Chapter 6
The Fossil Record of the Lymnaeidae: Revisiting a 200-Myr-Long Story of Success

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Abstract Here, I present a review of the global pre-Pleistocene fresh- to brackish-water fossil record of the gastropod family Lymnaeidae based on a thorough literature survey of over 450 scientific works. I discuss the putative origin of the family, assess diversity development through geological time (based on the fossil records of Europe and North America), and illustrate the family's geographic distribution over the past 200 Myr using paleogeographic maps. The following section deals with potential dispersal mechanisms to explain the family's disjunct fossil distribution. A final part is devoted to peculiar cases of morphological evolution toward limpet-like and/or strongly sculptured shells.

6.1 Introduction

Today, the Lymnaeidae are a diverse family in the world's fresh water (e.g., Pyron and Brown 2015; Aksenova et al. 2018; Vinarski et al. 2019; and other articles in this volume). The family is near globally distributed, whereas the northern hemisphere maintains a much higher diversity (Vinarski et al. 2019). Also morphologically, they are highly diverse and comprise a great variety of shell shapes (e.g., Baker 1911; Hubendick 1951; Correa et al. 2011; Campbell et al. 2017; Aksenova et al. 2018;

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Vinarski et al. 2019; Alda et al. 2023). Moreover, Lymnaeidae play a vital role in the transmission of liver fluke and are thus of medical importance (e.g., Correa et al. 2010; Mahulu et al. 2019).

Since lymnaeids occur in a great range of habitats, they are a common component of fossil freshwater communities and are often used as paleoecological indicators (e.g., Good 1987; Carobene et al. 2018; Salvador et al. 2018a; Esu and Girotti 2020; Kadolsky 2020; Rasser et al. 2020). Numerous species have been described from fossil deposits all around the globe (e.g., Wenz 1923). Yet, in spite of their high diversity and relevance to paleoecology, a thorough review of the family's diversity and distribution through geological time is absent.

Here, I review the literature to provide an overview over the global fossil record of lymnaeids and their geographic and stratigraphic distribution. Given the number of publications documenting lymnaeids in fossil deposits, the overview focuses on the pre-Pleistocene record. Although not including every single record in the literature, I sought to cover the complete geographic range of the family through time. I review the oldest records of fossil species attributed to the Lymnaeidae and discuss the family's potential origin. Based on the available data for Europe and North America, which contain particularly rich records, I reconstruct continental diversity through time. Lymnaeid distribution through time and space is illustrated via paleogeographic maps. Two further chapters deal with potential dispersal mechanisms and morphological evolution.

6.2 Material and Methods

Information for European and North American faunas was retrieved in the frame of a project dealing with diversification dynamics of freshwater gastropods over the past 200 Myr. This project aligns with a continuous effort to gather and complete an inventory of all fossil freshwater gastropods worldwide. Most of the taxonomic information has already been made available via MolluscaBase (MolluscaBase eds 2021). Data were mostly obtained directly from the literature. Additional information were derived from various online sources, but in all cases these data were checked for accuracy and correctness against the primary literature. In total, the data were derived from 454 scientific works (Supplementary Table S1).

Systematically, I include in this review all species currently classified in the Lymnaeidae. Since fossil (as well as recent) lymnaeids have been regularly mixed up with members of the terrestrial families Succineidae (e.g., Marshall 1926), Bulimulidae (e.g., Salvador et al. 2018b), and Oleacinidae (e.g., Wenz 1923; Harzhauser et al. 2014b), I follow the latest revisions to account for systematic changes. This concerns also some genera formerly placed in the family Clivunellidae (*Delminiella, Neoclivunella*, and *Neodelminiella*), now a monotypic family restricted to the Miocene of the Balkans (Harzhauser et al. 2016). *Neoclivunella* and *Neodelminiella* comprise limpet-shaped shells and are classified tentatively in the lymnaeid subfamily Valencienniinae (Harzhauser et al. 2016). That taxon is still poorly defined and its genus- and species-level taxonomy is not well resolved and depends on the author (e.g., Gorjanović-Kramberger 1923; Moos 1944; Taktakishvili 1967; Marinescu 1970). Because of their descent from a species belonging to the genus *Radix*, Bouchet et al. (2017) treated the Valenciennιinae as a synonym of Amphipepleinae. Here, I follow the traditional concept and treat the subfamily as distinct. In addition to the two abovementioned genera, I include here *Velutinopsis*, *Undulotheca*, *Hiscerus*, *Velutinellus*, *Provalenciennesia*, and *Valenciennius*. Despite the morphological similarity to *Delminiella* and the Valenciennιinae, the family Clivunellidae is believed to be closely related to Planorbidae (Harzhauser et al. 2016) and is thus not treated herein. The Mesozoic genus *Proauricula* Huckriede, 1967, which was considered a basal Basommatophora and probably predecessor of the Lymnaeidae by Bandel (1991), was lately reclassified in the Ellobiidae by Yu et al. (2021).

Stratigraphically, the review is limited to the pre-Pleistocene fossil record. With few exceptions (e.g., the Caspian Sea; Andrusov 1923), the Early Pleistocene faunas resemble in species composition the modern fauna (e.g., Taylor 1960, 1966; La Rocque 1963; Esu and Girotti 1975; Schlickum and Puisségur 1978; Dehm 1979). Only the overview of the number of fossil species discovered per year and decade is based on all fossil species. Data were derived from a MolluscaBase query for all fossil-only species (including nomina dubia, taxa inquirenda and temporary names, e.g., junior homonyms without replacement name; queried 7 November 2021; Supplementary Table S2).

Age classifications of the localities are based on the most recent assessments of the fossil-bearing strata. For most European sites, age data are available from Neubauer et al. (2015a, b, c, 2021). Stratigraphic data on formations in China were derived mostly from Zhang (2009). Based on the ages, paleocoordinates were estimated using the GPlates Portal under the PALEOMAP model (http://portal.gplates.org/service/d3_demo/?view=points).

The statistical analyses were performed using R v. 4.0.3 (R Core Team 2020). Diversity reconstructions are made only for Europe (including Turkey) and North America because of the paucity of data for the other continents as well as the uncertain stratigraphy or taxonomy of many of those records. Subspecies, doubtful records or identifications ("cf.", "aff."), nomina nuda and nomina dubia were not considered. Taxa inquirenda and temporary names were included. Range-through species richness binned over stratigraphic stages was calculated using the package divDyn v. 0.8.0 (Kocsis et al. 2019). In order to avoid a biased decrease of range-through richness toward the Pleistocene by assuming that all taxa went extinct at the end of the Pliocene, I included species occurring today in a separate Holocene time bin for the calculation. Data for the modern species was taken from MolluscaBase. Stage boundaries follow the International Chronostratigraphic Chart (July 2021; https://stratigraphy.org/chart).

Since all fossil time series are inevitably skewed by uneven preservation (Alroy 2010), I applied a subsampling approach to assess whether any observed diversity pattern is the result of sampling. For this purpose, I used the shareholder quorum subsampling (SQS) method of Alroy (2010) as implemented and advanced in the package divDyn using 1000 iterations and a quorum level varying between 0.3 and

0.7 at increments of 0.1. The SQS approach was only applied to the European dataset, since not enough data are available for other continents.

Genus-level diversity is not discussed herein due to the problems associated with genus classification in lymnaeids. While modern lymnaeid systematics rely on anatomical characters and results from molecular phylogenetics (e.g., Vinarski 2013; Aksenova et al. 2018), any fossil species classification is inevitably based on shell characters, which are often of limited value (see also Vinarski 2013 for an in-depth discussion of the subject). Most fossil species are placed in "standard" genera like *Lymnaea* or *Galba*, whereas probably very few of them actually belong in these genera.

Institutional abbreviations. MBFSZ – Mining and Geological Survey of Hungary, Budapest; NHMW – Natural History Museum Vienna; ZMBH – Zemaljski Muzej Bosne i Hercegovine, Sarajevo.

6.3 Diversity Through Time

The first fossil lymnaeids were described by Alexandre Brongniart in 1810 (Brongniart 1810). He introduced nine new species from Eocene and Oligocene deposits of the Paris Basin in France; all of them are still considered as valid. Since then, the number of species descriptions per year has almost linearly increased (Fig. 6.1a). Noteworthy publications advancing the number of species above average were contributed by Deshayes (1863), who described 15 species also from the Paleogene of the Paris Basin species, and Gorjanović-Kramberger (1901), who introduced eleven species for the Valencienniinae of Lake Pannon. Overall, with 18 described species each, these two authors introduced the most (still valid) fossil lymnaeid species (Fig. 6.1b).

The curve of new species descriptions is not saturated yet. Only since the year 2000, twenty new species of Lymnaeidae have been described from fossil freshwater deposits (Macaleț 2000; Pierce and Constenius 2001; Kovalenko 2004, 2017; Prysjazhnjuk et al. 2006; Pan and Zhu 2007; Harzhauser et al. 2012, 2014a, 2016; Neubauer et al. 2014, 2015d; Vinarski and Frolov 2017; Yu et al. 2021).

Altogether, 379 valid accepted species have been described over the 210 year-long history of fossil lymnaeid taxonomy (Supplementary Table S2). Of these, pre-Pleistocene distribution data are available for 376 species in 32 genera (of which 15 are only known from fossil species) and four subfamilies (Lymnaeinae, Amphipepleinae, Lancinae, and Valencienniinae) (Supplementary Table S1).

The species richness reconstructions showed similar tendencies for Europe and North America, yet in quite different magnitudes (Fig. 6.2). While the pre-Pleistocene European fossil record comprised altogether 262 species, only 56 species were recorded for North America. Species richness remained low in both continents during the Mesozoic and earliest Paleogene. No notable diversity decline was observed at the Cretaceous–Paleogene boundary, which contrasts a

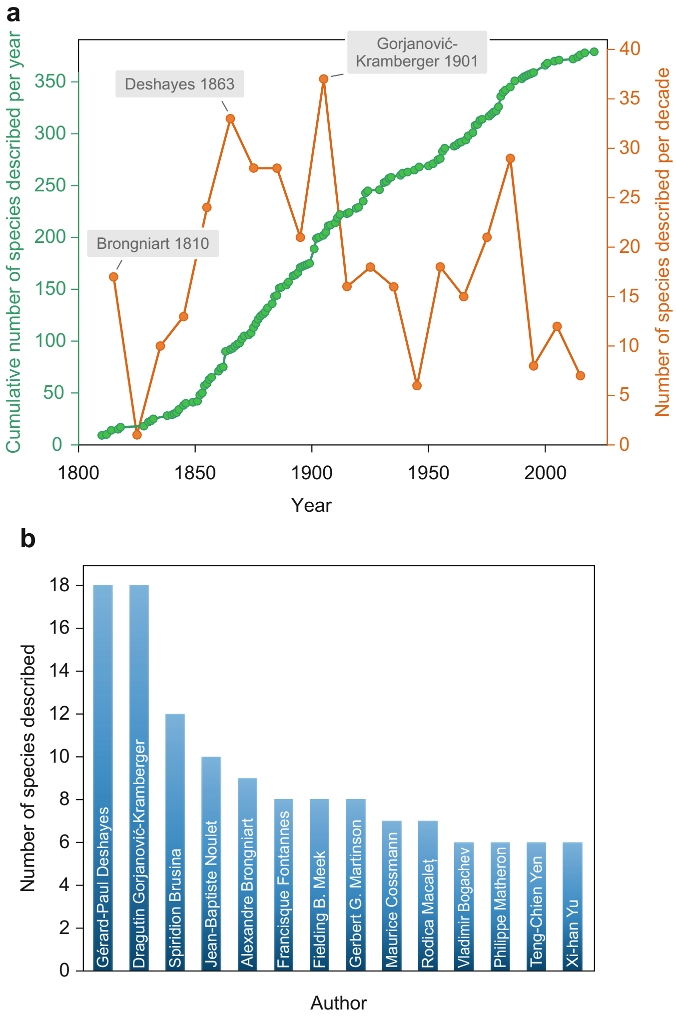

Fig. 6.1 (**a**) Number of lymnaeid species described per year (cumulative, green) and decade (orange). Indicated are additionally the three publications that have contributed the most to the number of species. (**b**) Authors that described more than five fossil lymnaeid species. Invalid or unavailable names (e.g., synonyms, nomina nuda) were not considered in any of the two plots

massive breakdown of the overall freshwater gastropod diversity in Europe (Neubauer et al. 2021).

Diversification speeded up about coevally in both continents in the Lutetian (Middle Eocene). In Europe, a diversity peak was reached with 45 species in the Rupelian. Diversity dropped in both continents toward the Oligocene–Miocene boundary and increased again during the Miocene. The all-time species richness peak was reached in both continents during the Tortonian. In Europe, this peak is

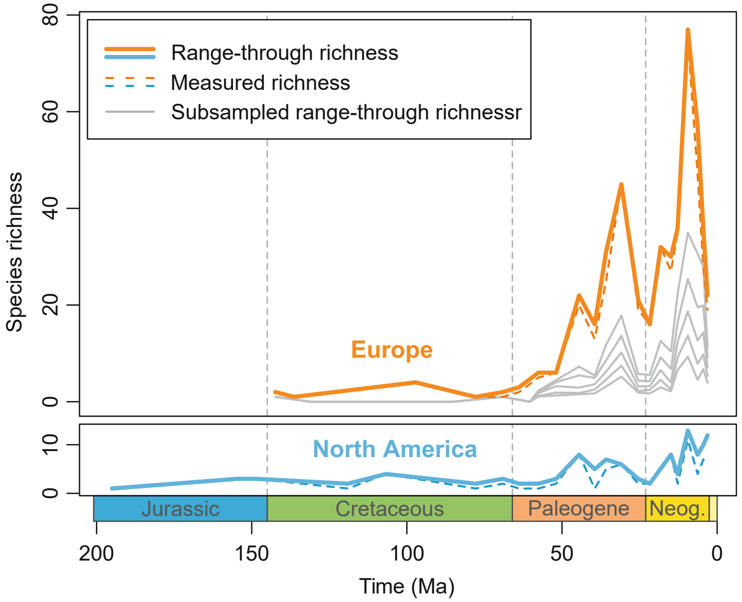

Fig. 6.2 Lymnaeidae species richness through geological time for Europe and North America, including subsampled richness for Europe (using quorum levels of 0.3, 0.4, 0.5, 0.6, and 0.7)

partly owed to major diversification events in Lake Pannon and the Dacian Basin. Hence, not all of the 77 species recorded for the Tortonian lived simultaneously.

The diversity trend for Europe derived from the raw data was confirmed by the subsampling (SQS) approach (Fig. 6.2), suggesting that the observed pattern is not biased by uneven sampling. There is unfortunately not enough data for North America to use subsampling to assess the reliability of the measured trend.

6.4 Geographic Distribution Through Time and the Origins of Lymnaeidae

In this chapter, I give an overview of the geographic distribution of Lymnaeidae from their first occurrence in the fossil record to the Pliocene, illustrated by a series of paleographic maps (Figs. 6.3, 6.4, 6.5, 6.6). Given the high number of records in some stratigraphic intervals, these maps are not exhaustive and do not contain all records as single points but are rather intended to cover the entire geographic range of lymnaeids in each interval. Also, the lymnaeid fossil record is clearly geographically biased toward Europe and North America (Supplementary Fig. S1). The spotty occurrences on other continents, such as Asia, where lymnaeids are common today (Vinarski et al. 2019), suggest a strong preservation, sampling, and/or research bias.

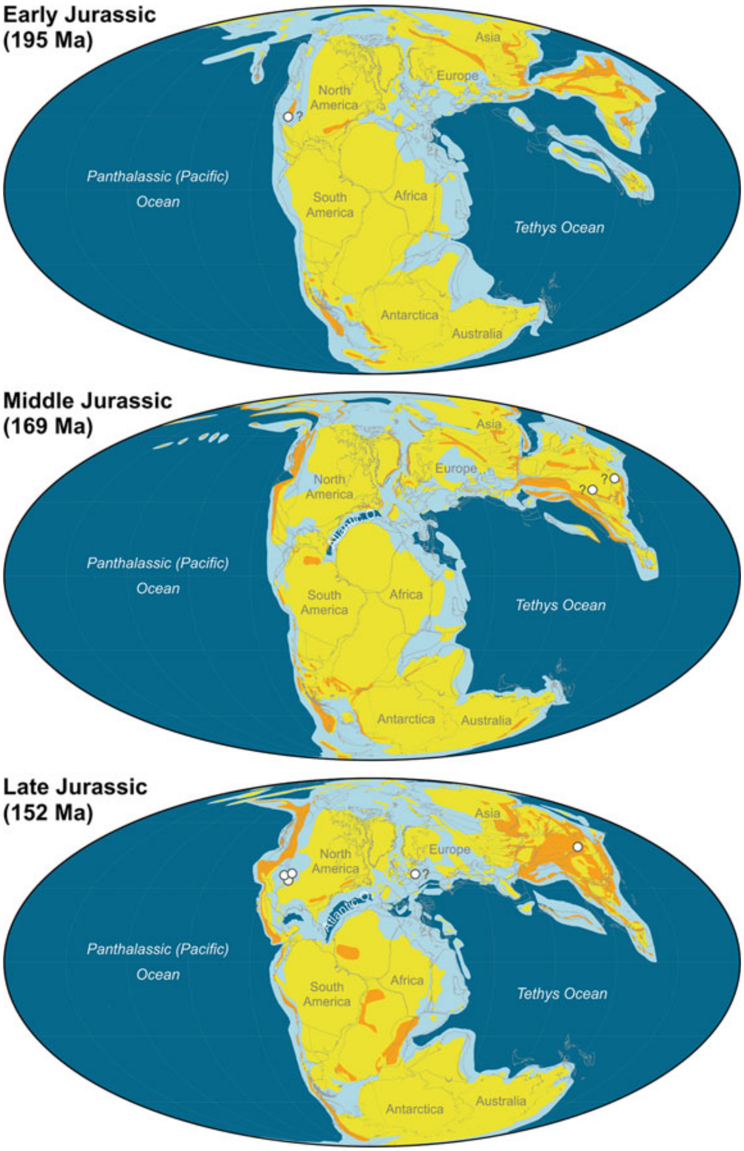

Fig. 6.3 Geographic distribution of Lymnaeidae in the Jurassic. Close-by localities are represented by single points. Question marks indicate species of uncertain lymnaeid affinity. Base map from Cao et al. (2017) used under Creative Commons Attribution 3.0 (CC BY 3.0) license. Yellow areas mark land masses, orange indicates mountain ranges

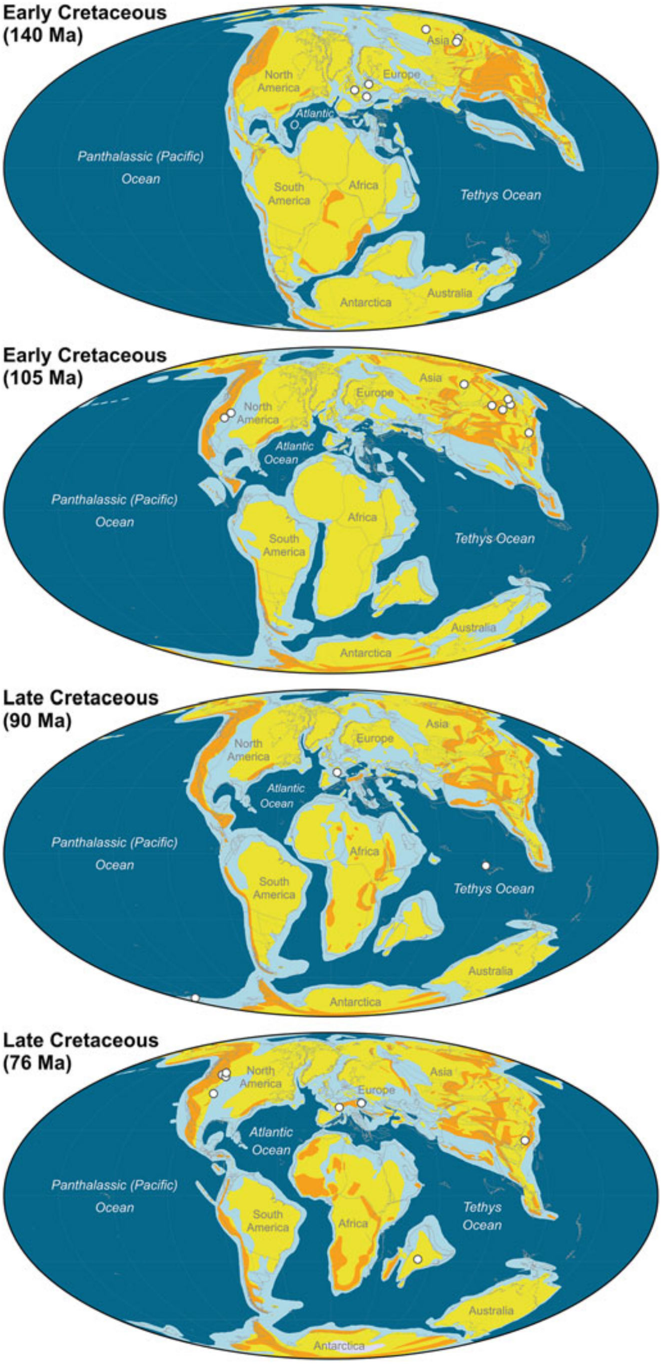

Fig. 6.4 Geographic distribution of Lymnaeidae in the Cretaceous. Close-by localities are represented by single points. Base map from Cao et al. (2017)

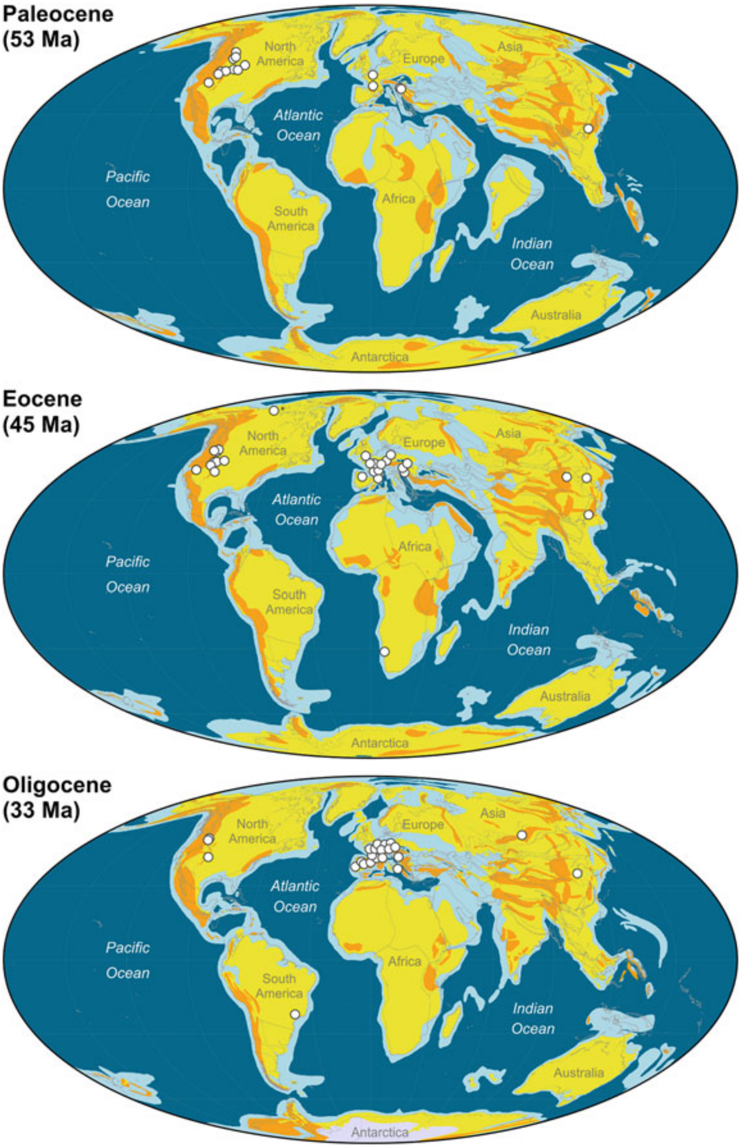

Fig. 6.5 Geographic distribution of Lymnaeidae in the Paleogene. Close-by localities are represented by single points. Asterisks mark localities with doubtful stratigraphic age. Base map from Cao et al. (2017)

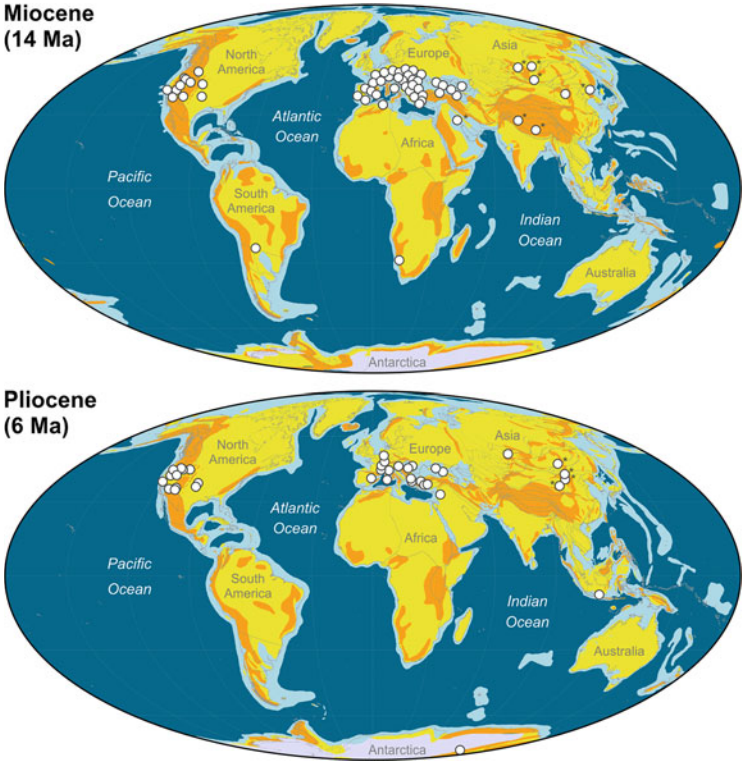

Fig. 6.6 Geographic distribution of Lymnaeidae in the Neogene. Close-by localities are represented by single points. Asterisks mark localities with doubtful stratigraphic age. Base map from Cao et al. (2017)

6.4.1 *Mesozoic Roots*

The ancestry of the Lymnaeidae is unresolved. Inaba (1969) hypothesized a late “pro-lymnaeid” ancestor, from which modern lineages arose starting already in the late Paleozoic, but without any evidence from fossils. Kruglov (2005) suggested an origin and initial diversification in the Triassic and hypothesized that the ancestor of Lymnaeidae is related to Chilinidae. This assumption would at least match the basal position of Chilinidae within the Hygrophila as indicated by phylogenies based on morphology and molecular data (Hubendick 1978; Nordsieck 1992; Jörger et al. 2010), although their fossil record is comparably sparse and young (Dayrat et al. 2011). However, the latest molecular phylogeny by Saadi et al. (2020) suggests that the ancestor of Lymnaeidae is more closely related with Physidae. Yet, the fossil record of that family only starts in the Late Jurassic (Huckriede 1967).

A Triassic origin of Lymnaeidae as supposed by Kruglov (2005) predates the fossil record of the family. The earliest putative mention of lymnaeids in the fossil record derives from the United States (Fig. 6.3). Robinson (1915) described the two species *Valvata gregorii* and *Limnaea hopii* from "Painted Desert beds" in Arizona, which he attributed to the Morrison Formation, suggesting a Late Jurassic age for the fossils. Yen (1951) later attributed these findings erroneously to the Upper Triassic Chinle Formation (Harshbarger et al. 1957). The stratigraphic mystery was finally solved by Harshbarger et al. (1957), who correlated the fossil-bearing strata with the silty facies of the Kayenta Formation, pointing toward an Early Jurassic (Pliensbachian) age (Marsh and Rowe 2018). However, the type material has apparently not been studied since the first description (see, e.g., Yen 1952, p. 27), and the illustrations and description provided by Robinson (1915) do not unequivocally ascertain placement in the Lymnaeidae.

The next oldest records of supposed Lymnaeidae come from the Middle Jurassic of China (Fig. 6.3). Pan (1977) described *Galba lufengensis* and *Galba yunnanensis* from the Zhanghe Formation and Hepingxiang Formation of Yunnan, and Yü and Pan (1980) recorded *Galba tongshangensis* from the Tongshan Group of Zhejiang. All these stratigraphic units are presently attributed to the Middle Jurassic (Zhang 2009). The preservation of these fossil species is poor (Yü and Pan 1980) and, as for Robinson's material above, the attribution to Lymnaeidae cannot be confirmed with certainty. In fact, *Galba lufengensis* resembles terrestrial succineids.

A careful revision of these earliest fossils is required to assess the origin of the Lymnaeidae. At least from the Late Jurassic onward, the number of lymnaeid records increases and they come from various continents (Fig. 6.3). This includes species from the Morrison Formation in the USA (White 1886; Yen 1952; Solem and Yochelson 1979; Gray 1988; Evanoff et al. 1998), the Tithonian of Shandong in China (Pan 1983) and, possibly, the Kimmeridgian of Lower Saxony in Germany (Huckriede 1967), involving several species undoubtedly belonging in the family Lymnaeidae.

Records from the Jurassic–Cretaceous boundary were derived from the Tithonian–Valanginian Purbeck Formation in southern England (Arkell 1941) and its stratigraphic equivalents (mostly of Berriasian age) in Switzerland (De Loriol and Jaccard 1865) and Germany (Dunker 1846) (Fig. 6.4). Early Cretaceous lymnaeids were documented from the Valanginian–Hauterivian and the Aptian–Albian of Siberia (Reis 1910; Martinson 1956, 1961), the Guantou, Yehe, Banlashan, Yixian and Xiazhuang formations of Zhejiang, Jilin, Liaoning and Beijing in China (Yü and Pan 1980; Zhu 1980; Yü 1987; Pan and Zhu 2007) and the Aptian–Albian Cloverly Formation (Yen 1946c, 1951) and the Albian Bear River Formation (White 1876; Yen 1954) in the USA. This also involves findings of Yen and Reeside (1946) and Yen (1952), who formerly attributed their fossils to the Morrison Formation, but Evanoff et al. (1998) identified the strata as belonging to the Cloverly Formation.

The Late Cretaceous (potentially) saw the first appearance of Lymnaeidae on the southern hemisphere (Fig. 6.4). Beu et al. (2014) reported an unidentified species from the Cenomanian of New Zealand, which they tentatively referred to the genus *Austropeplea*. Additional early Late Cretaceous records come from the Cenomanian of France (Repelin 1902; age after Fabre-Taxy 1948) and Myanmar (Yu et al. 2021). After a long stratigraphic gap, end-Cretaceous taxa appear in the Campanian–

Maastrichtian St. Mary River Formation (Whiteaves 1885; Tozer 1956), the Campanian–Danian Edmonton Group (Tozer 1956) and the Maastrichtian lower Willow Creek Formation (Tozer 1956) of Canada, the Maastrichtian Laramie Formation in the USA (Meek 1873), the Maastrichtian Nanxiong Formation of Guangdong, China (Yü 1977), the Maastrichtian of India (Sowerby 1840; Hislop 1860; Hartman et al. 2008), the Campanian–Maastrichtian (“Rognacien”) of France (Matheron 1843; Fabre-Taxy 1959), and the Maastrichtian of Hațeg in Romania (Pană et al. 2002). (Note that Pană et al. (2002) introduced a new genus and three new species names for Lymnaeidae but without describing them or designating type material, rendering all these names unavailable.)

6.4.2 The Paleogene Diversification

Rich Paleocene faunas containing Lymnaeidae have been documented from the USA and Canada, including the Green River Formation (White 1880; La Rocque 1960), Paskapoo Formation (Whiteaves 1885; Russell 1926; Tozer 1956), Devils Basin Formation (Love 1989) and Fort Union Formation (Meek and Hayden 1856; Yen 1948b; Bickel 1977) (Fig. 6.5). European records were derived from the “Liburnian” (Danian) of Croatia (Sandberger 1870–1875; Stache 1889) and the Thanetian of France, i.e., the “Sables de Bracheux” (Cossmann 1889; Glibert 1962) and the “Calcaire de Rilly” in the Paris Basin (Bayan 1870) and the “Calcaire à *Physa prisca*” in southern France (Noulet 1854; Rey and Villatte 1971). Only a single Paleocene record comes from Asia, namely from the Shanghu Formation of Guangdong, China (Yü 1977).

The Eocene diversification is represented by numerous localities in Europe and North America (Fig. 6.5). The majority of records come from the Paris Basin in France (e.g., Brongniart 1810; Deshayes 1863; Leriche 1899; Cossmann 1902; Jodot and Feugueur 1953; Glibert 1962) and the Hampshire Basin in southern England (e.g., Sowerby 1826–1829; Edwards 1852; Glibert 1962; Paul 1989; Munt 2014), as well as from the Upper Rhine Graben in Germany and France (e.g., Sandberger 1870–1875; Rollier 1910), the “Calcaires de Mas-Saintes-Puelles”, “Calcaire de Castres” and “Molasse de Castelnaudary” in southern France (Serres 1844; Noulet 1854, 1857; Jodot and Rey 1956), and the Anjou (Glibert 1962), Matelles (Rey 1962b) and Aix-en-Provence (Matheron 1843; Roule 1886; Rey 1962a) basins, amongst several others. In North America, several species have been reported from the Middle–Late Eocene of the Kishenehn Basin (Russell 1952, 1955; Pierce and Constenius 2001, 2014). Additional records come from the Upper Eocene Florissant Formation (Cockerell 1906, 1908), the Upper Eocene to Lower Oligocene White River Formation (Evans and Shumard 1856; Meek 1876) and several more localities in the mid-west (e.g., Yen 1946b, 1948a; Good 1987; Hartman and Roth 1998). Only three Asian regions have yielded Eocene lymnaeids. They are located in China (Guangdong and Hebei provinces; Yü and Pan 1982; Yü and Zhang 1982) and Korea (Suzuki 1949). Finally, Lymnaeidae first appeared in the fossil record of

Africa during the Eocene, with two species from the Lutetian of Namibia (Pickford et al. 2008).

During the Oligocene, Lymnaeidae maintain a diverse fossil record in France, specifically in the Paris Basin (e.g., Brongniart 1810; Deshayes 1863; Dollfus 1906, 1920; Glibert 1962; Lozouet and Maestrati 1981), the "Calcaires d'Albi" in southern France (e.g., Fontannes 1884), and the Limagne Basin (e.g., Rey 1965) (Fig. 6.5). Numerous findings have been reported from the Chattian "*Ramondi* Beds" and "Formation du Gypse d'Aix" in France, Switzerland, and Germany (e.g., Fontannes 1881, 1884; Douxami 1904; Jodot 1954; Rey 1965). Additional important records come from the Upper Rhine Graben in France (e.g., Sandberger 1870–1875; Gillet 1953; Jodot 1954), the Mainz Basin (e.g., Thomä 1845; Mödden et al. 2000), and the Hessian Depression in Germany (e.g., Dunker 1853) and Limburg in Belgium (Glibert and Heinzelin de Braucourt 1954; Janssen 1980; Marquet et al. 2008). Only few records come from outside central Europe; these include localities in Portugal (Roman 1907; Pais 2012), Spain (Almera 1894; Royo Gómez 1922; Esu 1984), and Italy (Sacco 1886; Esu and Girotti 2010). Comparably little is known about North American Oligocene Lymnaeidae. Only three species have been documented from the Renova Formation (Pierce 1993) and the Antero Formation (Russell 1938) in the USA. Similarly, only few Asian localities have yielded lymnaeids. Popova (1964, 1981) described a few taxa from the Upper Oligocene–Lower Miocene (?) Bayanday Formation of Siberia, and Yen (1969) documented one species from Shandong Province, China. Finally, an unidentified lymnaeid was found in the Upper Oligocene Tremembé Formation of São Paulo State, Brazil (Salvador et al. 2018b), being the oldest fossil Lymnaeidae of South America.

6.4.3 The Neogene Diversity Peak

The Miocene record of Lymnaeidae is by far the richest (Figs. 6.2 and 6.6), and the sheer number of records and works mentioning lymnaeid fossils makes a detailed listing impractical (Supplementary Table S1). The European Miocene fossil record includes 158 species from over 1340 records from 26 countries, spanning from Portugal in the West to the Caspian Sea in the East (Fig. 6.6). The majority of records come from Germany and France, particularly from the Aquitaine Basin (e.g., Grateloup 1828; d'Orbigny 1852; Degrange-Touzin 1892; Peyrot 1933; Wenz 1936), the Upper Freshwater Molasse (e.g., Klein 1853; Sandberger 1870–1875; Clessin 1885; Jooss 1913; Wenz 1935; Schlickum 1976; Salvador and Rasser 2016; Salvador et al. 2016), and the Mainz Basin (e.g., Thomä 1845; Braun 1851; Kadolsky 1989). Paleogeographically, most records were derived from the Late Miocene Lake Pannon. This huge long-lived brackish-water lake alone yielded over 50 species of Lymnaeidae, most of which are endemic to the lake (see also chap. 6.1). Important contributions were made by Brusina (1874, 1902), Gorjanović-Kramberger (1901, 1923), Pavlović (1927), Strausz (1942), Moos (1944), Stevanović (1951, 1955, 1990b, c), Bartha (1955, 1971), Papp (1956), Kochansky-Devidé and Pikija (1976), Sremac (1981), Marinescu (1973), Lennert et al. (1999), Vrsaljko (1999), and Botka et al. (2019), amongst many others. Further rich faunas were reported from the Dacian Basin in Romania (Krejci-Graf and Wenz 1932; Wenz 1942; Marinescu 1970; Hanganu 1972; Huică 1977; Marinescu and Papaianopol 1990; Macaleț 2000) and the Bakony Mountains in Hungary (Kókay 2006).

Important North American faunas yielding Miocene lymnaeids were described by Hanna (1923), Yen (1946a, 1947), Taylor (1954, 1957, 1966, 1983), Carr and Trimble (1963), Firby (1966), and Pierce (1993). A South American record comes from the Middle Miocene San José Formation of Argentina (Morton and Herbst 2003; Salvador et al. 2018b). Asian taxa were recorded by Suzuki (1949) from Korea, Willis (1967) from Iraq, and Yen (1969) from China. Additional reports of undefined Neogene age were made by Martinson (1954), Popova (1981), and Yü (1982) from Russia, Mongolia, and Tibet. Pickford (2008) reported two species from the Early Miocene of Namibia.

The Pliocene distribution reflects more or less the Miocene one, with many records in Europe and North America, a few in Asia and a single one in South America (Fig. 6.6). The center of European diversity is slightly shifted to the east compared to the Miocene, with the Dacian Basin holding the most diverse fauna (e.g., Macarovici 1940; Hanganu 1972; Macaleț 2000; Papaianopol et al. 2003; Van Baak et al. 2015). Additionally, the Transylvanian Basin in Romania (Jekelius 1932) and the Lower Rhône Basin in France (Serres 1853; Michaud 1855; Fontannes 1879, 1883) have yielded faunas rich in lymnaeids. The North American faunas mostly come from the Blancan deposits and were summarized by Taylor (1966). Additional records were listed by Henderson and Rodeck (1934), Nations (1974), Taylor and Smith (1981), and Love (1989). In Asia, taxa were documented from the Kyzylgir Formation in Siberia (Popova et al. 1970; Popova 1981), the Late Pliocene of Java (van Benthem Jutting 1937) and several localities in China (Ping 1931; Suzuki 1949; Zhu 1985; note that some of these records may range into the Early Pleistocene). Finally, an unidentified lymnaeid species was documented from the Pliocene Meyer Desert Formation of Antarctica by Ashworth and Preece (2003), representing the sole fossil record of that continent as yet.

6.5 Dispersal in the Fossil Record

When viewing the distribution patterns of Lymnaeidae in the fossil record and their spread from the presumed origin in the Early Jurassic of North America to nearly all over the world, the most obvious question is: how did they get there? Already during the Jurassic, the early Atlantic Ocean separated North America and Eurasia (Cao et al. 2017; Fig. 6.3). In fact, during most of the Mesozoic and Cenozoic, broad seaways isolated the continents, and only short intermittent phases of terrestrial pathways are known (Brikiatis 2014, 2016; Cao et al. 2017). However, these land bridges existed only between selected continents and it is unlikely that any of them offered hydrological connections allowing direct dispersal. A prime example of dispersal with an obvious lack of land connection is posed by the Pliocene occurrence of a lymnaeid on Antarctica (Ashworth and Preece 2003).

Dispersal in freshwater snails today knows active and passive pathways. Snails move actively along streams or are passively dispersed via ingestion and defecation by fish or waterbirds or via attachment to birds, mammals, amphibians, or even larger insects (e.g., Walther et al. 2008; Kappes and Haase 2012; van Leeuwen et al. 2012, 2013; Kolenda et al. 2017). Dispersal by both fish and waterfowl has already been witnessed for Lymnaeidae previously (Baker 1911; Kappes and Haase 2012; van Leeuwen and van der Velde 2012). Especially long-distance aerial dispersal is invoked to explain the pan-continental distribution of the family and disjunct occurrences on islands or in distant water bodies (Aksenova et al. 2018; Vinarski et al. 2021). Only Lancinae may form an exception here. In contrast to most lymnaeids, lancines have a poorly developed lung and probably do not survive transport outside of the water for long, constraining the possibility for dispersal by birds or mammals over long distances (Campbell et al. 2017).

As concerns fossil representatives, aerial dispersal has been proposed to explain the disjunct occurrence of *Delminiella* in Austria, separated from the remaining records in the Dinaride Lake System by a marine connection between the Mediterranean and Paratethys seas (Harzhauser et al. 2016). Similarly, Esu and Girotti (2018) suggested transport by waterfowl as likely mechanism to explain the occurrence of *Corymbina*, otherwise restricted to the Aegean region, in Lower Pliocene deposits of Italy. The Antarctic Pliocene record of a lymnaeid is likely a result of bird-mediated dispersal as well (Ashworth and Preece 2003) and the same might be true for many a disjunct occurrence in the Late Cretaceous or Cenozoic (Taylor 1988). However, waterfowl did not originate before the Late Cretaceous (Claramunt and Cracraft 2015). The mechanisms for dispersal prior to their evolution remain enigmatic.

Migrating land vertebrates, amphibians, or insects may have constituted viable options to reach water bodies not hydrologically connected, but it is unclear how lymnaeids could disperse across large distances and seaways. Early Cretaceous birds show similar anatomical features as modern migratory birds, but it is uncertain if they also underwent long-distance migration (Falk 2011). A possible yet so far entirely unsupported hypothesis involves pterosaurs (Yu et al. 2021). Some species of pterosaurs were likely capable of long-distance travels (Witton and Habib 2010), and some of them probably contributed to angiosperm seed dispersal during the Cretaceous (Fleming and Lips 1991). A few species probably fed on mollusks (Bestwick et al. 2018). Perhaps, freshwater mollusks could have been dispersed via ingestion and defecation or via attachment to the feet, just like in modern birds. However, to support this hypothesis a joint fossil record of gastropod and pterosaur species would be necessary.

Another aerial dispersal alternative may be offered by strong winds and storms. Several examples are known of terrestrial and freshwater mollusks and even fishes to be transported via storms (Rees 1965; Ożgo et al. 2016). Although the number of records is still anecdotal, Ożgo et al. (2016) considered storms a possible means of long-distance dispersal, at least for terrestrial gastropods. However, the chance that storms pick up lymnaeids and deliver them safely to new freshwater environments might be comparatively low.

6.6 Exploring the Limits of Morphological Disparity

The typical lymnaeid shell, both today and in the fossil record, is smooth and turbiniform. However, a number of "special cases" of morphological evolution happened over the long evolutionary history of the Lymnaeidae. Four of these are detailed in this chapter.

6.6.1 Valencienniinae

Probably the most outstanding among those cases is the evolution of the Valencienniinae. This subfamily originated during the Early Tortonian (Late Miocene) in early Lake Pannon from a small ancestor species currently attributed to the genus *Radix* (Gorjanović-Kramberger 1923; Moos 1944; Taktakishvili 1967; Marinescu 1970; Neubauer et al. 2016). During the c. 7-Myr-lifetime of the long-lived Lake Pannon, several evolutionary lineages evolved from that ancestor exhibiting widely expanded apertures and/or limpet-shaped shells (Fig. 6.7a–c, f, i). This also involved a massive size increase over time: starting from about 20 mm in height (Gorjanović-Kramberger 1890), some species developed shell sizes of up to 132 mm (Taktakishvili 1967). As such, they are among the largest non-marine aquatic snails ever recorded. Some of the species also developed a peculiar siphonal fold (Fig. 6.7c) and/or sculpture in the form of strong concentric ribs (Fig. 6.7a–c, f), both of which are rare features among lymnaeids in general.

While starting in Lake Pannon, these lineages were not confined to it. Several species have been reported from the Upper Miocene and Pliocene of the Dacian Basin (Krejci-Graf and Wenz 1932; Marinescu 1970; Hanganu 1972; Huică 1977; Marinescu and Papaianopol 1990; Papaianopol and Marinescu 1995) and Black Sea Basin (Rousseau 1842; Sinzov 1875; Davitashvili 1930; Taktakishvili 1967; Özsayar 1977). During the Pontian (latest Miocene), the subfamily expanded as far as the Kura Basin in Azerbaijan in the East (Davitashvili 1931). The last known occurrence is *Valenciennius kujalnicus* Taktakishvili, 1962 from the lower Kuyalnikian (latest Pliocene to earliest Pleistocene) of the Gurian region in Georgia (Taktakishvili 1967). ("?*Valenciennesia metochiana*" Pavlović, 1933 from the Middle Miocene Peć Series in Kosovo is probably not related with the Valencienniinae; a revision is required.)

Because of the sequential appearance of (morpho-)species of these evolutionary lineages, the individual species have been used as biostratigraphic markers (Moos 1944; Taktakishvili 1967; Botka et al. 2019). In the Black Sea Basin, stratigraphers

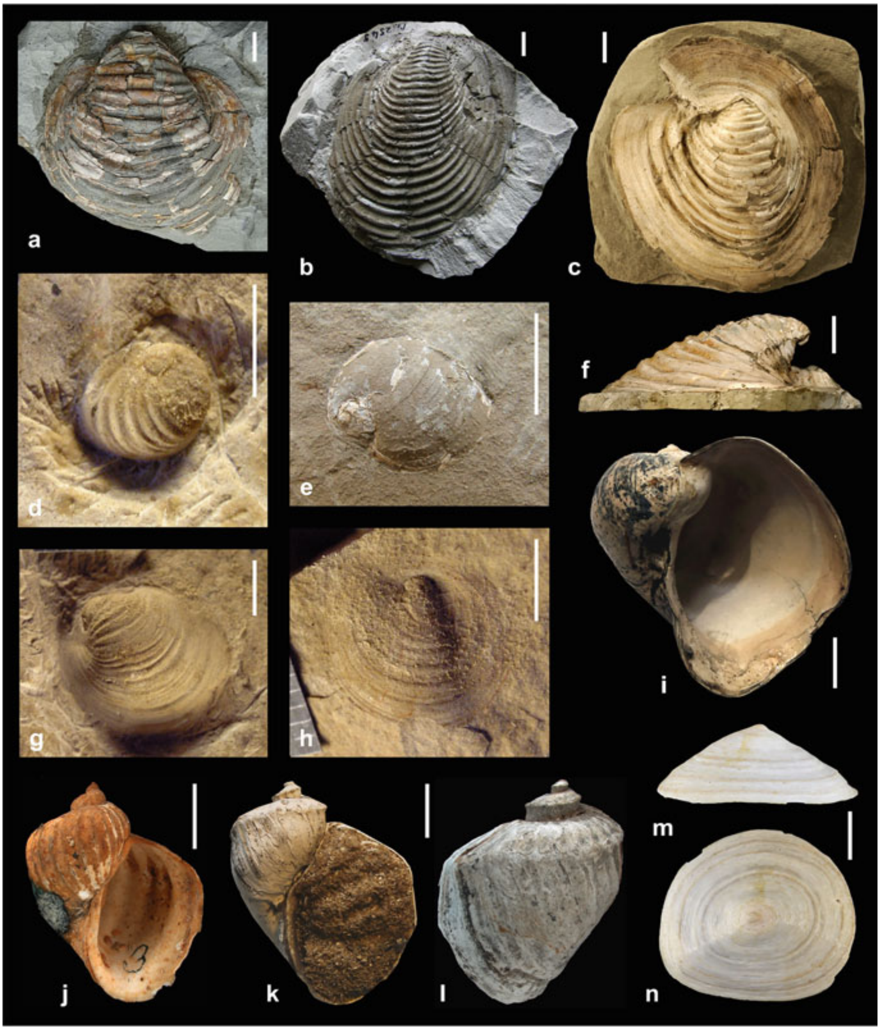

Fig. 6.7 Examples of lymnaeid species with extraordinary morphological adaptations. (**a**) *Undulotheca halavatsi* (Gorjanović-Kramberger, 1901), Guşteriţa, Romania, Late Miocene, coll. Botka (no number) (from Botka et al. 2019). (**b**) *Provalenciennesia arthaberi* (Gorjanović-Kramberger, 1901), Beočin, Serbia, Late Miocene, MBFSZ Pl. 2545. (**c**) *Valenciennius reussi* Neumayr in Neumayr and Paul, 1875, Tirol, Romania, Late Miocene, NHMW 1900/IX/5 (from Vermeij 2017). (**d**) *Delminiella* cf. *soklici*, Podhum, Bosnia, and Herzegovina, Early Miocene, ZMBH Mg3657. (**e**) *Velutinopsis velutina* (Deshayes, 1838), Mihalţ, Romania, Late Miocene, coll. Botka. (**f**) *Valenciennius reussi*, Okrugljak near Zagreb, Croatia, Late Miocene, NHMW 1888/XIV/2. (**i**) *Radix kobelti* (Brusina, 1884), Okrugljak near Zagreb, Croatia, Late Miocene, NHMW 1888/XIV/9. (**g**) *Delminiella soklici* Kochansky-Devidé and Slišković, 1972, Vučipolje near Tomislavgrad, Bosnia, and Herzegovina, Early Miocene, holotype, ZMBH Mg3631 (from Harzhauser et al. 2016). (**h**) *Delminiella excentrica* Kochansky-Devidé and Slišković, 1972, Eminovo selo near Tomislavgrad, Bosnia and Herzegovina, Early Miocene, holotype, ZMBH Mg3623 (from Harzhauser et al. 2016). (**j**) *Corymbina bicarinata* (Fuchs, 1877), Livanates, Greece, Early Pleistocene, holotype, NHMW 1878/XX/3. (**k, l**) *Corymbina elegans* (Cantraine, 1841), Livanates, Greece, Early Pleistocene, NHMW 1878/XX/1 (label reads "*Lymnaeus Adelinae*", a

even used to distinguish lower and upper "*Valenciennius* clays" in Pontian strata (Seninski 1905; Stevanović 1990a; Popov et al. 2016).

Little is known about the causes for that peculiar morphological diversification. In Lake Pannon, the Valencienniinae seem to be constricted to deep-water (sublittoral and profundal) environments (Harzhauser and Mandic 2008; Cziczer et al. 2009). One hypothesis is that the broad, flattened shell is an adaptation to life on mudgrounds in deeper settings (Marinescu 1970; Müller et al. 1999). Cziczer et al. (2009) proposed, in turn, that the limpet-like shape serves floating or swimming in the water column.

6.6.2 *Delminiella*

A similar case of morphological evolution toward a limpet-like shell is found in the Early Miocene genus *Delminiella* (Fig. 6.7d, g, h). Unlike for Valencienniinae, no ancestor–descendant relationship is known for that genus, but a lymnaeid ancestor has been proposed (Harzhauser et al. 2016). The genus is known by three species only; two occur in the Dinaride Lake System in Croatia and Bosnia and Herzegovina (Kochansky-Devidé and Slišković 1972), the third one is endemic to the paleo-lake Lavant in southern Austria (Harzhauser et al. 2016). They are all much smaller than Valencienniinae and range around 15 mm in maximum diameter. All species have widely expanded apertures and concentric growth lines or riblets, and all retain a small, coiled apex (Kochansky-Devidé and Slišković 1972; Harzhauser et al. 2016; Fig. 6.7d, g, h).

In the Dinaride Lake System, their appearance in the fossil record parallels the evolution of the similarly limpet-shaped but presumably unrelated family Clivunellidae. In the Livno and Tomislavgrad basins in Bosnia and Herzegovina, *Clivunella* and *Delminiella* even co-occur in the same strata (Kochansky-Devidé and Slišković 1972). In contrast to the alleged deep-water Valencienniinae, *Delminiella* (as well as Clivunellidae) are suggested to be more generalist species that lived in a greater variety of paleohabitats (Harzhauser et al. 2016). They occurred in muddy lake bottoms in deeper water with intermittent low oxygen levels (De Leeuw et al. 2011) and in littoral settings alike (Bulić and Jurišić-Polšak 2009).

Fig. 6.7 (continued) junior objective synonym of *C. elegans*). (**m, n**) *Lanx kirbyi* Hanna and Gester, 1963, Dorris, California, Early Pleistocene, paratype, CASG 34807.02 (formerly CASG 12451). Photos by D. Botka (a, b), CAS (m, n), O. Mandic (d, g, h), T.A. Neubauer (j, l), A. Schumacher (c), M. Vinarski (f, i, k). Scale bars = 10 mm (a–c, f), 5 mm (d, e, g–n)

6.6.3 *Lancinae*

Similar to Valencienniinae and *Delminiella*, the subfamily Lancinae comprises limpet-like shells (Vermeij 2017). Species of that group have completely lost coiling and are the only true patelliform lymnaeids (Campbell et al. 2017; Fig. 6.7m, n). Shells are smooth aside from concentric growth lines. Because of their close resemblance of "true" freshwater limpets, species of Lancinae have been previously placed in the planorbid subfamily Ancylinae (Campbell et al. 2017).

Lancinae are restricted to North America and include the three genera *Lanx*, *Fisherola,* and *Idaholanx* (Campbell et al. 2017), of which only *Lanx* is known to have a fossil record. Four fossil species are recognized and their appearance in the fossil record is patchy, which might indicate that not all of them belong to the same genus. This is especially true for the oldest record of the genus and subfamily, *Lanx nevadensis* MacNeil, 1939 from the Lower Cretaceous of Nevada (MacNeil 1939). Given that molecular data indicate a close relationship between Lancinae and Lymnaeinae (Saadi et al. 2020), it is unlikely that the subfamily originated already in the Cretaceous. Probably, *Lanx nevadensis* does not belong in Lancinae; its systematic position still needs to be assessed.

The stratigraphically next occurrence of (probably true) Lancinae derives from Middle Miocene strata of California, over 100 Myryounger (Firby 1966). Further occurrences have been documented from the Late Miocene, Pliocene, and Pleistocene of the western USA (Hannibal 1912; Hanna 1922; Yen 1944, 1947; Hanna and Gester 1963; Taylor 1966, 1981; Fig. 6.7m, n). Today, Lancinae dwell primarily in cool, flowing, well-oxygenated water, often in rivers, springs or spring-influenced areas of the Pacific drainage region, where they are commonly found under stones or attached to them (Taylor 1981; Burch 1982; Campbell et al. 2017).

6.6.4 *Corymbina*

A different type of morphospace expansion is exhibited by the fossil genus *Corymbina* (syn. *Adelina* Cantraine, 1841, non Dejean, 1835; *Adelinella* Wenz, 1922). The genus includes five species that are characterized by the presence of strong axial ribs, sometimes accompanied by a spiral keel (Fig. 6.7j–l). Most species have a classical lymnaeid-type shell, but some forms developed a detached aperture or an even uncoiled body whorl (Willmann 1981). The genus is mostly confined to the Aegean region (Greece and Turkey), where it occurs in Middle Miocene to Middle Pleistocene strata (Oppenheim 1919; Willmann 1981; Schütt and Kavuşan 1984; Esu and Girotti 2020). Two exceptions of disjunct occurrences were found in the Sarmatian (late Middle Miocene) of Romania (Marinescu 1992) and the early Pliocene of Italy (Esu and Girotti 2018). Because of the limited occurrence in space and time, the genus has been used for biostratigraphic correlations between Greek and Turkish Neogene strata (Willmann 1981, 1982; Böger 1983).

6.7 Synthesis

The fossil record of Lymnaeidae is patchy but indicates a widespread distribution over long periods of time of the family's evolutionary history. Given the paucity of freshwater deposits over large parts of the globe, especially in the Mesozoic, we know little about the family's origin, early history, and distribution. The earliest supposed member of the family occurred during the Early Jurassic in North America. Already in the course of the Jurassic the Lymnaeidae spread to Europe and Asia. Diversity remained low until the early Paleogene until the family started to diversify during the Middle Eocene—approximately 150 Myr after its (presumed) origin. The all-time peak of lymnaeid diversity was reached in the Late Miocene and coincided with major morphological diversification of the subfamily Valenciennіinae. The resulting species developed partly huge and strongly ribbed, limpet-like shells and were probably adapted to dysoxic deep-water settings. The associated evolutionary lineages evolved in long-lived lakes, which are widely considered natural laboratories of evolution (e.g., Michel et al. 1992; Harzhauser et al. 2013; Van Damme and Gautier 2013; Jenny et al. 2020). A similar yet smaller event of morphological diversification happened during the Early Miocene in central to southeastern Europe (genus *Delminiella*). The earliest supposed member of the North American Lancinae, a small subfamily of truly patelliform species that still exists today, dates back to the Early Cretaceous.

The disjunct distribution of Lymnaeidae through geological time is strongly shaped by long-distance dispersal. During the Late Cretaceous to Cenozoic, waterfowl probably constituted the main vector, suggested by numerous examples of isolated occurrences. In fact, the diversification of waterfowl and development of migratory routes may have contributed markedly to the diversification of Lymnaeidae. Conversely, the mechanisms for long-distance dispersal prior to waterfowl evolution remain doubtful and potentially involve Mesozoic ornithurine birds, pterosaurs, or storms. However, the patchy Mesozoic fossil record and the uncertainties regarding the systematic classification of early alleged lymnaeids further complicate the reconstruction of dispersal pathways.

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