Chapter 2
General Characteristics of the Family Lymnaeidae

Maxim V. Vinarski and Jean-Pierre Pointier

Abstract The article provides a brief introduction to the Lymnaeidae and contains short reviews of taxonomy, the fossil record, morphology, biogeography, and ecology of these snails, with an emphasis on the extant representatives of the family.

The aim of this chapter is to provide the reader with a brief and general overview to the family Lymnaeidae, in other words to give an introductory reading to the subjects discussed in the rest of the book.

2.1 Taxonomic Position of the Family

Lymnaeidae Rafinesque, 1815 is a relatively speciose family of aquatic snails belonging to a large group informally known as the "pulmonate snails" (Pulmonata). The main diagnostic feature (synapomorphy) of the subclass Pulmonata was thought to be their mode of respiration based on the utilization of atmospheric air and the use of lungs as an organ of breathing. Since 1816, when Georges Cuvier proposed a new system of the Gastropoda based on morphology of the respiratory system (Cuvier 1816), a taxon named Pulmonata figured in almost each version of classification, though the rank of this group might have been varied. Cuvier (1816) and many of his followers ranked it as an order (e.g., Fischer 1880–1887; Pelseneer 1905), whereas in the twentieth century systematics the Pulmonata have usually been treated as a

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subclass of Gastropoda (Prosobranchia and Opisthobranchia constituted the two other subclasses) [Thiele 1929, 1931 and many subsequent taxonomists]. An alternative, albeit somewhat less popular, approach was to build the system of Gastropoda on the gross morphology of the nervous system. The use of this criterion led Spengel (1881) to distribute gastropods between two subclasses—Streptoneura (with *chiastoneury*, i.e. crossing of the cerebrovisceral commissures caused by the torsion process) and Euthyneura (without chiastoneury), and such a division was accepted by some workers of the early-mid-twentieth century (Grobben 1910; Ivanov 1940; Taylor and Sohl 1962).

Most often, the subclass (or order) Pulmonata was divided into two subgroupings—Basommatophora (chiefly aquatic forms) and Stylommatophora (almost exclusively terrestrial). In this classical scheme, the Lymnaeidae, alongside with such families as Acroloxidae, Planorbidae, Physidae, and several else, constituted Basommatophora (Thiele 1931; Hubendick 1978; Salvini-Plawen 1980). This classification has been challenged in the 1970s–1980s (Golikov and Starobogatov, 1975, 1988; Minichev and Starobogatov 1979; Salvini-Plawen 1980; Haszprunar 1988; Ponder and Lindberg 1997; reviewed in Ponder and Lindberg 2008), and now the class Gastropoda is divided into several subclasses, none of which is identical to Pulmonata of the older authors. The current system of Gastropoda is grounded chiefly on the results of molecular phylogenetic research, according to which Pulmonata is a part of a larger group called Heterobranchia (Ponder and Lindberg 2008). It is ranked as a subclass by Bouchet et al. (2017). Heterobranchia is the taxon embracing virtually all representatives of the former subclasses Opisthobranchia and Pulmonata. Thus, traditional "Pulmonata" has become an abandoned concept. According to Schrödl (2013, p. 162), "traditional Pulmonata most likely has failed from a phylogenetic point of view, and thus should be avoided in a systematic, taxonomic and classificatory context." However, it does not prevent from using the informal term "pulmonate snails." Basommatophora is also an outdated concept; in the current taxonomy, the higher group to which the Lymnaeidae belongs is Hygrophila (Box 2.1). Historically, Hygrophila constituted a subset of the old "Basommatophora," a taxon uniting all families of freshwater basommatophoran gastropods (Thiele 1931).

2.2 Evolutionary Origin of the Family and Its Fossil Record

The direct ancestors of the family Lymnaeidae are unknown. According to Kruglov (2005), the origin and initial diversification of this group should be dated to the Triassic Period, and possible progenitors of the lymnaeids were some *Chilina*-like gastropods. It correlates well with the basal position of Chilinidae within Hygrophila revealed in both morphology- and molecular-based phylogenies (Hubendick 1978; Nordsieck 1992; Jörger et al. 2010; Saadi et al. 2020).

The oldest known lymnaeid remains are dated as early Jurassic and come from the western USA. Paleontologists classify these fossil species as belonging to extant genera *Galba* and *Lymnaea* (Robinson 1915; Yen and Reeside 1946; Tracey et al. 1993), which, however, must be treated with great caution. As it has been revealed during recent molecular phylogenetic studies on the living Lymnaeidae, shell characters are not a good source of phylogenetic signal; phylogenetically distant genera may demonstrate convergent similarity in their shell shape and proportions (see below). The estimates of the geological age of particular lymnaeid genera obtained by independent approaches can be quite different. For example, Martinson (1961) described three fossil species of the genus *Radix* from the Upper Cretaceous of Siberia. On the other hand, a fossil-calibrated phylogeny presented by Aksenova et al. (2018) dates the origin of this genus to the mid-Eocene, and the mean age of divergence between *Radix* and its sister clade, which includes eight lymnaeid genera, is 58.2 Ma, which corresponds to the Paleocene. However, this is just the mean age, the confidence interval for this estimate is quite broad and ranges from ca. 45 to 73 Ma, which involves also the latest Cretaceous.

As of 01.10.2022, 360 fossil lymnaeid species are accepted as valid (MolluscaBase 2022). Around 15 extinct genera of the Lymnaeidae have been described, including those forming a conchologically aberrant subfamily, Valencienniinae Gorjanović-Kramberger, 1923 (sometimes ranked as a family; see Taktakishvili 1967), known from the Pliocene of southeast Europe (Fig. 2.1).

2.3 Diversity and Taxonomic Structure of the Extant Lymnaeidae

According to Hubendick (1951) and Kruglov and Starobogatov (1981, 1993), the extant Lymnaeidae are distributed among only two genera—*Lymnaea* and *Lanx* Clessin, 1882 (Hubendick 1951), or *Lymnaea* and *Aenigmomphiscola* (Kruglov and Starobogatov, 1993). Today, most taxonomists tend to split the family Lymnaeidae into a series of genera, the actual number of which is, however, unknown since the integrative revision of the taxonomic structure of this family has not been completed yet. The most recent published estimates counted 20 to 25 extant lymnaeid genera (Ponder and Waterhouse 1997; Vinarski 2013; Vinarski et al. 2019), but in the course of a molecular phylogenetic study (Aksenova et al. 2018), the number of valid genera increased, mainly due to elevation of rank of some taxa previously treated as subgenera (*Ampullaceana*, *Kamtschaticana*, and some other). Two new lymnaeid genera, *Idaholanx* Clark, Campbell & Lydeard, 2017, and *Tibetoradix* Bolotov, Vinarski & Aksenova, 2018, have recently been described. Therefore, for the time being, it is reasonable to estimate the generic richness of living lymnaeids to lie between 30 and 35 valid genera.

To estimate the lymnaeid species richness in the recent fauna is even more difficult. The estimates available from the literature vary from only 40 (Hubendick 1951) to about 100 (Strong et al. 2008) and even more than 200 valid species worldwide (Kruglov 2005). As of 01.11.2021, MolluscaBase (2022) lists 161 species

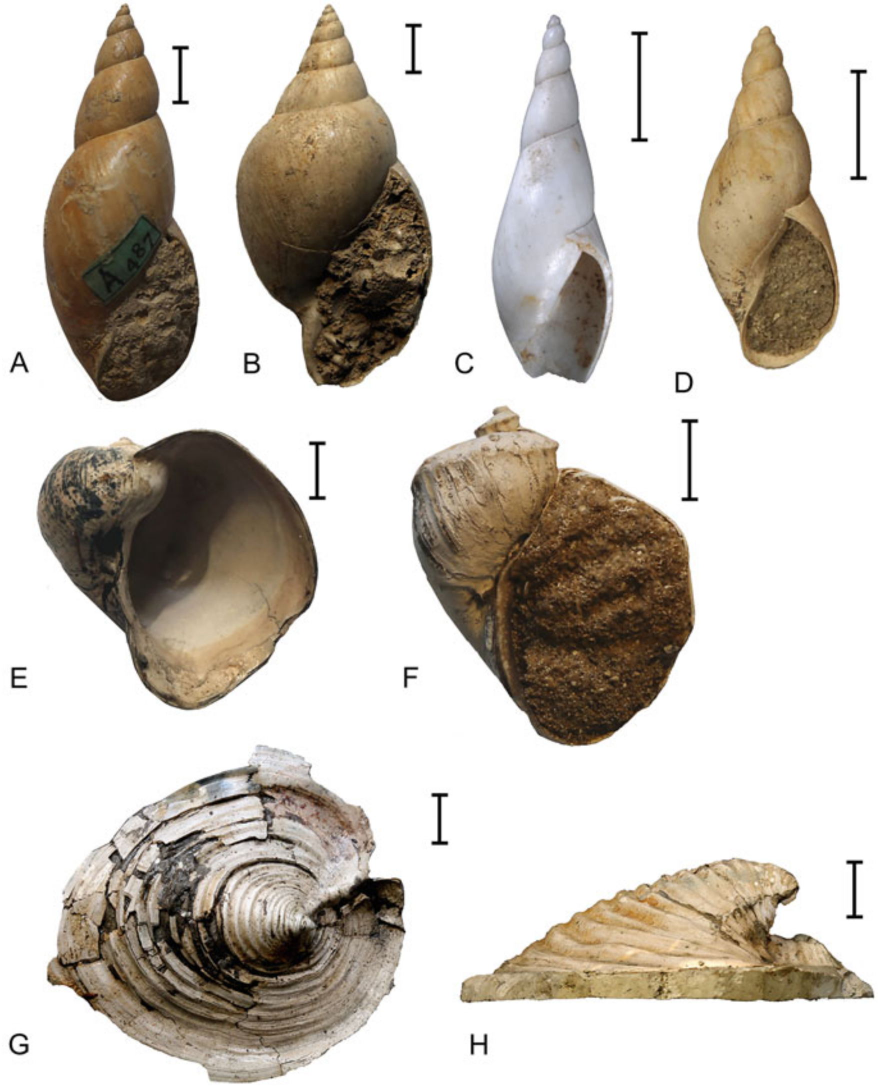

Fig. 2.1 A selection of fossil lymnaeid shells. (**a**) *Stagnicola longiscatus* (Brongniart, 1810), Eocene of England. (**b**) *Lymnaea caudata* F.E. Edwards, 1852, Eocene of England. (**c**) *L. megarensis* Gaudry in Gaudry et Fischer, 1867, Pliocene of Greece. (**d**) *Lymnaea bogatschevi* Vinarski et Frolov, 2017, late Miocene of South Russia. (**e**) *Radix kobelti* (Brusina, 1884), Pliocene of Croatia. (**f**) *Corymbina bicarinata* (Fuchs, 1887), Pliocene of Greece. (**g, h**) *Valenciennius reussi* Neumayr in Neumayr et Paul, 1875, Pliocene of Croatia. Two different specimens in two views. All shells, except E, are from the collection of the Natural History Museum in Vienna. E – from collection of the Zoological Institute, Russian Academy of Sciences, St. Petersburg. Scale bars 5 mm. Photos: Maxim V. Vinarski

of Lymnaeidae flagged as "accepted." In order to understand this number properly, one needs to keep in mind that a great portion of these taxa were described in the nineteenth to the first half of the twentieth centuries, when shell characters served as the virtually sole basis for species delineation. The validity of some of the accepted species still requires to be confirmed.

The synonymy rate among living Lymnaeidae is rather high. According to MolluscaBase, there are 1050 unaccepted species names, which is 6.5 times higher than the number of accepted species. This synonymy rate would increase substantially, if all unaccepted taxa of the "variety" rank, introduced in the past, are taken into account (it would be impossible to make such a calculation here since a large portion of these "varieties" has still not been indexed in MB).

On the other hand, recent integrative taxonomic studies (Campbell et al. 2017; Aksenova et al. 2018, 2019; Mahulu et al. 2019) have resulted in description of several new species of lymnaeid snails (or resurrection of the old-forgotten ones), and there are all reasons to believe that this process is not finished yet. Furthermore, instances of the so-called taxonomic crypsis have been detected among lymnaeids (Correa et al. 2010, 2011; Aksenova et al. 2018; Alda et al. 2018, 2021), which means that at least some "traditional" species of this family may, in fact, represent complexes of several distinct species. Since 2005, a series of new lymnaeid species, still not supported by molecular data, has been described (e.g., Glöer and Yildirim 2006; Glöer and Pešić 2008; Vinarski 2011; Qian et al. 2012). Therefore, an estimate of 200–225 living lymnaeid species in the world's fauna seems realistic.

The internal taxonomic structure of the extant Lymnaeidae has been considered differently by various authors. Traditionally, most systematists did not divide it into subfamilies (Hubendick 1951; Starobogatov 1967; Kruglov and Starobogatov 1993; Jackiewicz 1998; Ponder and Waterhouse 1997). The most controversial was the taxonomic status and rank of a peculiar North American group of limpet lymnaeids (the genera *Lanx* and *Fisherola* Hannibal, 1912). Both conchologically and anatomically, these limpets seem to be rather distinct from the rest of the Lymnaeidae. For example, this group is characterized by the presence of two prostates (H.B. Baker 1925; Starobogatov 1967). Hannibal (1914) proposed to erect a separate subfamily, Lancinae, whose rank was subsequently elevated to the family (Pilsbry 1925; Thiele 1931). Later on, the family status for this group was accepted by Taylor and Sohl (1962) and Starobogatov (1967).

On the other hand, Walter (1969, p. 5), in his thorough morphological study of the North American lymnaeids, concluded that "the limpet-like lymnaeids are more closely related to some species of '*Stagnicola*' than are some species of '*Stagnicola*' to each other" and therefore the author proposed "to reject the taxa Lancinae and *Lanx*." His point of view, however, was so radical that no malacologist shared it.

Recently, Campbell et al. (2017) showed that this group does not constitute a separate family within the Lymnaeoidea. Though the phylogenetic relationships of this group to other Lymnaeidae are not resolved yet, it represents a monophyletic and morphologically divergent clade that may be characterized by some synapomorphies (Campbell et al. 2017). Campbell et al. (2017) proposed to retain it as a subfamily of the Lymnaeidae, and their opinion was followed by Bouchet et al. (2017) and Vinarski et al. (2019).

The most recent phylogenetic study by Saadi et al. (2020) did not resolve the internal taxonomic structure of the Lymnaeidae. The authors showed that the subfamily Lymnaeinae may be not monophyletic, but the set of genera included in their study is too limited to warrant a thorough conclusion on the phylogenetic relationships among Lymnaeidae.

The current system of the living Lymnaeidae, as it is accepted by Bouchet et al. (2017) and MolluscaBase (2022), is summarized in Box 2.2. The contributors to this book, in the main, used this classification, however, in some cases they followed their own views on the volume and taxonomic position of particular genera and subgenera. Aksenova et al. (2023) propose an updated and more detailed version of this system, whose reliability and workability will be evaluated in the nearest future.

2.4 Shell and Soft Body Morphology Features

The vast majority of freshwater species of Gastropoda, including lymnaeids, are shell-bearing animals. Following Burch (1989), one can divide the overall diversity of shell morphologies observed among freshwater snails into four general categories. *Neritiform* shells vary in shape from hemispherical to globose; their spires are very low and small and sometimes become virtually invisible (Fig. 2.2a). *Ancyliform* (*limpet-shaped*) shells are uncoiled, have a shape of cap or obtuse cone (see Fig. 2.2c). *Planorbiform* (*discoidal*) shells, with sunken spire, are coiled in the same plane (see Fig. 2.2b), whereas *turbospiral* (*conic*) shells have a more or less raised spire. Both spire height and whorl number in turbospiral shells are very variable, which creates a plethora of conchological variants even within a single family. Most lymnaeid snails possess turbospiral shells that may take various shapes, from slender and subulate to subglobose (Fig. 2.3). The shell of the lymnaeid genus *Lantzia* may be described as neritiform (see Fig. 2.3l), while auriculate shells occupy an intermediate position in the shell morphospace, being a transition from conic to neritiform (see Fig. 2.3k). The limpet-shaped forms among living lymnaeids are known exclusively from North America where three genera, forming the subfamily Lancinae, occur (see Fig. 2.2c). In the late Miocene and Pliocene, ancyliform lymnaeids were living in large lacustrine basins of south-eastern Europe; most limpets of this group have been placed into the genus *Valenciennius* Rousseau, 1842 (see Fig. 2.1g,h) and other, closely allied, genera (Gorjanović-Kramberger 1923; Moos 1944; Taktakishvili 1967; Marinescu 1969; Harzhauser et al. 2016). As Lancinae and Valencienniinae belong to two distant phylogenetic lineages, separated both in space and time, it is clear that the limpet-shaped form among lymnaeids evolved convergently from coiled ancestors (which was a common situation within the class Gastropoda, see Vermeij 2017).

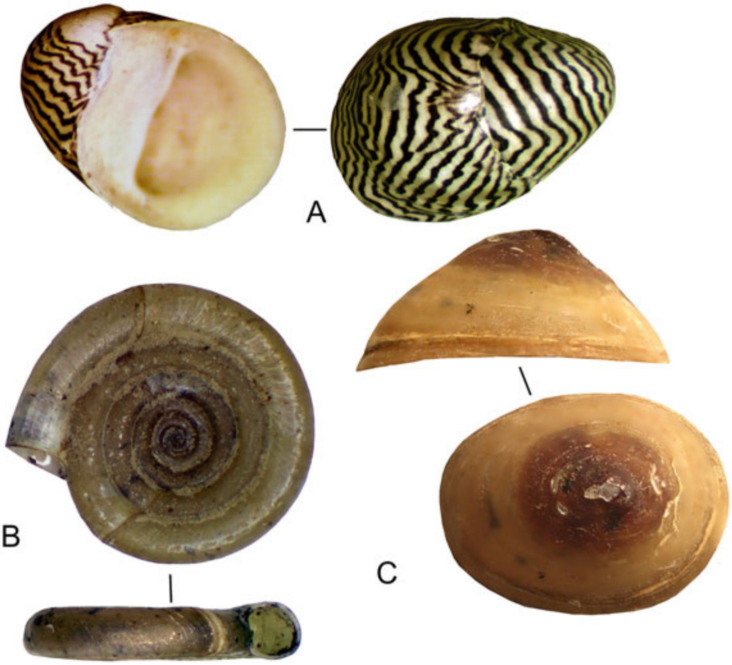

Fig. 2.2 Examples of neritiform (a), planorbiform (b), and ancyliform (c) shell. (**a**) *Theodoxus pallasi* (Neritidae). (**b**) *Anisus leucostoma* (Planorbidae). (**c**) *Lanx subrotundatus* (Lymnaeidae: Lancinae). This figure is not in a scale. Photos: Maxim V. Vinarski

The absolute shell size within the discussed family varies considerably. Its largest representatives in the recent fauna belong to the genus *Lymnaea*; their shells may reach 60–65 mm height. Shells of fossil Valencienniinae may have been even larger (up to 132 mm in diameter; see Taktakishvili 1967). On the other hand, shell height of species of the genus *Galba* rarely exceeds 10 mm (in most cases, the adult shells are 5–8 mm height). The majority of extant pond snails are, however, animals of medium size; their shell heights lie between 10 and 20–22 mm.

It should be remembered that the absolute shell size is a very plastic variable, and a number of abiotic and biotic factors are known to affect size. For example, the so-called *parasitic castration* may lead to development of unusually large individuals of pond snails (Wilson and Denison 1980). An opposite trend is *dwarfism,* which has been discovered in various species of the family. Dwarf morphs are known in lymnaeid populations inhabiting geothermal springs (Bolotov et al. 2012; Aksenova et al. 2017; Vinarski et al. 2023), in deep alpine lakes (Geyer 1923, 1929), and, occasionally, may represent a result of starvation (*Hungerformen* of Kobelt 1871). Typically, a dwarf individual is 1.5–2.0 times smaller than its congeners from populations living under "normal" conditions (Fig. 2.4). Most probably, this "thermal dwarfism" must be explained by the shortening of the life cycle of snails and their shift to neotenic reproduction (Vinarski et al. 2023). Large-

Fig. 2.3 Diversity of lymnaeid shell shapes. (**a**) Subulate (*Acella haldemani*). (**b**) Cylindric (*Omphiscola glabra*). (**c**) Turriculate (*Lymnaea taurica*). (**d, e**) High-conical (two morphotypes of *Lymnaea stagnalis*). (**f–h**) Ovate-conical (*Bulimnea megasoma*, *Pseudosuccinea columella*, *Ampullaceana lagotis*). (**i**) Ovoid (*Ampullaceana balthica*). (**j**) Ear-shaped, of auriculate (*Radix auricularia*). (**k**) Globose (*Myxas glutinosa*). (**l**) Neritiform (*Lantzia carinata*). (**a–g**) belong to the subfamily Lymnaeinae; (**h–l**) – to the subfamily Amphipepleinae. Scale bars 2 mm. Photos: Maxim V. Vinarski

scale spatial trends in shell size have been revealed in some widespread lymnaeid species. Generally, the absolute shell size tends to decrease in the south-north direction, which contradicts the predictions of Bergmann's rule (Vinarski 2012a, b; Vinarski and Kramarenko 2019). This relationship between shell size and latitude has been explained by reduction of the growth season (i.e., a warm period when shell growth is possible) in high latitudes. This reduction leads to formation of a climatically-driven "converse Bergmann" cline of shell size found in lymnaeids and some other aquatic pulmonates (Vinarski and Kramarenko 2019).

However, some clear exceptions from this general size gradient can be mentioned. The largest recent lymnaeid species, *Lymnaea stagnalis,* is native to the temperate belt of the North Hemisphere and is almost totally absent from the tropic latitudes (Hubendick 1951). On the other hand, the fauna of the Lymnaeidae of Hawaii, the islands lying at 20^0 N, consists of small-sized species, whose mean shell length is between 5 and 10 mm. Only rare individuals of these species can reach 15 mm height (Hubendick 1952). Possibly, this is a consequence of the so-called island rule that predicts that the insular endemics are generally diminutive in absolute size as compared to their relatives of the mainlands (Lomolino 2005; McClain et al. 2006; Lomolino et al. 2013; and references therein).

The lymnaeids are notoriously known as a group demonstrating enormous variability in shell shape and proportions, both at the intrapopulational and intraspecific level. Many shell characters of these snails are subject to local adaptation, and the observed conchological variability is typically merely direct effects of the ambient conditions on a plastic phenotype (though some distinct conchological

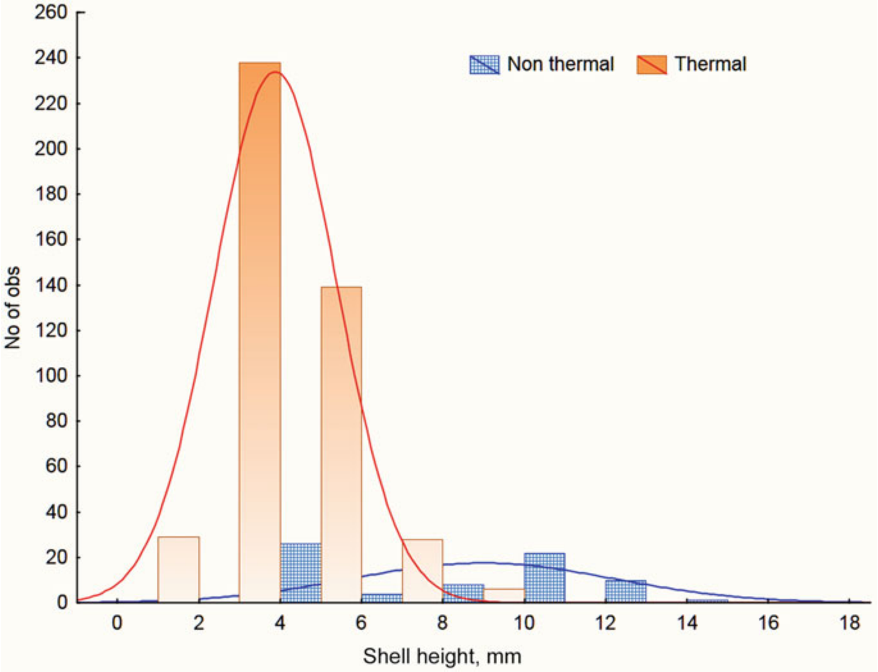

Fig. 2.4 Shell height distribution in *Ampullaceana balthica* individuals from thermal (water temperature range + 15… + 38 ° C) and non-thermal (water temperature range + 5… + 7 ° C) waterbodies of Island. (after Vinarski et al. 2023; modified)

variants may well have a hereditary basis). In a large body of water, like Lake Konstanz (= Bodensee) in Germany and Switzerland, the extent of intraspecific variation may be colossal (Fig. 2.5). In smaller habitats, the conchological disparity within a population is usually less prominent, though some patterns of variation may be discerned. Typically, shells can be arranged into a continuous series of phenotypes, varying from relatively slender and high-spired to more inflated and low-spired shapes (Fig. 2.6). In the past, it was not an uncommon situation when shells corresponding to the opposite extremes of variation were classified as belonging to two distinct varieties or even species. The biometrical analysis usually shows that all individual shells actually belong to a continuum, and the values of the measured traits follow the normal distribution pattern.

The variability in shell surface coloration and sculpture can also be very prominent at the intraspecific level. As a rule, it lacks any taxonomic value, though there are data that the pattern of shell microsculpture may be species-specific in some lymnaeids (Jackiewicz and Koralewska-Batura 1995; Jackiewicz 1998).

Examples of the *convergent* and *parallel* shell evolution are widespread among lymnaeid snails. The genera *Aenigmomphiscola* and *Omphiscola* represent one of the most salient instances. The structure of the copulatory apparatus in these genera is strikingly different, whereas their shells are almost indistinguishable (Kruglov and

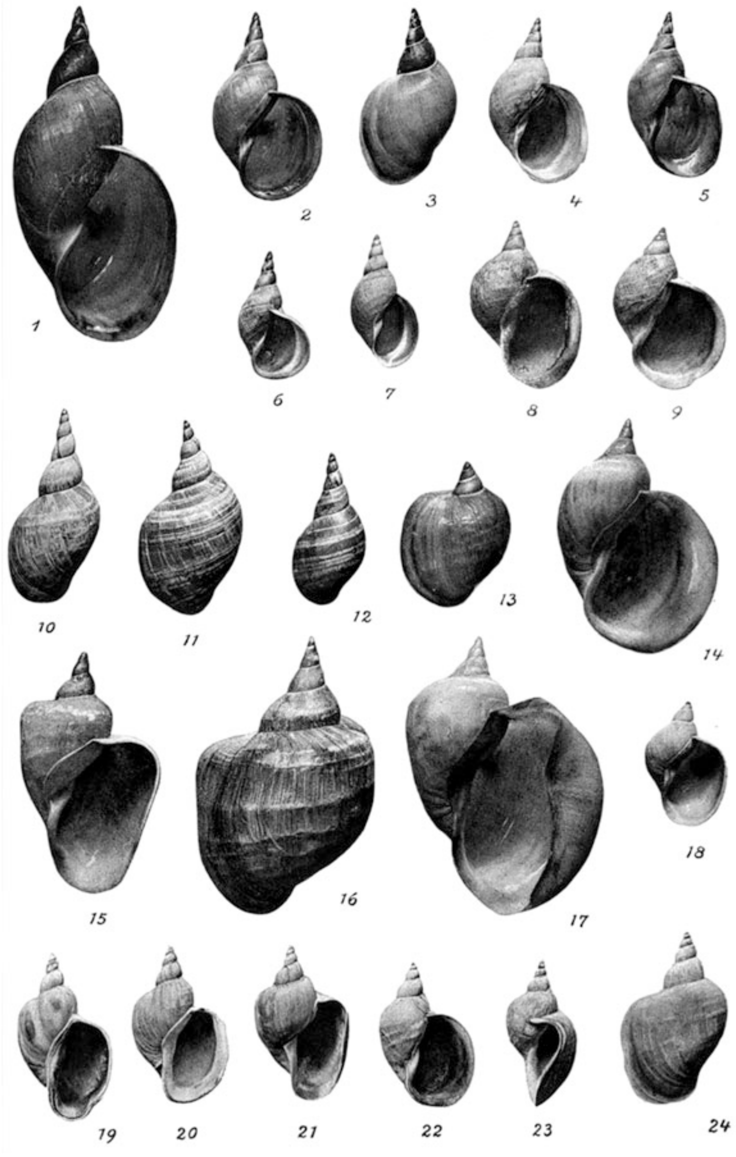

Fig. 2.5 Conchological disparity of *Lymnaea stagnalis* from Lake Konstanz. A "typical" form (= *L. stagnalis* f. *normalis perfecta*) is given under No. 1. After Geyer (1929), with modifications

Starobogatov 1981). A molecular phylogenetic study has brought evidence of the sister relationship between the two genera (Vinarski et al. 2011); most probably, they share the same shell morphology which was inherited from their common ancestor. Similar shell morphologies have been developed in lymnaeid species belonging to phylogenetically distant genera and living in different continents (Figs. 2.7 and 2.8).

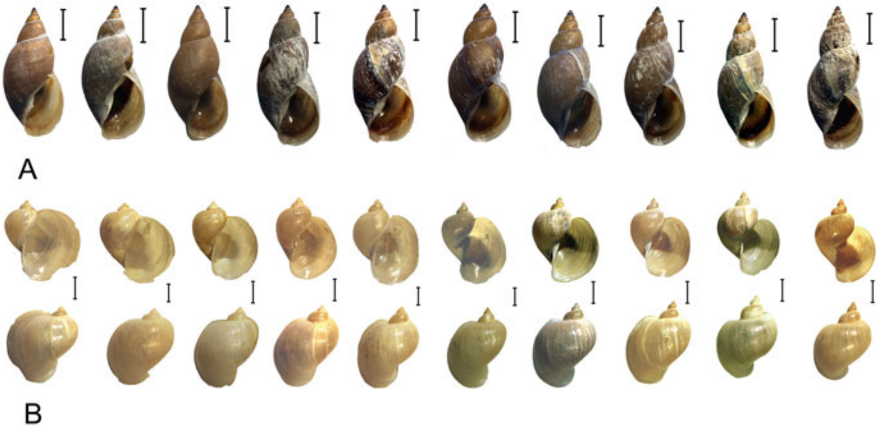

Fig. 2.6 Intrapopulation shell variation in two lymnaeid species: *Stagnicola palustris* (A) and *Radix auricularia* (B). (**a**) Russia, Tula Region, the Yasskoye Lake. (**b**) Mongolia, the Khar-Us-Nuur Lake. Scale bars 2 mm. Photos: Maxim V. Vinarski

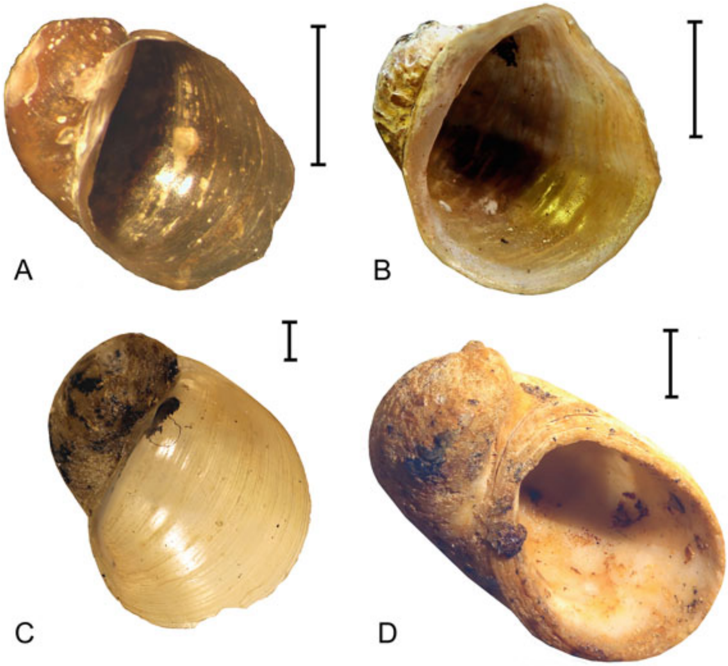

Fig. 2.7 Neritiform and subneritiform shells independently developed in phylogenetically and geographically distant lymnaeid species. (**a**) *Erinna newcombi*, Hawaii. (**b**) *Lantzia carinata*, Reunion Island. (**c**) *Radix onychia*, Japan, Biwa Lake. (**d**) *Peregriana subonychia*. Russia, Neogene of the Altay Mts. Scale bars 2 mm. Photos: Maxim V. Vinarski

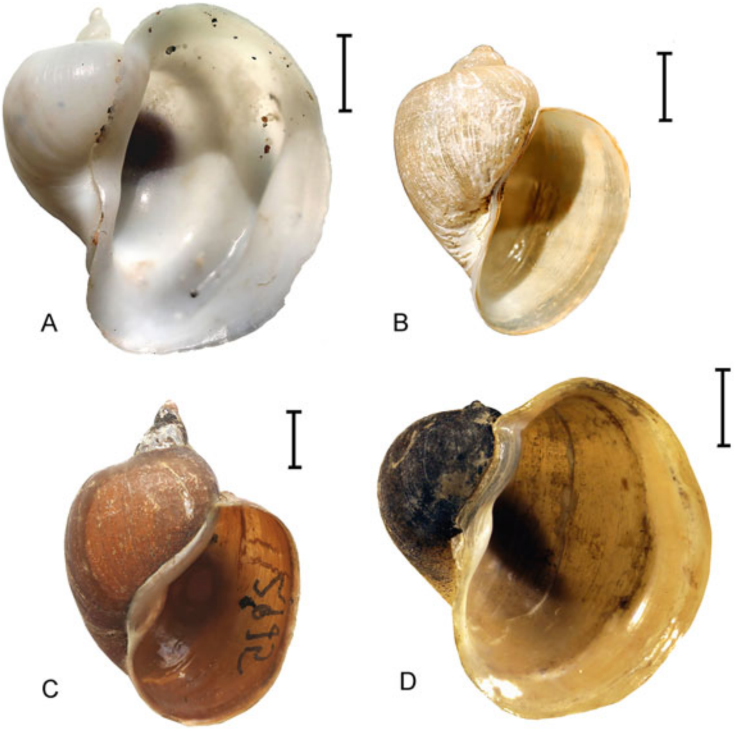

Fig. 2.8 Auriculate shells independently developed in phylogenetically and geographically distant lymnaeid species. (**a**) *Radix obliquata*, Kyrgyzstan, Issyk-Kul' Lake. (**b**) *Ladislavella emarginata* f. *mighelsi*, USA, Square Lake, Maine. (**c**) *Lymnaea stagnalis* f. *lacustris*, Russia, Karelia, Svyatozero Lake. (**d**) *Ampullaceana ampla*, Sweden, Östergotland. Scale bars 5 mm. Photos: Maxim V. Vinarski

The vast majority of the lymnaeid species have dextral (= right-coiled) shells, however, for a small group known as the subgenus *Pseudisidora* (*Pseudobulinus* Kruglov & Starobogatov, 1993), sinistrality is a diagnostic trait. It is endemic to Hawaii and, most probably, includes only one valid species—*Pseudisidora* (*Pseudobulinus*) *reticulata* (Gould, 1848) [Fig. 2.9]. In other lymnaeid species, sinistral (= left-coiled) individuals may occasionally arise as a consequence of a single-gene mutation (see Freeman and Lundelius 1982; Pierce 1996; Asami et al. 2008; Davison et al. 2009; Kuroda and Abe 2020 for reviews of sinistrality in the Lymnaeidae). Some recent results hint that the sinistrality can be the ancestral state for the family of pond snails (Davison et al. 2016), though the recent *Pseudobulinus*, with their narrow endemicity, do not seem a good candidature for the lymnaeid ancestral group and, most probably, their sinistrality is a secondary trait. Unfortunately, the fossil record gives us no data on the assumed left-coiled lymnaeid ancestors.

Within the Hygrophila, the direction of shell coiling typically (but not always) corresponds to the type of asymmetry of the soft body. Species of the families

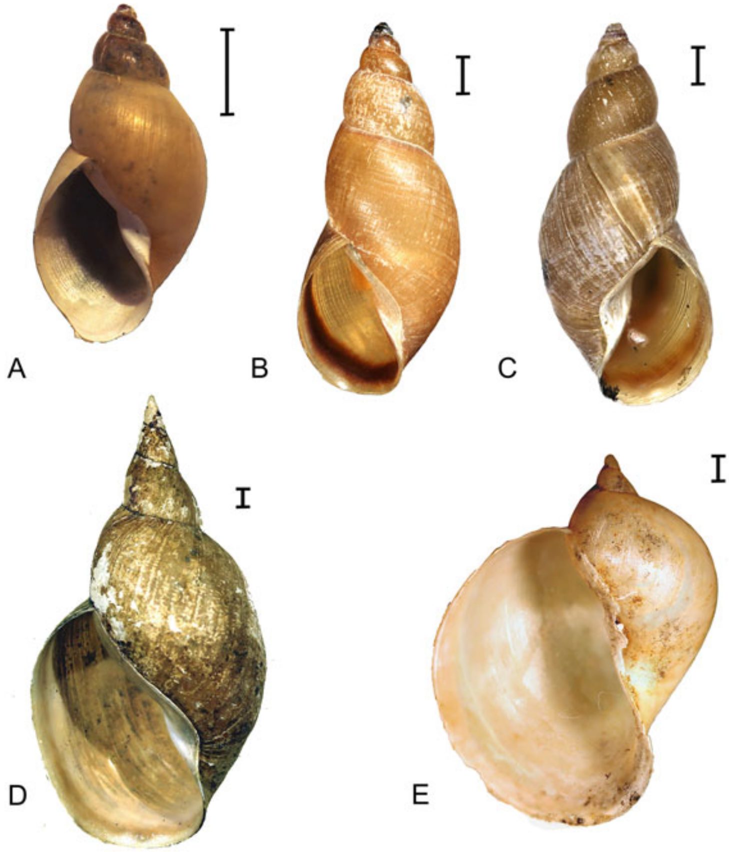

Fig. 2.9 Sinistral individuals of lymnaeid snails. (**a**) *Pseudisidora reticulata*, Hawaii. (**b, c**) *Stagnicola saridalensis*, Russia, Western Siberia (sinistral and dextral specimens). (**d**) *Lymnaea stagnalis*. Russia, vicinity of St. Petersburg. (**e**) *Radix auricularia*. England, Northamptonshire. Scale bars 2 mm. Photos: Maxim V. Vinarski (**a, c-d**), Peter Glöer (**b**)

Chilinidae, Latiidae, Lymnaeidae, and Acroloxidae are conchologically and anatomically dextral, so that the genital, anal, and respiratory openings are on the right side of the body. In contrast, the families Bulinidae, Physidae, and Planorbidae include anatomically sinistral species, and in some of them the shell is right-handed, but in this case, it is designated as *pseudodextral*.

The body plan of the Lymnaeidae represents a specific case of the Hygrophila body plan; the latter has been described in many sources (Ivanov 1940; Duncan 1960; Starobogatov 1967; Franc 1968; Hubendick 1978; Nordsieck 1992; Ponder et al. 2020) that allows us to omit a detailed anatomical characterization of the family (see also anatomical accounts presented in Hubendick 1951, 1978; Jackiewicz 1954, 1998; Walter 1969; Stadnichenko, 2004; Kruglov 2005). Walter's paper (1969) especially merits to be mentioned here since it represents a minutely and richly

Fig. 2.10 A crawling individual of the mammoth pond snail, *Bulimnea megasoma* (Say, 1824). Canada, Ontario Province, the Cart Lake near Cobalt Town. Photo: Maxim V. Vinarski

illustrated descriptive monograph of the anatomy of a certain lymnaeid species, *Lymnaea* (*Ladislavella* of the current system) *catascopium* (Say, 1817).

The body of a lymnaeid snail divides into three main parts—the head, the foot, and the visceral mass covered by the mantle. In a living animal, the whole visceral mass is hidden within its shell (Fig. 2.10). In some groups, like the genus *Myxas* (the gelatinous lymnaeid snails), the mantle is greatly extended and can be reflected over the shell, covering it except for a small oval space on the upper side of the last whorl. The head bears a pair of flat tentacles, triangular in outline, and a pair of eyes located at the tentacle bases. The foot is a muscular organ allowing snails to crawl over a substrate. The coloration of both foot and head is usually homogeneous and varies from pale yellow or light-grayish to almost black, while the mantle surface may exhibit a more complex pattern of coloration, with light spots or small "freckles" against a dark background, and vice versa (Falniowski 1980a, b; Jackiewicz 1993; Schniebs et al. 2011). Within a species, some, more or less distinct, "types" of pigmentation can be distinguished (e.g., in *Ampullaceana balthica*; see Schniebs et al. 2011). Some authors reported some stable intraspecific differences in the mantle pigmentation pattern (Roszkowski 1914; Falniowski 1980a, b). For example, the mantle pigmentation pattern between isolates of Cuban *Pseudosuccinea columella* susceptible and resistant to *Fasciola hepatica* infection was analyzed by Gutiérrez et al. (2003). These authors showed that the distribution pattern of the spots was clearly different between resistant and susceptible isolates, whereas some other researchers questioned the usefulness of this character as a diagnostic one (Schniebs et al. 2011).

The mantle cavity in the pulmonate snails has been transformed into an unpaired "lung," an adaptation to air-breathing. In all lymnaeids, except *Pseudobulinus*, it is located on the right side of the body and opens via the *pneumostome* (*mantle pore*). The atmospheric air is usually used as the oxygen source, however, in some situations, it is not easy for pond snails (for example, for those living in large lakes of tectonic origin, at considerable depths) to rise to the water surface for breathing. A classic example of this is the Lake Geneva lymnaeids, living at depths of 40–200 m (Russell-Hunter 1964). Under such circumstances, the mantle cavity becomes filled by water and thus acts similarly to the "adaptive gill" (*pseudobranch*) of some other Hygrophila belonging to Acroloxidae, Bulinidae, and Planorbidae (Starobogatov 1967). The cutaneous respiration is another—not alternative to the described above—mechanism of oxygen uptake (Russell-Hunter 1978). This acts especially effectively in species (like those of *Myxas*) with the mantle reflected over the shell (Stadnichenko 2004).

The lung also functions as a hydrostatic apparatus. A change in the volume of air in the lung leads to a change in the buoyancy of the animal, and also allows it to hold the shell in a certain position in relation to the substrate (Checa and Jiménez-Jiménez, 1997).

Figure 2.11 depicts the general topography of the internal organs of a lymnaeid mollusc.

The alimentary system starts from a relatively small mouth, which is located ventrally in the frontal part of the head. The mouth leads to the oral cavity containing brown-colored *jaws* made of conchiolin. Their function is to grind up large pieces of food. The *buccal mass*, or *pharynx* (see Fig. 2.11), incorporates the *radula*, which is a protrusile tonguelike structure serving as a device for getting the food by means of substrate scraping (see Ivanov 1990 for a detailed review on the functional morphology and evolution of the molluscan radula). The radula tears or rasps food particles and then pulls them into the mouth. Solem (1974) describes in detail the biomechanics of this process in herbivorous pulmonate snails. The radula is mounted on a cartilaginous *odontophore* and consists of hundreds to thousands of minute teeth.

Hubendick (1978, p. 13) described the lymnaeid radula (like the radulas of other Hygrophila) as being "of a primitive type with numerous small and comparatively simple teeth of fairly similar shape in each cross row" (Fig. 2.12). The teeth of the lymnaeid radula form transversal rows, up to several dozens, each of them has a more or less identical structure. The *central* (*rachidian*) cusp is situated medially and divides a row into two virtually symmetrical halves containing approximately the same number of individual teeth. The rachidial tooth (see Fig. 2.12) is smaller than the *lateral teeth* located on either side of the latter. The *marginal teeth* are situated externally of the lateral ones. Some authors (e.g., Stadnichenko 2004) distinguish the third group of teeth, the *interstitial* ones, positioned between the lateral and marginal ones.

The rachidian teeth bear a single cusp or two cusps (*monocuspid* or *bicuspid* tooth), while the lateral ones have either two or three (*tricuspid*) well-developed cusps. Typically, these cusps are of uneven size, with the central cusp being the most

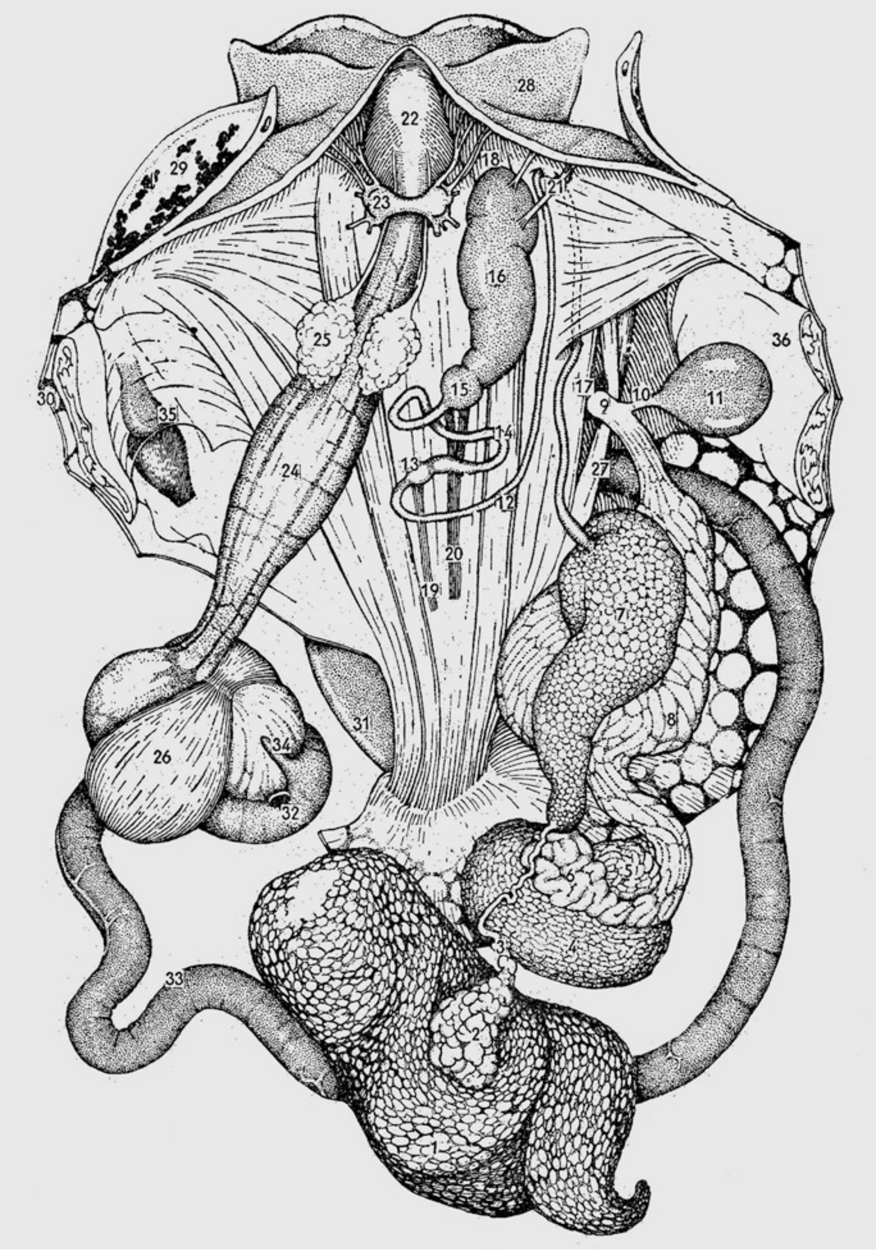

Fig. 2.11 Internal anatomy of *Ampullaceana balthica* (Poland, vicinities of Poznań). After Jackiewicz (1954), slightly modified. Explanation of numbers: 1 – liver; 2 – hermaphroditic gland; 3 – hermaphroditic duct with the seminal vesicles; 4 – albumen gland; 5 – nidamental gland; 6 – uterus; 7 – prostate; 8 – pyriform body; 9 – vagina; 10 – spermathecal duct; 11 – spermatheca (*bursa copulatrix*); 12 – *vas deferens*; 13 – bulbous termination of the penis sheath; 14 – penis sheath; 15 – bulbous termination of the praeputium; 16 – praeputium; 17 – female gonopore; 18 – male gonopore; 19 – retractor of the penis sheath; 20 – retractor of the praeputium; 21 – protractor; 22 – buccal mass (*pharynx*); 23 – cerebral ganglia; 24 – esophagus; 25 – salivary

developed. The marginal teeth cusps are weakly developed, their number varies from 1 to 6, rarely more.

Each individual radula may be described by means of a simple formula indicating the number of lateral and marginal teeth and the number of cusps which are bearing. Jackiewicz (1998, p. 15) provided an example of a radula studied in a specimen of *Stagnicola corvus*. "The length and the width of this radula are 4.27 mm and 1.93 mm, respectively. There are 87 longitudinal and 118 transversal rows. The shell height and width were 31.83 and 14.00 mm, respectively. Radula size is directly proportional to the specimen size." The radular formula of this specimen was (where M—marginal teeth; L—lateral teeth):

$$\begin{array}{cccccccc} (\mathrm{M}) & (\mathrm{L}) & (\mathrm{C}) & (\mathrm{L}) & (\mathrm{M}) & & & \\ \underline{32} & \underline{11} & 1 & \underline{11} & \underline{32} & = & 43\text{-C-}43, & \text{where} \\ 3\text{-}5 & 2\text{-}3 & & 2\text{-}3 & 3\text{-}5 & & & \end{array}$$

the numbers in the middle line are equal to the numbers of teeth in a half-row, and the numbers in the lower line correspond to the number of cusps.

The morphology of the radula is subject to some ontogenetic changes; some abnormalities of the radular structure are sometimes occurring (Jackiewicz 1998; Stadnichenko 2004).

The significance of the lymnaeid radular morphology for the classification of the family had long been considered low if not negligible (Annandale and Rao 1925; Roszkowski 1929; Hubendick 1951; Jackiewicz 1998; but see Yakchali and Deilamy 2012). In the late 1950s, Berrie (1959) demonstrated biometrically that the radular morphology may vary intraspecifically, and two separate populations of the same species may be so different in this respect that "they could legitimately be established as separate subspecies" (Berrie 1959, p. 403). On the other hand, the intraspecific differences are sometimes not prominent and not always stable, and, in some studied cases, the revealed distinctions in the radular morphology do not fit the branching pattern of a phylogenetic tree (e. g., see Vinarski et al. 2022). At the family level, the radular morphology of the lymnaeids has been characterized as "strikingly uniform" (Hubendick 1951, p. 38). The lack of the taxonomic signal in the radular morphology was reported in other groups of Pulmonata (e.g., terrestrial family Helicidae; see Schileyko 1972).

Three main parts of the alimentary system lie posterior to the pharynx—esophagus, stomach, and intestine. The *salivary glands* ducts open laterally into the pharynx, somewhat anterior to the esophagus. The *esophagus* is a muscular tube-like organ, usually rather long and dark-pigmented. The lymnaeid *stomach* is a relatively large and well-muscled organ, typically of rounded shape, consisting of three parts (crop, stomach s.str., and gizzard). The gizzard has a blind pocket called

Fig. 2.11 (continued) glands; 26 – stomach; 27 – anal opening; 28 – tentacle; 29 – mantle collar; 30 – mantle over the mantle cavity; 31 – foot; 32 – liver duct outlet; 33 – intestine; 34 – cecum; 35 – heart; 36 – lung

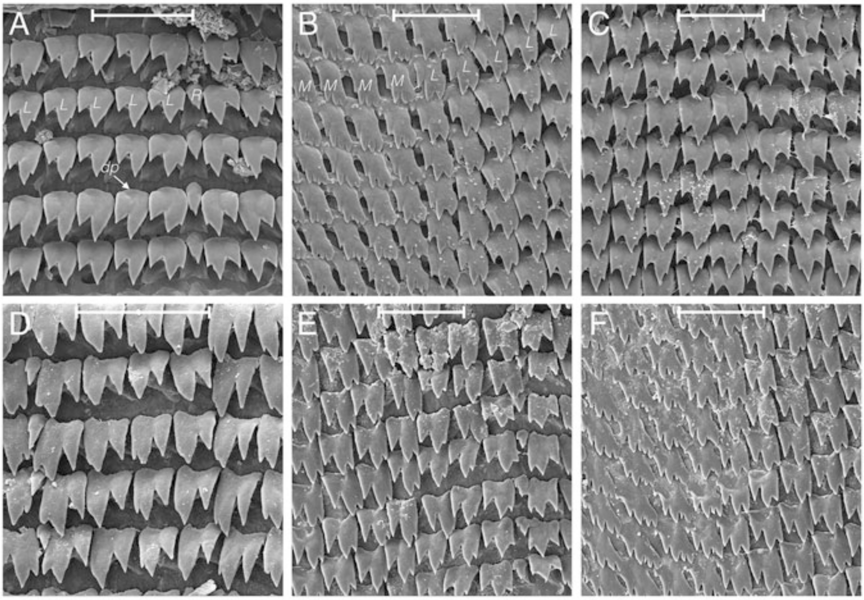

Fig. 2.12 Fragments of radulae of *Tibetoradix kruglovi* (**a–c**) and *T. imitator* (**d–f**). Abbreviations: *dp* – distal part of tooth, *L* – lateral tooth, *M* – marginal tooth, *R* – rachidian (central) tooth. Scale bars = 40 μm. Photos: Ivan O. Nekhaev

the *cecum*. The stomach is followed by the *intestine*, a long and thin duct of almost the same length as the esophagus. The posterior end of the intestine forms the *rectum*; the *anal opening* is located on the right side of the soft body, close to the head (see Fig. 2.11).

A large well-developed digestive gland called the *hepatopancreas*, or, expressing less technically, the liver, occupies the upper part of the visceral mass located within the upper whorls of the shell. This is the largest internal organ in most (if not all) snails. The lymnaeid hepatopancreas is bilobate, dark-brown colored; its ducts open into the gizzard. The main function of the hepatopancreas is the intracellular digestion of fats and proteins, whereas the digestion of carbohydrates takes place in the gizzard (Kruglov 2005).

The lymnaeids are potentially omnivorous snails, but vegetative food dominates in their diet. Larger species (like *L. stagnalis*) may feed on dead corpses of other animals, including representatives of their own species (Baker 1911; Frömming 1956; Tsikhon-Lukanina 1987; Stadnichenko 2004). The instances of their feeding on egg masses of other snails are known (Frömming 1956). In some representatives of the family, the detritivory becomes the dominant, if not obligate, feeding mode. A typical lymnaeid snail is a grazer, scraping its food from the substrate using the radula.

The circulatory system is open, of the lacunar type. It consists of the heart, blood vessels, the sinus system, and the lacunae. There is a well-developed arterial system, consisting of vessels with developed walls (aorta, arteries), but venous vessels, as a rule, lack their own walls. The *heart* is a relatively simple bicameral organ serving as a blood pump. It is located on the left side of the soft body between the lung and the kidney and is surrounded by the *pericardium* filled with fluid. The heart *ventricle* is followed by the aorta which further divides into two arteries, the anterior and the posterior ones, both subdivide into arteries of the second order. The arteries bring the *hemolymph* (the body fluid analogous to blood of vertebrates), through the sinus system, to the various internal organs. Next, the hemolymph returns to the lung through the weakly branched pulmonary veins. In the lung, it is oxygenated and returns to the heart.

The hemolymph of the Lymnaeidae has two main components—the hemolymph plasma, containing the oxygen-carrying protein hemocyanin, and the hemocytes (amoebocytes). The latter are responsible for diverse aspects of molluscan life such as immune response, biomineralization, shell formation, and regeneration processes. Recently, Machałowski and Jesionowski (2021) published a detailed review article on the mollusc hemolymph and its constituents, which we recommend as a further reading on this topic.

The central organ of ***the excretory system*** is the *kidney*, or *nephridium*, which is described as a large unpaired sac-like organ of spongy structure (Jackiewicz 1998). This is situated together with the lung and the pericardium in the last whorl of the visceral mass. The kidney is tripartite, its duct (ureter) opens as a pore on the right side of the snail's body, near the pneumostome and opposite the anal opening.

The nervous system is of scattered-nodular type, and it tends to concentrate into a cerebral ring around the esophagus, which consists of separate ganglia. The ganglia are connected by transverse *commissures* and longitudinal *connectives*, the latter being relatively short, as a result of which the ganglia are located close to each other. The tendency of the fusion of these ganglia leading to the further concentration of the nervous system is observed among the Hygrophila (Hubendick 1978). In the Lymnaeidae, the central nervous system consists of paired brain or *cerebral ganglia*, foot or *pedal ganglia*, lateral or *pleural ganglia*, *parietal ganglia* and *esophageal* or *buccal* ganglia as well as solitary *visceral (or abdominal) ganglion*. The large cerebral ganglia, located just behind the pharynx on the dorsal side of the body, innervate the front of the head, the copulatory apparatus, and sensory organs. The pleural ganglia innervate the mantle, the pedal ganglia innervate the leg muscles, the pallial ganglia innervate the edge of the mantle, osphradium, pneumatic bridge, etc. Finally, the abdominal ganglion, which occupies the extreme posterior position in the cerebral ring, innervates almost all organs of the visceral sac. A pair of very small buccal ganglia lies under the esophagus and innervates the pharynx, esophagus, and salivary glands.

The sensory organs of the Lymnaeidae are represented by sensitive cells scattered over the body surface and especially numerous on the tentacles, along the edges of the mouth, mantle, and foot. These cells perform tactile, olfactory, and gustatory functions. The head tentacles, of triangular shape, are a specialized organ of touch and smell. In the mantle cavity lies a specialized organ of chemical sense—*osphradium*, which determines the composition of water supplied to the lung, perceiving fluctuations in osmotic pressure and the dissolved oxygen concentration. There are paired organs of balance and seismic and audio reception—*statocysts* (*otocysts*), located in the front of the foot in the immediate vicinity of the pedal ganglia. They are hollow vesicles lined with epithelial ciliary cells that perform a receptor function. The cavity of the statocyst is filled with liquid statolymph, in are located *statoconia*—small auditory stones, which, when the equilibrium is disturbed, change their position and press on the receptor cells. In larger species, like *Lymnaea stagnalis*, the number of statoconia can reach 700. The organs of vision are represented by a pair of eyes located at the base of the tentacles. The eyes are responsible for photoreception, but they are not able to create visual images; therefore, the lymnaeid snails cannot distinguish the shape of objects. The dermal (non-ocular) photoreceptor system was described in *Lymnaea stagnalis* (Chono et al. 2002).

At the classical, i.e., pre-molecular, stage of the lymnaeid taxonomy, the ***reproductive system*** was considered the most important source of the taxonomic and phylogenetic signal in the family (Baker 1911; Hubendick 1951; Walter 1969; Paraense 1976, 1982, 1984, 1994, 1995; Kruglov and Starobogatov 1981; Jackiewicz 1998; Kruglov 2005; Pointier 2015; Pointier and Vázquez 2020). Though the recent "integrative" studies have shown that the significance of the reproductive anatomy is not as prominent as it was thought in the last century, the features of the lymnaeid genitals remain an important tool for species identification, at least in some genera (i.e., *Stagnicola*, *Galba*).

Figure 2.13a illustrates the general morphology of the lymnaeid reproductive system.

All freshwater pulmonates, not excluding the lymnaeids, are dioecious snails, and their reproductive system is based on a common *Bauplan* (Duncan 1960; Starobogatov 1967; Hubendick 1978; Jordaens et al. 2007).

An unpaired hermaphroditic organ—the gonad (*hermaphroditic gland*, *ovotestis*) is located apically in the visceral sac and in most cases is immersed in the tissues of the hepatopancreas. The gonad is divided into separate lobes—*diverticulae* opening into the gonadial ducts, and the latter into the *hermaphroditic duct*, which forms more or less numerous swellings—seminal vesicles (see Fig. 2.13). At the end of the hermaphroditic duct, the reproductive system is divided into the male and female ducts, emerging from a small formation called the *quadrivium*. The hermaphroditic duct and the duct of the albuminoid gland open into the quadrivium, which forms a special extension—the fertilizing pocket.

The proximal part of the male genital duct is represented by the *prostate* (see Fig. 2.13c)—a sac-like gland that produces seminal fluid. The lancine snails have two prostates of different structure. There may be one, two, or many folds inside the prostate, formed by the prostate wall, usually in its widened part. In some genera (*Omphiscola*, *Pseudosuccinea*), the prostate lacks any folds (Paraense 1983; Kruglov and Starobogatov 1993; Jackiewicz 1998). The prostate is followed by the *vas deferens*, which, near the female genital opening, plunges into the integument of the body and reaches the male genital opening, where it leaves the muscle tissue and opens into the *copulatory apparatus* (see Fig. 2.13b), the morphology of which is relatively uniform within the family (but see Kruglov and Starobogatov 1981). The copulatory apparatus consists of a tubular *penis* (see Fig. 2.13d,e), embedded into the *penis sheath*, and a *praeputium* opening outward with the male genital opening. In the normal state,

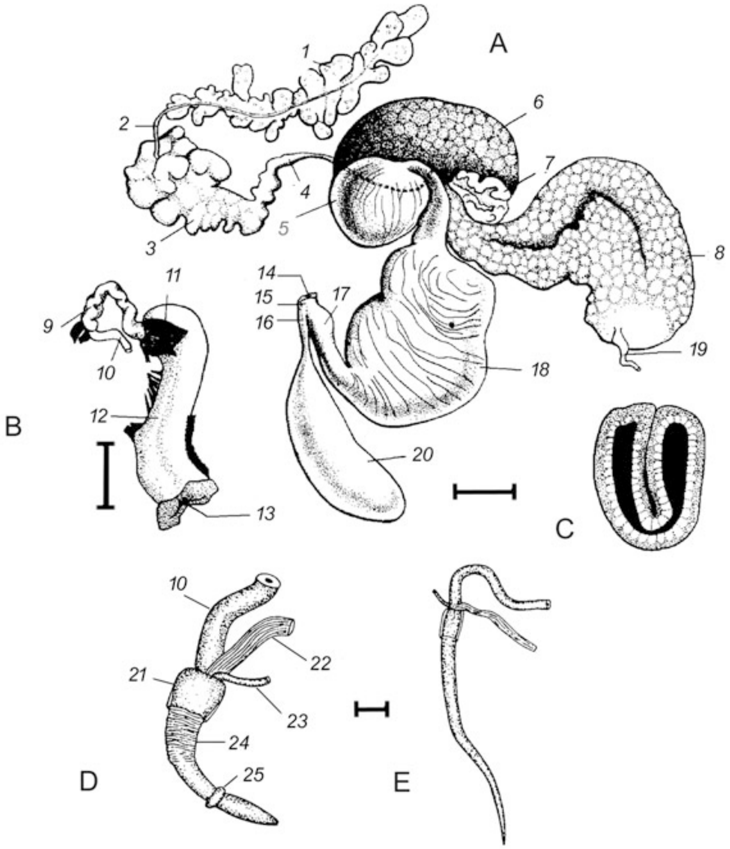

Fig. 2.13 The reproductive anatomy of the lymnaeid snails: The distal part of the reproductive system (**a**), the copulatory apparatus (**b**), and cross-section through the prostate (**c**) of *Ampullaceana fontinalis* (**a**–**c**), and the penises of *Lymnaea stagnalis* (**d**) and *Myxas glutinosa* (**e**). After Beriozkina and Starobogatov (1988) and Andreeva et al. (2010), slightly modified. Scale bars 0.5 mm (D, E), 1 mm (A–C). Explanation of numbers: 1 – hermaphroditic gland; 2 – the distal part of the hermaphroditic duct; 3 – seminal vesicles; 4 – the proximal part of the hermaphroditic duct; 5 – nidamental gland; 6 – albumen gland; 7 – the labyrinth of the oviduct; 8 – prostate; 9 – penis sheath; 10 – the distal part of the spermathecal duct; 11 – the praeputium retractor; 12 – praeputium; 13 – male gonopore; 14 – female gonopore; 15 – vagina; 16 – spermathecal duct; 17 – provagina; 18 – uterus; 19 – the proximal part of the spermathecal duct; 20 – spermatheca (*bursa copulatrix*); 21 – the base of the penis; 22 – the penis sheath retractor; 23 – the penial nerve; 24 – penis; 25 – the fixative swelling (present not in all species)

the copulatory apparatus is immersed inside the soft body, and it turns outward during copulation. Two annular folds—*velum* (outer) and *sarcobellum* (inner)—are situated on the border of the penis sheath and the praeuputium. Various lymnaeid genera differ from each other in relation to the degree of development of these folds; sometimes (like in the genus *Omphiscola*) the velum can completely disappear (Kruglov and Starobogatov 1981; Jackiewicz 1998).

The most peculiar penial morphology is observed in a small group of lymnaeids separated in a genus of its own, *Aenigmomphiscola* Kruglov et Starobogatov, 1981. Two extant species of this genus are endemic to Russia and Kazakhstan (Vinarski and Grebennikov 2012). In these snails, the velum is asymmetrically enlarged and forms a so-called *praeputial organ* (Kruglov and Starobogatov 1981; Vinarski et al. 2011). According to Kruglov (2005), it plays the role of a sucker that holds the individuals during copulation. A praeputial organ performing a similar function is also present in species of the genus *Planorbarius* Dumeril, 1806 and *Segmentina* Fleming, 1818 of the family Planorbidae (Stadnichenko 1990; Maksimova and Yakovleva 1991). In some groups that do not have a praeputial organ, the fixative swelling, or ring, develops on the penis (Fig. 2.13d).

In the proximal part of the penis sheath, there are glandular deepenings called the *proximal chambers*. The penis sheath becomes noticeably swollen at the proximal end when the chambers are well-developed. Several muscle retractors approach the copulatory apparatus from the outside.

The female reproductive tract in the Lymnaeidae is represented by the *oviduct*, the enlarged part of which is called the *uterus*. The uterus begins after the point of confluence of the nidamental gland duct into the oviduct and passes into the *provagina*, which opens outward (see Fig. 2.13a). The proximal part of the provagina, near the female genital opening, receives the seminal duct.

The *chromosomal diversity* within the family Lymnaeidae has been studied intensively during the past 50–60 years (Inaba 1969; Patterson and Burch 1978; Garbar and Korniushin 2003; Garbar et al. 2004). This diversity appeared relatively low as compared to that found in some other Hygrophila families. Most lymnaeid species possess 17 or 18 pairs of chromosomes, and the extant subfamilies can be characterized using the chromosome number. Thus, representatives of the subfamily Amphipepleinae (= Radicinae) typically have 17 (sometimes 16) chromosome pairs, whereas in the Lymnaeidae the typical haploid number is 18 (some species have $n = 19$) [Vinarski 2013]. The low chromosome number is characteristic for the most Hygrophila families (Burch 1960; Burch et al. 1960; Patterson and Burch 1978; Thiriot-Quiévreux 2003; Garbar et al. 2004) and thus can be considered a plesiomorphic character (Nordsieck 1992). The exception is some polyploid species of the families Bulinidae and Planorbidae (the genera *Ancylus*, *Bulinus*, *Gyraulus*). In these groups, tetraploid, hexaploid and even octoploid species are known (Burch et al. 1960; Goldman et al. 1983; Burch and Jung 1993).

Though the chromosome number as such cannot be used as a unique taxonomic characteristic of a genus or species in the Lymnaeidae, some interspecific differences in other karyological characters can be reported. For example, the European species of the genus *Stagnicola* can be distinguished on the basis of their NF (= *nombre fundamentale*), i.e., the number of the chromosome arms. Thus, *Stagnicola palustris* and *S. corvus* share the same chromosome number ($n = 18$) but their NFs are different, equal to 72 and 60, respectively (Garbar et al. 2004). Some morphological features of the chromosomes allow one to distinguish two conchologically indistinguishable genera, *Stagnicola* and *Catascopia* (= *Ladislavella* of the current system) [Garbar et al. 2004].

The life cycles of the Lymnaeidae are relatively uniform. These molluscs are typical *r*-strategists characterized by relatively short life spans, high fecundity, increased rate of food consumption, and fast generation turnover. Under natural conditions, the life cycle duration in the family varies between one and 2 years (Russell-Hunter 1978; Beriozkina and Starobogatov 1988). The number of generations per year is also variable and depends on local conditions.

The dioecy of the Lymnaeidae and their ability to reproduce by self-fertilization have often been considered as an adaptation to life in non-permanent waterbodies as well as to rapid colonization of novel habitats (Boss 1978; Beriozkina and Starobogatov 1992; Heller 1993; Jarne et al. 1993; Jordaens et al. 2007; Vinarski et al. 2021). Despite the simultaneous hermaphroditism of freshwater Pulmonata, self-fertilization (*autogamy*) is not obligatory for these animals (Jarne et al. 1993). In most cases, cross-fertilization (*allogamy*) prevails, in which one individual plays the role of a "male" and the other as a "female," but the possibility of autogamy remains though its frequency varies among different species (Beriozkina and Starobogatov 1988; Jordaens et al. 2007). The ability to self-fertilize also determines the phenomenon of *aphally*—the absence of the copulatory apparatus, which is known in some representatives of Hygrophila (Harutyunova 1977; Starobogatov et al. 1989).

In the vast majority of aquatic pulmonates, embryonic development occurs outside the body of the parent. In the oviduct, a fertilized egg is covered by a series of protective membranes that form an egg capsule (Beriozkina 2002). Then, individual egg capsules combine under a common membrane secreted by the glands of the distal part of the oviduct, and form a separate clutch, called *an egg mass* (or *egg cluster*, or *egg capsule*, or *syncapsule*). The number of egg capsules in an egg mass varies considerably and, as a rule, depends on the body size of the molluscs. In large species of Lymnaeidae, such as *Lymnaea stagnalis*, the number of egg capsules per egg mass can exceed 100 (Beriozkina and Starobogatov 1988; Kruglov and Starobogatov 1992), and in some representatives of the genus *Radix* it reaches 250 (Prozorova 1992). On the other hand, species of the genus *Galba* are characterized by the small size of egg masses and, as a consequence, the small number of egg capsules (Kruglov and Starobogatov 1992). Nutrients are concentrated outside the egg capsules, usually in the protein matrix of the egg mass, which is eaten by juveniles before leaving the syncapsule (Beriozkina 2002).

The lymnaeid egg masses demonstrate a marked diversity in their size and structure within the family (Fig. 2.14). The data on the morphology of egg masses of different representatives of the Lymnaeidae can be found in the literature (Nekrasov 1927, Piechocki 1979; Beriozkina and Starobogatov 1981, 1988; Kruglov and Starobogatov 1985, 1992; Prozorova 1992; Jackiewicz 1998). Some authors have considered them species-specific. In the 1980s, there were attempts in the USSR to use the structure of the egg masses as a diagnostic tool for the identification of the lymnaeid (and other freshwater pulmonate) species of Eastern Europe (Beriozkina and Starobogatov 1981, 1988). A diagnostic key for the lymnaeids based on size and some qualitative features of the egg masses was even proposed (Beriozkina & Starobogatov 1988, p. 232–234).

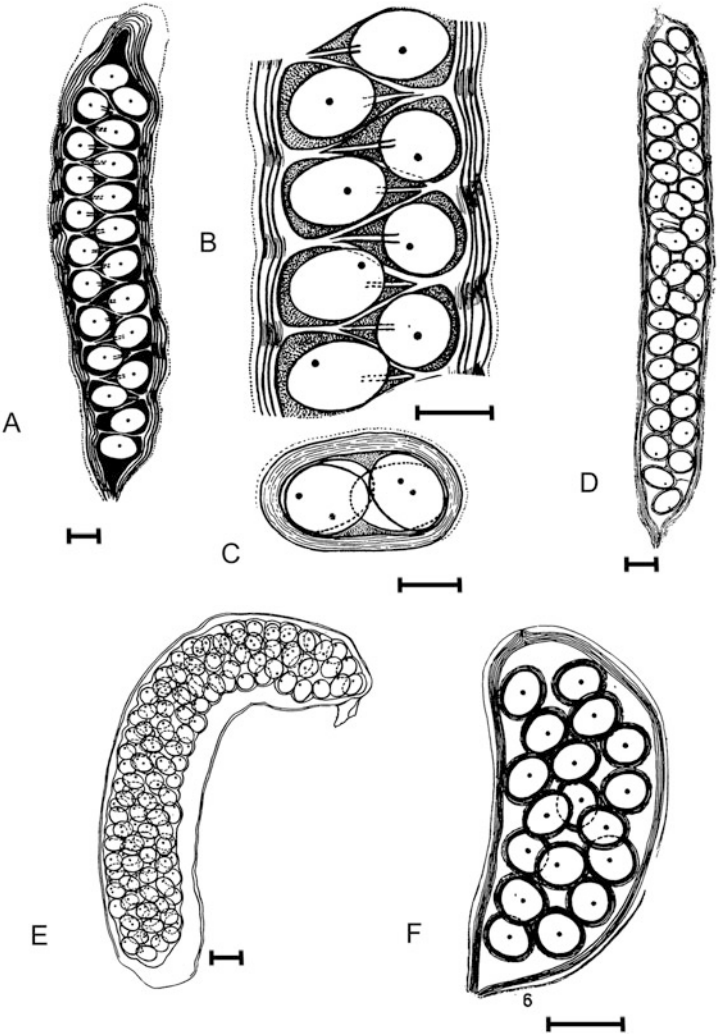

Fig. 2.14 The structure of the egg masses in *Myxas glutinosa* (**a**–**c**), *Lymnaea stagnalis* (**d**), *Radix auricularia* (**e**), and *Stagnicola palustri*s (**f**). After Beriozkina and Starobogatov (1988), slightly modified. Scale bars 1 mm. (**a, d**–**f**) General views. (**b**). The middle region of an egg mass (enlarged). (**c**). Cross-section through an egg mass

However, the latest research has revealed that the idea of the species specificity of the egg masses morphology was incorrect. In one of the latest publications, Beriozkina (2019) explicitly revised her earlier views and stated that "the high degree of variability [of egg masses of pulmonate snails] questions the use of their morphology as a species criterion. At the same time, this morphology retains its significance as a characteristic of the subgenera" (Beriozkina 2019, p. 40).

2.5 Elements of Biogeography and Ecology

The modern range of the family can be classified as "subcosmopolitan." The lymnaeids are distributed in waterbodies of all continents, except for the Antarctic (Starobogatov 1970; Banarescu 1990; Strong et al. 2008; Vinarski et al. 2019). The most species-rich faunas of this family are those of North America, Central Asia, South-East Asia, and Europe, whereas Africa and South America maintain a relatively low species richness of the Lymnaeidae. In the Northern hemisphere, the family is represented far north of the Polar circle, though these snails are not found in many Arctic islands (Vinarski et al. 2021). It has been thought that the Lymnaeidae obey the global species richness gradient, i.e. the pattern of decline in species richness toward the poles (Hubendick 1962; Starobogatov 1970; Vinarski et al. 2012), however, actually, the form of the relationship between the number of lymnaeid species and the latitude is not linear. In the equatorial parts of Africa and South America, the species richness of the family is considerably lower than in the temperate latitudes. It is also characteristic of tropical Asia. In the Northern hemisphere, the Lymnaeidae tend to concentrate in the latitudes lying between 30 and 60 degrees. In the Southern hemisphere, the highest number of lymnaeid species is observed in Australia.

The altitudinal range of the family is rather wide. The lymnaeids are found in some of the deepest continental depressions lying below the sea level (i.e., Turfan Depression in Western China; Vinarski, pers. observations). The highest occurrences of the family are known in the Himalaya and Tibet plateau. The genus *Tibetoradix* Bolotov, Vinarski & Aksenova, 2018, is a unique example of a freshwater mollusc genus adapted to live under high-altitude conditions. In Tibet Plateau, the species of this genus are distributed vertically between 3544 and 4749 m a.s.l. (Vinarski et al. 2022). Another example is *Galba cousini*, endemic to the northern part of the Andes Cordillera (Venezuela, Colombia, and Ecuador), which occurs at altitudes ranging from 2500 to 4200 m a.s.l. (Pointier 2015).

The lymnaeids (and other freshwater pulmonates) use different mechanisms of their dispersal, ranging from the "natural" vectors (birds, fish, large flying insects) to dissemination with humans' transport vehicles and aquarium trade (Malone 1965; Starobogatov 1970; Boag 1986; Madsen and Frandsen 1989; Brown 2007; Kappes and Haase 2012; Ng et al. 2016; Patoka et al. 2017). Many species use rivers and streams for their passive dispersal, drifting downstream (Starobogatov 1970; Shikov 1977). Large rivers flowing in latitudinal direction have long been thought to serve as the main vectors of dispersal of continental molluscs in the south-north direction (Vinarski et al. 2012, 2021).

Some representatives of the family are effective invaders, distributed today far outside their native range. The most widespread of them is *Pseudosuccinea columella*, a North American species, which is currently distributed in Europe, South America, South Africa, Australia, New Zealand, and some other countries (Lounnas et al. 2017; Vinarski et al. 2019). *Lymnaea stagnalis*, a Holarctic species, whose range lies mainly within the Northern Hemisphere temperate zone, has been introduced to Australia, New Zealand, and Cameroon (Hubendick 1951; Climo and Pullan 1972; Tchakonté et al. 2014). *Radix auricularia*, another Eurasian species, is known now from North America and New Zealand (Hubendick 1951; Burch 1989; Mills et al. 1993). This list of invasive lymnaeids is far from being complete.

The main factors limiting the dispersal of freshwater pulmonates are the chemical composition of water, temperature, and oxygen regimes of waterbodies (Aho 1978a, b; Beriozkina and Starobogatov 1988; Pip 1993; Økland 1990; Økland and Økland 1997; Dillon 2000). One of the most important chemical elements for molluscs is calcium. A number of studies returned strong positive correlations between the abundance and/or diversity of freshwater molluscs and calcium concentration (Dillon 2000). Calcium ions absorbed by animals from the water in the form of carbonate salts are used to build the shell (Russell-Hunter 1964; Økland 1990). Many lymnaeid species are calciphiles and do not occur in habitats with a low content of this element (below 20 mg/l). According to Briers (2003), such species as *Lymnaea stagnalis*, *Radix auricularia*, and *Myxas glutinosa* belong to this ecological group.

It has been experimentally established that a decrease in the concentration of calcium ions to 1.04 mg/l leads to its negative balance in the body and the death of snails (Kruglov 2005). The number of lymnaeid species in waterbodies poor in calcium is reduced in comparison with habitats where there is no deficiency of this element (Russell-Hunter 1964; Aho 1978a, b; Økland 1990).

The optimal hydrogen-ion concentration (pH) values for freshwater Pulmonata are 6.9–8.0. When it decreases to 6.0–6.5, it results in in vivo destruction of the shell material and high embryonic mortality (Kruglov 2005). Under pH = 4.7–4.9, significantly lower adult growth rates and reduced gross fecundity are observed (Hunter 1990). Freshwater molluscs are totally absent from waterbodies with $\text{pH} < 4.0$ (Salazkin 1969). At the same time, the reactions of molluscs to the effect of this factor are often species- and genus-specific (Salazkin 1969; Økland 1990; Kruglov 2005). For example, the gelatinous pond snail, *Myxas glutinosa*, exhibits low resistance to water acidification which was revealed under experimental conditions (Berezina 2001). On the other hand, such species as *Lymnaea stagnalis* and *Galba truncatula* in Norway were found to dwell in a wide pH range, from 4.4 to 8.8. Both species demonstrated increased frequency of occurrence in waterbodies with pH values = 7.4–8.8 (Økland 1990).

The presence of oxygen dissolved in water is necessary for the normal embryonic development of the Lymnaeidae (Stadnichenko 2006), therefore, these snails cannot survive anoxic conditions, despite their possibility of breathing atmospheric air.

The Lymnaeidae is a group of ecologically plastic snails able to dwell in various aquatic environments, whose range embraces almost the entire spectrum of waterbody types (large lakes and ponds, reservoirs, rivers and streams, brooks, ephemeral pools, etc.). Certain representatives of the genera *Galba* and *Orientogalba* are, in fact, amphibiotic snails, living on various wet surfaces like shores of rivers and streams, moistened stones near waterfalls, and other similar habitats. On the other hand, only a few lymnaeid species are known to inhabit the giant ancient lakes (Ohrid, Baikal, Lugu) [Schütt 1974; Albrecht et al. 2008;

Vinarski 2018; Wiese et al. 2020], and generally the Lymnaeidae do not form in such waterbodies endemic species flocks as it is characteristic for other families of freshwater snails—Planorbidae, Acroloxidae, Thiaridae, Viviparidae (Boss 1978). Possibly the only freshwater environment not conquered by lymnaeid snails is the subterranean waterbodies, including the cave streams and lakes.

Lymnaeids overwinter buried in the ground, often among the roots of aquatic plants. The activity of molluscs in winter is sharply reduced, they, as a rule, stop feeding, the intensity of gas exchange also decreases, and their lung is filled with water. Such a state resembling anabiosis is regarded as the "hibernation" (Ivanov 1940), "dormancy" (Storey 1972), or, to use a term coined by Boss (1974), "oblomovism" of molluscs. If the waterbody does not freeze to the bottom, then some snails can remain motile and feed under the ice (Russell-Hunter 1964; Stadnichenko 2006).

In relatively large waterbodies, the lymnaeids, similar to other freshwater pulmonates, tend to concentrate in the shallow zone near the shore, well warmed up and rich with vegetation and light. However, in large lakes, these snails may occur at depths 250–280 m (Russell-Hunter 1978). Most representatives of the family are phytophilous snails though potentially may live on different substrata (submerged stones, deadwood, plastic and metal objects of anthropogenic origin, and so on). The lymnaeids inhabiting non-permanent habitats are adapted to summer aestivation that helps them survive when their waterbody is dried up. The snails are waiting out the dry period in moist soil or among dead leaves and stems of aquatic plants (Cheatum 1934; McMahon 1983; Alyakrinskaya 2004). According to different authors, the duration of stay in an anhydrous environment varies significantly among freshwater pulmonates, ranging from 1 month to 390 days (Alyakrinskaya 2004). Despite these adaptations, the survival rate of molluscs during the unfavorable dry season is very low.

Though this family is commonly classified among freshwater molluscs, some Lymnaeidae demonstrate a considerable salinity tolerance. A classical example is the lymnaeids found in brackish water environments, for instance, in the Baltic Sea, under salinity around 2‰ or even higher (Clessin 1878; Dregol'skaya et al. 1988). In the Issyk-Kul Lake in Central Asia (Kyrgyzstan), the lymnaeid *Radix obliquata* lives under salinity 5.8–5.9‰ (Pavlova 1983). In Northern Kazakhstan, several representatives of the family were found in mineralized lakes with salinity equal to 4.95‰ (Andreeva et al. 2010). According to Taktakishvili (1967), *Valenciennius*, the giant Neogene lymnaeid of south-east Europe (see above), was essentially a marine mollusc adapted to rather deep-sea conditions. Taktakishvili argued that the unique morphological characteristics of this genus, including their gigantism and limpet-like shape, evolved as an adaptation to living under increased salinity and at considerable depths.

The family demonstrate some instances of profound thermal adaptation, i.e. living in the hot waterbodies (lakes, ponds, streams) situated in geothermal sites scattered throughout the world—in North America (Alaska, Yellowstone Park), Iceland, Kamchatka Peninsula, Tibet Plateau, Pamir, etc. (Starmühlner 1957; von Oheimb et al. 2011; Aksenova et al. 2016, 2017; Vinarski et al. 2023). Hydrothermal habitats are characterized by high temperature (typically >20–25 ° C) that is maintained the year round, without drastic seasonal fluctuations. From the biological point of view, they represent a very peculiar environment, and animals need to develop special adaptations in order to be able to conquer it (Mitchell 1974; Bolotov et al. 2012). Formation of ecological ("thermal") races in such habitats is a common outcome of their colonization by various lymnaeid species (Vinarski et al. 2023). In earlier times, such races often were described as separate species (Boubee 1833; Kruglov and Starobogatov 1989), but the recent molecular studies show that, in most cases, they should be classified merely as ecotypes of widespread species (Aksenova et al. 2017). In total, 17 species of the family representing several genera and all extant subfamilies were found to form populations in geothermal sites around the world (Table 2.1).

The practical significance of the family is multifarious. The public health research is focused on the lymnaeids as intermediate hosts of trematode larvae, many species of which cause serious diseases in humans, domestic and wild animals. The classical instance of this is the host–parasite relationships between *Galba truncatula* and *Fasciola hepatica*, the main causative agent of fasciolosis. Except for *G. truncatula*, a number of other lymnaeid species are found to transmit the larvae of *F. hepatica* and other fasciolids, however, the suitability of different species for the larvae is unequal (Bargues and Mas-Coma 2005; Kruglov 2005; Malcicka 2015; Vázquez et al. 2018). Such opportunism in host choice is characteristic of many other trematode species. For example, the obligate hosts of the trematode *Echinostoma revolutum* Looss, 1899 are molluscs of two families (Lymnaeidae, Planorbidae), and additional hosts are several other families of freshwater molluscs (Bithyniidae, Viviparidae, and some families of bivalves) and even dragonfly larvae (Sudarikov et al. 2002).

And, vice versa, a single lymnaeid species may serve as a host for many trematode larvae belonging to different genera and families (Stadnichenko 2004; Kruglov 2005; Żbikowska 2011). For example, in the northern and central parts of Poland *Lymnaea stagnalis* hosts 14 species of Trematoda (Żbikowska 2007), in Ukraine, this snail harbors 21 species of parasites (Stadnichenko 2004), whereas the full spectrum of trematode species parasitizing this snail species throughout its range is 35 (Kruglov 2005). It is assumed (Faltýnková et al. 2008) that the most important factors determining the species richness of trematode larvae in molluscs are the host body size (the larger the snail, the greater the number of trematode species infect a given host species) and the density of mollusc populations. The number of cercariae produced by a mollusk directly depends on the size of the animal, temperature, season, and other factors. According to Shigin (1971), a large individual of *Lymnaea stagnalis* is capable of producing up to 13.5 million *Diplostomum spathaceum* (Rudolphi, 1819) cercariae during its life.

Many species of lymnaeids play a significant role in the aquatic food webs, being the destructors of vegetation and detritus and serving as the food item for many species of fish, waterfowl, and predatory macroinvertebrates. These snails are used as biological indicators of water pollution and ecosystem health. The shells of fossil lymnaeids are useful for the purposes of biostratigraphy.

The great pond snail, *Lymnaea stagnalis*, is actively used as a standard model object for the studies in neurophysiology, ecotoxicology, developmental biology, biomineralization, and some other branches of science (Meshcheryakov 1990;

Table 2.1 A list of lymnaeid species inhabiting the geothermal sites in various continents

Species	Country, region	Source of data
Ampullaceana balthica (Linnaeus, 1758)	Iceland, French Pyrenees	Bolotov et al. 2017
A. lagotis (Schrank, 1803)	Northeast European Russia; East Kazakhstan	Vinarski et al. 2023
Austropeplea tomentosa (L. Pfeiffer, 1855)	New Zealand	Winterbourn 1968
Galba truncatula (O.F. Müller, 1774)	Austria, Iceland, Hungary	Pinter 1979; Hafner et al. 1986
Kamtschaticana kamtschatica (Middendorff, 1851)	Russian Far East	Aksenova et al. 2016
Ladislavella catascopium (Say, 1817)	USA (Yellowstone Park), Kamchatka Peninsula, Canada (British Columbia and Yukon Provinces)	Brues 1927; Vinarski et al. 2016, 2023
Ladislavella elodes (Say, 1821)	USA, Nevada, Yellowstone Park	Brues 1928, 1932
Lanx patelloides (I. Lea, 1856)	USA, California	Brues 1932
Lymnaea stagnalis (Linnaeus, 1758)	Austria	Hafner et al. 1986
Peregriana peregra (O.F. Müller, 1774)	Croatia	Krkać 1979
Pseudosuccinea columella (Say, 1817)	Austria	Hafner et al. 1986
Radix alticola (Izzatullaev, Kruglov & Starobogatov, 1983)	Tajikistan, Nepal	Aksenova et al. 2018
R. auricularia (Linnaeus, 1758)	Europe (Austria), Russia (Baikal area, Kamchatka), Afghanistan; Tibet	Weber 1910; Likharev and Starobogatov 1967; Hafner et al. 1986; Aksenova et al. 2016, 2017; von Oheimb et al. 2016
R. rubiginosa (Michelin, 1831)	Indonesia, Sulawesi and Sumatra Islands	Brues 1939
R. rufescens (Gray, 1822)[a]	India, Himalaya	Chatterjee et al., 2022
Stagnicola palustris (O.F. Müller, 1774)	Austria, Hungary	Pinter 1979; Hafner et al. 1986
Tibetoradix kozlovi Vinarski, Bolotov et Aksenova, 2018	China, Tibetan Plateau	Vinarski et al. 2022

[a] Referred to as *Lymnaea acuminata* (Lamarck, 1822) [see Chatterjee et al., 2022]

Amorim et al. 2019; Fodor et al. 2020; Kuroda and Abe 2020; Rivi et al. 2021). The use of other lymnaeid species as laboratory animals is much less widespread, though one can cite classical experiments on the heredity of shell sinistrality made by Boycott and his colleagues (Boycott and Diver 1923, 1927; Boycott et al. 1930). The model object of their research was another species, *Peregriana peregra* (Freeman and Lundelius 1982).

Most aspects of the Lymnaeidae biology, ecology, morphology, and distribution, reviewed in this chapter only cursory, will be discussed in detail in the following chapters of this book.

Box 2.1 Taxonomic Position of the Lymnaeidae Within the Class Gastropoda, According to Opinions of Different Systematists

Thiele (1931)	Taylor and Sohl (1962)
Class: Gastropoda Cuvier, 1795	**Class:** Gastropoda Cuvier, 1795
Subclass: Pulmonata Cuvier, 1817	**Subclass**: Euthyneura Spengel, 1881
Order: Basommatophora Keferstein, 1865	**Order**: Basommatophora Keferstein, 1865
Superfamily: Lymnaeoidea Rafinesque, 1815	**Superfamily**: Lymnaeacea Rafinesque, 1815
Family: Lymnaeidae Rafinesque, 1815	**Family**: Lymnaeidae Rafinesque, 1815
Hubendick (1978)	Nordsieck (1992)
Class: Gastropoda Cuvier, 1795	**Class:** Gastropoda Cuvier, 1795
Subclass: Pulmonata Cuvier, 1817	**Subclass**: Pulmonata Cuvier, 1817
Order: Basommatophora Keferstein, 1865	**Superorder**: Basommatophora Keferstein, 1865
Superfamily: Lymnaeacea Rafinesque, 1815	**Order**: Hygrophila A. Férussac, 1822
Family: Lymnaeidae Rafinesque, 1815	**Infraorder**: Branchiopulmonata Minichev & Starobogatov, 1975
	Superfamily: Lymnaeacea Rafinesque, 1815
	Family: Lymnaeidae Rafinesque, 1815
Golikov and Starobogatov (1988)	Bouchet et al. (2017)
Class: Gastropoda Cuvier, 1795	**Class:** Gastropoda Cuvier, 1795
Subclass: Pulmonata Cuvier, 1817	**Subclass**: Heterobranchia Burmeister, 1837
Superorder: Lymnaeiformii A. Férussac, 1822	**Cohort**: Tectipleura Schrödl et al., 2011
Order: Lymnaeiformes A. Férussac, 1822	**Subcohort**: Panpulmonata Jörger et al., 2010
Family: Lymnaeidae Rafinesque, 1815	**Superorder**: Hygrophila A. Férussac, 1822
	Superfamily: Lymnaeoidea Rafinesque, 1815
	Family: Lymnaeidae Rafinesque, 1815

Box 2.2 The Taxonomic Structure of the Extant Lymnaeidae Accepted in MolluscaBase (2022)[a]

Family Lymnaeidae Rafinesque, 1815[b]		
Subfamily Lymnaeinae	Subfamily Amphipepleinae Pini, 1877 (= Radicinae Vinarski 2013)	Subfamily Lancinae Hannibal 1914
Acella Haldeman, 1841 *Aenigmomphiscola* Kruglov et Starobogatov, 1981 *Bulimnea* Haldeman, 1841 *Erinna* H. & A. Adams, 1855 *Galba* Schrank, 1803 (subgenera *Galba* s.str., *Bakerilymnaea* Weyrauch, 1964; *Pseudogalba* F.C. Baker, 1913; *Sibirigalba* Kruglov et Starobogatov, 1985)[c] *Hinkleyia* F.C. Baker, 1928 *Ladislavella* B. Dybowski, 1913 *Lymnaea* Lamarck, 1799 *Omphiscola* Rafinesque, 1819 *Pectinidens* Pislbry, 1911 *Pseudisidora* Thiele, 1931 *Pseudosuccinea* F.C. Baker, 1908 *Stagnicola* Jeffreys, 1830 *Walterigalba* Kruglov et Starobogatov, 1985	*Ampullaceana* Servain, 1882 *Austropeplea* Cotton, 1942 (subgenera *Austropeplea* s. str., *Kutikina* Ponder et Waterhouse, 1997) *Bullastra* Bergh, 1901 *Kamtschaticana* Kruglov et Starobogatov, 1984 *Lantzia* Jousseaume, 1872 *Limnobulla* Kruglov et Starobogatov, 1985 *Myxas* G.B. Sowerby I, 1822 *Orientogalba* Kruglov et Starobogatov, 1985 *Peregriana* Servain, 1882 *Racesina* Vinarski et Bolotov, 2018 *Radix* Montfort, 1810 (subgenera *Radix* s.str. and *Exsertiana* Bourguignat, 1883) *Tibetoradix* Bolotov, Vinarski et Aksenova, 2018	*Idaholanx* Clark, Campbell et Lydeard, 2017 *Fisherola* Hannibal, 1912 *Lanx* Clessin, 1882

[a] The genera are given in alphabetical order which does not reflect their phylogenetic relationships. Please note that this classification is somewhat different from an updated version proposed in this book (Aksenova et al. 2023). In particular, Aksenova et al. (2023) reject the subfamily Lancinae and rank it as a tribe Lancini within the Lymnaeinae.

[b] The fourth subfamily, Valencienniinae, is completely extinct

[c] The subgeneric classification of *Galba* requires a revision

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