to classification of the family. None else than Kruglov and Starobogatov (1985) tried to use the method of crossing experiment for delineation of lymnaeid species. In doing so, they followed the “biological species concept” that proposes to delimit species on the basis of their reproductive isolation, which may be established experimentally. The authors attempted to demonstrate that *Lymnaea stagnalis* in Europe is a complex of several species, at least two of which, *L. stagnalis* s. str., and *L. fragilis* (Linnaeus, 1758), are reproductively isolated (Kruglov and Starobogatov 1985). The authors, however, acknowledged that this method has serious limitations when applied to hermaphroditic animals like aquatic pulmonate snails. The reason is that “their capacity for self-fertilization leads to difficulty in deciding whether the progeny is the result of self-fertilization or cross-fertilization between different forms” (Kruglov and Starobogatov 1985, p. 22). It can explain why the method has never gained much popularity among students of the lymnaeid snails.

Another approach, advocated by Kruglov (1986, 2005), was grounded on the so-called parasitological criterion. It was assumed that different species of parasitic trematodes are species-specific in their host choice, and each species of pond snails has its own specific circle of trematode larvae. If a larva infests a “wrong” host, it dies. Thus, observed differences in infestation by trematodes may be viewed as indirect evidence for taxonomic distinctness of two or more forms of lymnaeids (Kruglov 1986). However, recent parasitological and molecular studies showed that lymnaeid species serving as intermediate hosts of *Fasciola hepatica* are widely distributed across their phylogeny and basically, all clades contain species that have proven to be naturally or experimentally infected with the parasite (Correa et al. 2010).

A quite another approach to species delimitation used in the twentieth century zoological systematics was the biochemical one (Throckmorton 1968). In the 1960s–1980s, three basic types of experimental biochemical taxonomy techniques had been applied to freshwater Mollusca: chromatography, electrophoresis, and immunology (serology). Davis (1978) and Meier-Brook (1993) published reviews of these techniques in application to aquatic gastropods, with many examples of their practical usage for recognizing species. All these methods were directed toward identification of genotypic characters, including amino acid analysis of proteins, allowing thereby to characterize populations, species, or higher taxa of molluscs, and

to assess relationships among them (Davis 1978). Allozyme electrophoresis was the most popular technique. Davis (1994, p. 3) recommended it as “an ideal tool for population genetics as applied to delineating species.” A good illustration of this recommendation may be found in a population genetic study that was performed on populations of *Galba* species from several Neotropical countries. This study using starch gel electrophoresis analyzed populations from Venezuela, Cuba, Guadeloupe, Dominican Republic, and Bolivia as well as several *G. truncatula* samples collected from France, Portugal, and Morocco for comparison (Jabbour-Zahab et al. 1997). Multilocus enzyme electrophoresis was determined for 282 snails at 18 loci. Two genotypic groups could be differentiated by their multilocus genotypes (i) a Western genotypic group associating samples from Venezuela, Guadeloupe, Cuba, and Dominican Republic (*G. cubensis*) and (ii) an Eastern genotypic group associating samples from France, Portugal, and Morocco (*G. truncatula*). Surprisingly, the Northern Bolivian Altiplano populations formerly identified as *G. viator* did not present any divergence with the Portuguese sample and belong entirely to the Eastern genetic group (*G. truncatula*). These results showed that the lymnaeids coming from the Northern Bolivian Altiplano undoubtedly belong to the *G. truncatula* species (Jabbour-Zahab et al. 1997). In some countries, allozyme electrophoresis was exploited in the lymnaeid studies until quite recently (Mezhzherin et al. 2008) but today it is completely replaced by more advanced methods based on DNA sequencing.

Cytotaxonomy also had attracted many practitioners in the lymnaeid systematics of the last century (Perrot and Perrot 1938; Inaba 1969; Patterson and Burch 1978; Meier-Brook 1993) and was still in some use at the dawn of the new millennium (Garbar and Korniushev 2002; Garbar et al. 2004). Inaba (1969) attempted to reconstruct the phylogeny of the family based on cytotoxic and biogeographic evidence.

As it was mentioned above, since the last decade of the twentieth century, the molecular methods started to be actively used in the reviewed field. The current taxonomic work on the Lymnaeidae is based either on a strictly molecular approach (Bargues et al. 2006; Pfenninger et al. 2006; Puslednik et al. 2009; Correa et al., 2010) or on the “integrated” taxonomic scrutiny combining analysis of genetic, morphological, and zoogeographical information (Bargues et al. 2011; Correa et al. 2011; Schniebs et al. 2011, 2013; Vinarski et al. 2016; Campbell et al. 2017; Aksenova et al. 2018). The molecular methods also dominate in the studies of speciation and biogeography of lymnaeid snails (e.g., Albrecht et al. 2008; Cordellier and Pfenninger 2009; von Oheimb et al. 2011; Aksenova et al. 2018; Mahulu et al. 2019). The most recent advances in the fields of systematics and phylogeny of the family will be reviewed in subsequent chapters. Box 1.2 summarizes the most important works on the Lymnaeidae published over the last 120 years.

Of course, the lymnaeid studies of the last 50–70 years were not focused solely on taxonomy and phylogeny. The great pond snail, *L. stagnalis*, appeared to be a laboratory animal very suitable as a model object for studies in genetics, physiology, embryology, and some other experimental branches of biology (Freeman and Lundelius 1982; Meshcheryakov 1990; Fodor et al. 2020). Though this snail never

reached a popularity in the laboratories comparable to that of the fruit fly or *Caenorhabditis elegans*, some important discoveries resulted from experiments with the great pond snail. A classical example is Alfred Sturtevant's (1891–1970) work, in which the phenomenon of “maternal inheritance” was discovered (Sturtevant 1923). Experimental works on the inheritance of sinistrality in lymnaeid snails, performed in England by Arthur Edwin Boycott (1877–1938) and his co-workers (Boycott and Diver 1923, 1927; Boycott et al. 1930), became a further substantial contribution to understanding of this phenomenon (reviewed briefly in Gurdon 2005).

Around a century ago, some lymnaeid species, whose shells were easy to obtain in large quantities, constituted an important object for studies in variability of animal populations. These works were significant for the advance of biometric methods and the progress of the “population thinking” in zoology. The students tried to reveal both the patterns of conchological variation and the factors that may govern them (Zhadin 1923; H. Wagner 1929; Boettger 1930; Peters 1938a; see review in Arthur 1982).

But the most important field of the applied lymnaeid studies is, surely, that aimed at revealing the complex relationships between trematode larvae and their mollusc hosts. The parasitological significance of the pond snails and their impact on public health in various countries are enormous and will be reviewed in detail in the second part of this book. Only a short historical introduction to these studies is worthy to provide here.

The history of studies of Trematoda parasitizing freshwater snails can be traced back to the late seventeenth century. Swammerdam (1738) discovered, described, and depicted some trematode larvae found inside bodies of aquatic Gastropoda. (The adult worms living inside organisms of humans and warm-blooded animals were known much earlier; see Grove 1990). The work on description of their diversity had continued during the next two centuries, but the life cycle of the trematodes and the role of snails as their reservoir hosts and vectors remained obscure until the end of the nineteenth century. For instance, Govert Bidloo (1649–1713), the Dutch physician, in 1688 expressed his opinion that the worms bred in moist earth then were swallowed together with their eggs in water by herbivorous animals such a sheep, stags, calves, and wild boars (Grove 1990). Fischer (1880, pp. 111–112) enlisted several trematode species whose larvae occur in molluscs, however all species included into his list use waterfowl and frogs, not humans or domestic animals, as their definitive hosts.

The liver fluke, *Fasciola hepatica*, became the first trematode in which the life cycle was understood. After a long series of investigations and fruitless attempts of various authors to work out the extremely complex development of this parasite, Rudolf Leuckart (1822–1898) in Germany and Algernon Thomas (1857–1937) in England, who had been working quite independently of each other, published papers (both appeared in October 1882; see Leuckart, 1882; Thomas, 1882) on this subject. Due to the efforts of these two students, the key role of the lymnaeid *Galba truncatula* (O.F. Müller, 1774) in the transmission of the parasite was firmly established. In the last century, this mollusc, also known as the dwarf pond snail

(or the mud snail), became a focus of very intensive research in different countries of Europe (i.e., Patzer 1927; Zhadin and Pankratova 1931; Peters 1938b). Similar studies, involving other representatives of the genus *Galba*, were made in non-European countries, for example in Colombia (Brumpt et al. 1940).

Shortly after this discovery, many species of the Lymnaeidae were found to transmit other species of Trematoda of medical and veterinary importance (such as *Fasciola gigantica*, a cause of tropical fascioliasis, and *Fascioloides magna*, or the giant liver fluke). The family of pond snails is considered as one of the most significant from the point of view of public health, second only to planorbids (= Planorbidae s. lato, including bulinid snails) [Brown 1978; Bargues and Mas-Coma 2005; Vázquez et al. 2018].

Research on the role of molluscs as intermediate hosts of *Fasciola hepatica* has subsequently evolved as a result of successive outbreaks of animal or human distomatosis and the development of new analytical techniques. Until the 1980s, many species of Lymnaeidae were tested to determine their potential role as host snails in the parasite cycle (Kendall 1950; Berghen 1964; Boray, 1969, 1978; Busson et al. 1982; Kruglov 2005). Studies on several species of lymnaeids have also been carried out on various continents in order to know the characteristics of the environment in which they live, namely the life cycle of snails, the vegetation of their habitats, the associated fauna and the factors which act on snail ecology (Mehl 1932; Zhadin 1923; Roberts 1950; Chowaniec and Drozd 1958; Stefanski 1959; Bednarz 1960; Over 1962, 1967; Erhardová-Kotrlá 1971; Pécheur 1974; de Kock et al. 1974; Smith 1981 for *G. truncatula*). The occurrence of an outbreak of human and animal distomatosis in 1968–1969 in central France (Dreyfuss et al. 2015b) prompted studies on the control of molluscs in order to determine whether methods of biological control (predators, competitors) had to be used alone or in combination with molluscicides which were already known at that time (Mage et al. 1989; Rondelaud et al. 2006). Additional research was carried out on histological sections of lymnaeids in order to determine the kinetics of the various larval stages which follow one another in the body of the snail (Rondelaud and Barthe 1982; Rondelaud et al. 2009) and the pathology that the parasite induces in the latter (Sindou et al. 1991). The development of modern analytical techniques (electrophoresis, molecular biology) since the 1990s has made it possible to determine whether the DNA or RNA of the parasite is present in the bodies of the snails studied (Caron et al. 2008; Kim et al. 2014; Alba et al. 2015, for example). The current development of PCR (polymerase-chain reaction) has changed the conventional methods (dissection, cercarial shedding) used by the authors to test for the presence of the parasite in molluscs (Caron et al. 2008). The PCR indicates whether miracidia have penetrated the lymnaeid, even if the larval forms have degenerated later in the body of the snail. However, its use alone does not permit the determination of whether a lymnaeid species in a given region is a potential intermediate host capable of transmitting the parasite or a non-target mollusc into which the miracidia have penetrated through a decoy effect.

Box 1.1 Enumeration of Lymnaeid Species Described During 1758–1803 (Only Species Accepted Today as Valid Are Included)

Original name (in brackets – combination accepted in current taxonomy)	Type locality	Authority
<i>Buccinum glabrum</i> (<i>Omphiscola glabra</i>)	Denmark	O.F. Müller (1774)
<i>Buccinum glutinosum</i> (<i>Myxas glutinosa</i>)	Denmark	O.F. Müller (1774)
<i>Buccinum lagotis</i> (<i>Ampullaceana lagotis</i>)	Germany	Schrank (1803)
<i>Buccinum palustre</i> (<i>Stagnicola palustris</i>)	Denmark	O.F. Müller (1774)
<i>Buccinum peregrum</i> (<i>Peregriana peregra</i>)	Denmark	O.F. Müller (1774)
<i>Buccinum truncatulum</i> (<i>Galba truncatula</i>)	Denmark	O.F. Müller (1774)
<i>Helix auricularia</i> (<i>Radix auricularia</i>)	Europe	Linnaeus (1758)
<i>Helix balthica</i> (<i>Ampullaceana balthica</i>)	Sweden	Linnaeus (1758)
<i>Helix corvus</i> (<i>Stagnicola corvus</i>)	Germany	Gmelin (1791)
<i>Helix stagnalis</i> (<i>Lymnaea stagnalis</i>)	Europe	Linnaeus (1758)

Box 1.2 A Short Index to the Lymnaeid Literature of the Last 120 Years

Field of study	References
Morphology	Boettger 1944; Jackiewicz 1954, 1993, 1998; Hubendick 1951, 1978; Walter 1969; Falniowski 1980; Meshcheryakov 1990; Kruglov 2005
Phylogeny and taxonomy	Dall 1905; FC Baker 1911; Thiele 1931; Hubendick 1951, 1978; Starobogatov 1967; Inaba 1969; Kruglov and Starobogatov 1993a, 1993b; Barges and Mas-Coma 1997, 2005; Ponder and Waterhouse 1997; Jackiewicz 1993, 1998; Remigio 2002; Barges et al. 2003; Garbar et al. 2004; Kruglov 2005; Pusednik et al. 2009; Correa et al. 2010; Dayrat et al. 2011; Vinarski 2013; Bouchet et al. 2017; Campbell et al. 2017; Aksenova et al. 2018; Saadi et al. 2020; Alda et al. 2021; Saito et al. 2021
Nomenclature and type series	Hubendick 1951; Sitnikova et al. 2012, 2014; Vinarski et al. 2013; Vinarski 2016; Eschner et al. 2020
Biogeography and ecology	Roszkowski 1928; Boycott 1936; Frömring 1956; Over 1967; Starobogatov 1970; Russell-Hunter 1964, 1978; McMahon 1983; Beriozkina and Starobogatov 1988; Banarescu 1990; Økland 1990; Dillon 2000; Stadnichenko 2006; Strong et al. 2008; Aksenova et al. 2018; Lounnas et al. 2017, 2018; Vinarski et al. 2019; Alda et al. 2021

(continued)

Fossil record	FC Baker 1911, Wenz 1923; Korobkov 1955; Wenz and Zilch 1959–1960; Pchelintsev and Korobkov 1960; Taktakishvili 1967; Gray 1988; Taylor 1988
Most important regional surveys	Yen 1939; Boettger 1944; Hubendick 1951; Brandt 1974; Burch 1989; Subba Rao 1989; Økland 1990; Kruglov and Starobogatov 1993a, 1993b; Brown 1994; Jackiewicz 1998; Glöer 2002, 2019; Gittenberger et al. 2004; Stadnichenko 2004; Kruglov 2005; Khokhutkin et al. 2009; Andreeva et al. 2010; Thompson 2011; Welter-Schultes 2012; Johnson et al. 2013; Pointier 2015; Piechocki and Wawrzyniak-Wydrowska 2016; Vinarski and Kantor 2016; Vinarski 2019; Pointier and Vázquez 2020; Vinarski et al. 2020
Parasitological significance	Mozley 1957; Wright 1971; Brown 1978, 1994; Malek 1980; Mas-Coma and Bargues 1997; Kruglov 2005; Dreyfuss et al. 2015a; Pointier 2015; Caron et al. 2017; Vázquez et al. 2018; Celi-Eraza et al. 2020; Alba et al. 2019; Vázquez et al. 2019; Pereira et al. 2020

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