

Chapter 8

Patterns and Processes of Speciation in Lymnaeidae



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Abstract In the present chapter, we aimed to summarize the current knowledge of patterns and processes of speciation in the gastropod family Lymnaeidae. Using selected case studies, we evaluated biodiversity and speciation patterns at both large and small spatial scale. We outlined adaptations to extreme and isolated environments and examined the studies dealing with speciation processes in lymnaeid gastropods.

Despite being widespread globally, the family is not very speciose and species flocks or small-scale radiations are an absolute exception. The family obtained a nearly cosmopolitan but mainly Northern Hemispheric distribution, with both widespread and narrow-range taxa. Adaptation to special or extreme habitats illustrates the importance of ecology in lymnaeid speciation. Whereas the prevailing geographical mode is allopatry, with likely cases of parapatry, no evidence currently exists for sympatric speciation in Lymnaeidae. Niche conservatism seems to be pronounced in some lineages and supports the assumption that speciation by adapting to different selective regimes is a common phenomenon. Mechanisms involved in speciation include biotic interactions such as in host–parasite pairs, leading to co-evolution in various species.

Lymnaea stagnalis, and increasingly some species of *Radix*, serve as model systems in developmental biology and neurophysiology and are thus among the gastropods spearheaded for genomic and transcriptomic analyses, allowing for a genome-level perspective on various biological aspects. All these new developments in the “omics” era will, in the near future, improve our understanding of speciation mechanisms in lymnaeids and beyond.

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8.1 Introduction

Lymnaeidae represent a major group of predominantly freshwater pulmonate gastropods (Hydrophila) that reached a factual cosmopolitan distribution throughout their roughly 200 million years of evolution (Zilch 1960; Taylor 1988; Tracey et al. 1993). While being present on all continents, formerly including Antarctica as suggested by Pliocene fossils (Ashworth and Preece 2003), members of this group fulfill several ecological functions (Taylor 1988; Vinarski et al. 2023 Chap. 7 of this book). Moreover, many species have biomedical importance since they serve as intermediate hosts for diseases relevant for both animals and humans (Brown 1994), of which fascioliasis is the most well-known, affecting millions of people worldwide (Vázquez et al. 2023, this book).

Lymnaeidae have been recognized for their pronounced shell-shape plasticity. This morphological variability together with an anatomical uniformity has led to very different approaches and estimates of both species and generic diversity in both extant (Hubendick 1951, 1978; Kruglov 2005; Vinarski 2013) and extinct taxa (Zilch 1960; Walter 1968; Neubauer 2023, this book). Given that most nominal species in the family were delineated on a strictly conchological basis, it is thus not surprising that estimates of global species richness of Lymnaeidae vary from only 40 (Hubendick 1951) to about 100 (Strong et al. 2008) or even not less than 200 species (Kruglov 2005). However, there has been some progress in recent years when studies on lymnaeid systematics are increasingly phylogeny-based and conducted in an integrative taxonomic framework (e.g., Remigio and Blair 1997; Bargues et al. 2003, 2007, 2013; Correa et al. 2010; Aksenova et al. 2018; Vinarski et al. 2020; Vinarski et al. 2022). Nevertheless, controversy exists about the generic-level composition of the family. Depending on the underlying assumptions, authors have used systems recognizing a single genus *Lymnaea* (e.g., Walter 1968), two genera (Hubendick 1951; Kruglov 2005), or far more than these (e.g., Burch 1989; Correa et al. 2010; Vinarski 2013). However, in recent years, the latter approach became more and more dominating (see, e.g., Puslednik et al. 2009; von Oheimb et al. 2011; Vinarski 2013; Aksenova et al. 2018; Vinarski et al. 2019).

Following a multi-genus concept with 32 recognized recent genera, an analysis of their occurrences across 22 zoogeographical freshwater regions (Fig. 8.1) highlights the unequal distribution patterns of generic diversity of worldwide Lymnaeidae (Fig. 8.2, Table 8.1) that contrasts a general latitudinal diversity gradient (Hillebrand 2004). The majority of genera are found in the Northern Hemisphere, i.e., the Holarctic region. Here, eastern North America, western North America, the Euro-Mediterranean subregion, and Siberia are particular biodiversity hotspots with 9 or 10 genera being present. Regions of intermediate diversity are found both in large regions such as northern North America, East and Central Asia but also comparatively small ones such as western Mongolia and Lake Baikal (Fig. 8.1). In sharp

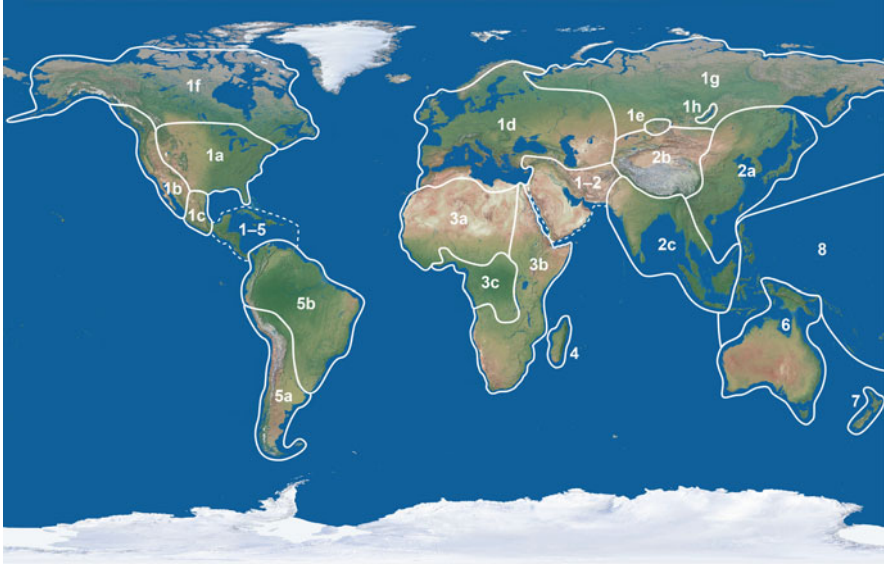


Fig. 8.1 Accepted zoogeographical freshwater regions after Bănărescu (1990) and Schäfer (1997). 1 – Holarctic region: 1a – Eastern North American subregion, 1b – Western North American subregion, 1c – Central Mexican subregion, 1d – Euro-Mediterranean subregion, 1e – Western Mongolian subregion, 1f – Arctic North American subregion, 1g – Siberian subregion, 1h – Baikal subregion; 2 – Sino-Indian region: 2a – East Asian subregion, 2b – High Asian subregion, 2c – South Asian subregion; 1–2: Western Asian transitional area; 3 – Ethiopian (African) region: 3a – West Africa, 3b – South East Africa, 3c – Central Africa; 4 – Malagasy region; 5 – Neotropical (South American) region: 5a – Andean-Patagonian subregion, 5b – Guayana-Brazilian subregion; 1–5: Middle American/Antillean transitional area; 6 – Australian region; 7 – New Zealand region; 8 – Indo-West Pacific region

contrast are those, mostly southern continental, regions that are inhabited by only one or two genera of Lymnaeidae, namely Africa, the Australian, and New Zealandian regions. Note, however, that there are other non-indigenous genera present in Africa (Appleton and Miranda 2015), and depending on taxonomic treatment, there might be more genera recognized for Australia (Puslednik et al. 2009).

Whereas the biogeography of Lymnaeidae has been summarized elsewhere (Vinarski et al. 2019; Vinarski et al. 2023, this book Chap. 7), the major aim of the present chapter is to review prominent patterns of speciation in selected case studies and the underlying mechanisms that led to the disparately distributed biodiversity of these gastropods. Given the wealth of literature that is currently available, such a review is naturally biased and not intended to be complete, but rather to provide an overview.

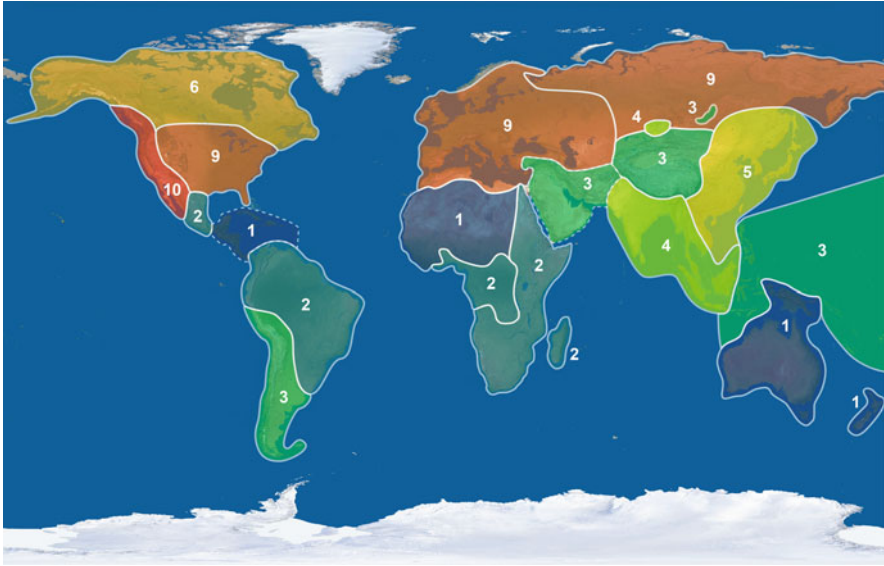


Fig. 8.2 Generic-level global diversity of Lymnaeidae (modified map of Fig. 8.1). Note the latitudinal gradient showing a generally decreasing diversity towards the South. Genera accounted for the respective freshwater zoogeographical regions are listed in Table 8.1

8.2 Speciation Patterns

8.2.1 Large-Scale Patterns

Global distribution patterns of generic biodiversity (Fig. 8.2 and Table 8.1) are also reflected on the species level (Hubendick 1951). Some species occupy very large ranges, some of them constantly extending their distribution anthropogenically, such as *Pseudosuccinea columella* (e.g., Lounnas et al. 2017). In contrast, small range endemics exist, especially in special and extreme habitats (see below). Moreover, the latitudinal biodiversity gradient observed (Fig. 8.2) is also present below the genus level, i.e., the total number of recognized species decreases toward the South (Vinarski et al. 2019). Given their biological characteristics and particularly their dispersal capacity, reproductive mode, and ecological flexibility, it has long been recognized that Lymnaeidae tend to speciate comparatively less often than caenogastropods (e.g., Boss 1978; Strong et al. 2008). In fact, there are no conspicuous species flocks known among the 32 recognized genera (but see below).

A superspecies concept has often been applied for widespread species such as *Radix auricularia* (Hubendick 1951) and *Lymnaea stagnalis* (Vinarski 2015). However, a detailed examination of seemingly widespread lymnaeid species has repeatedly revealed the existence of cryptic species or species complexes. A typical example is the endemic genus *Tibetoradix*, which originally was considered to belong to *Radix* and to be represented by only a single species, namely *Lymnaea*

Table 8.1 Distribution table of the 32 recognized lymnaeid genera across 22 accepted zoogeographical freshwater regions (see Fig. 8.1 and text for details). Note that Madagascar (region 4) includes surrounding archipelagos such as the Mascarene Islands and that the Hawaiian Islands and other Pacific isolated archipelagos are subsumed under Indo-West-Pacific (region 8). The nomenclature largely follows Vinarski et al. (2019), with additions from Vinarski et al. (2020) for radicine taxa

Genus	Zoogeographical freshwater regions																Total regions per genus						
	1a	1b	1c	1d	1e	1f	1g	1h	2a	2b	2c	1-2	3a	3b	3c	4		5a	5b	1-5	6	7	8
<i>Lymnaea</i>	1	1		1	1	1	1		1														7
<i>Acella</i>	1																						1
<i>Aenigmomphiscola</i>			1				1																2
<i>Bakerilymnaea</i>	1	1				1																	3
<i>Bulinnea</i>	1	1																					2
<i>Erimna</i>																						1	1
<i>Galba</i>				1			1				1			1	1		1	1					7
<i>Hinkleyia</i>	1	1				1											?	?					3
<i>Ladislavella</i>	1	1	1		1	1	1	1	1														8
<i>Omphiscola</i>				1																			1
<i>Pseudoisidora</i>																							1
<i>Pseudosuccinea</i>	1		1			1												1	1				5
<i>Sibirigalba</i>							1		1														3
<i>Sphaerogalba</i>	1	1																					2
<i>Stagnicola</i>				1			1	1			1	1											5
<i>Walterigalba</i>	1	1				1																	3
<i>Lanx</i>		1																					1
<i>Fisherola</i>	1	1																					1
<i>Idaholanx</i>	1																						1
<i>Myxas</i>				1																			1
<i>Ampullaceana</i>										1													1

(continued)

Table 8.1 (continued)

Genus	Zoogeographical freshwater regions																Total regions per genus						
	1a	1b	1c	1d	1e	1f	1g	1h	2a	2b	2c	1-2	3a	3b	3c	4		5a	5b	1-5	6	7	8
<i>Austropelea</i>																				1	1		2
<i>Bullastra</i>										1												1	2
<i>Kamchaticana</i>						1																	1
<i>Lantzia</i>															1								1
<i>Linnobulla</i>																1							1
<i>Orientogalba</i>								1		1													2
<i>Pectitidens</i>																1							1
<i>Peregriana</i>			1																				2
<i>Racesina</i>			1							1	1												3
<i>Radix</i>			1	1			1	1	1	1			1	1	1	1							10
<i>Tibetoradix</i>									1														1
Generic diversity	9	10	2	9	4	6	9	3	5	3	4	3	1	2	2	2	3	2	1	1	1	1	3

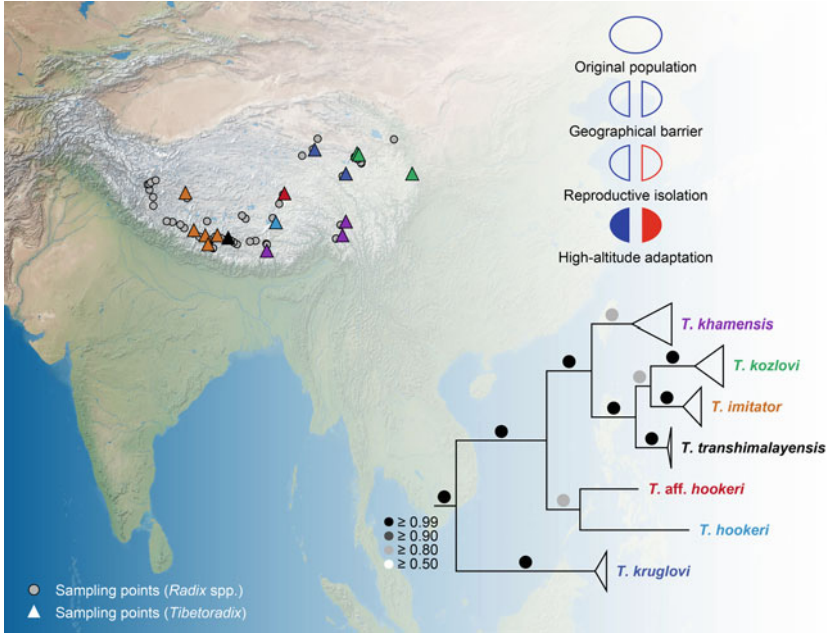


Fig. 8.3 *Tibetoradix* and other lymnaeids on the Tibetan Plateau. The molecular phylogeny (bottom-right) and the respective sampling (triangles in map) were redrawn after Vinarski et al. (2022). The remaining lymnaeid sampling points (gray circles in map) were compiled from the literature (von Oheimb et al. 2011; Clewing et al. 2016). For *Tibetoradix*, a process of allopatric speciation and high-altitude adaptation has been assumed (scheme on top-right), which resulted in a comparatively high number of species that are “trapped” in their environment (see Vinarski et al. 2022 for a discussion)

hookeri. However, new sampling from the Tibetan Plateau resulted in the recurrent number of six known species endemic to the plateau and small adjacent regions (Vinarski et al. 2022). Allopatric speciation, competitive exclusion, and high-altitude adaptation are interpreted for the pattern observed on the Tibetan Plateau (Fig. 8.3). Thereby, competitive exclusion likely prohibits the co-occurrence of several lineages (von Oheimb et al. 2011; Clewing et al. 2016; Vinarski et al. 2022), while adaptation to high altitudes probably reduces the chances of dispersal into lower regions (Vinarski et al. 2022).

Another prime example for misinterpreted widespread species relates to *Galba truncatula*, a species that turned out to hide several congeners, among them *G. schirazensis*, an overlooked species (Bargues et al. 2013) that is even invasive (Lounnas et al. 2018). In Africa, *G. truncatula* has been confused with *G. mweruensis*, a species occurring in high-altitude mountains of eastern and South Africa (Fig. 8.4). According to Mahulu et al. (2019), sub-tropical Africa has been colonized only once in either the Pliocene or possibly as early as the Miocene. From here on, diversification within *G. mweruensis* started finally in the

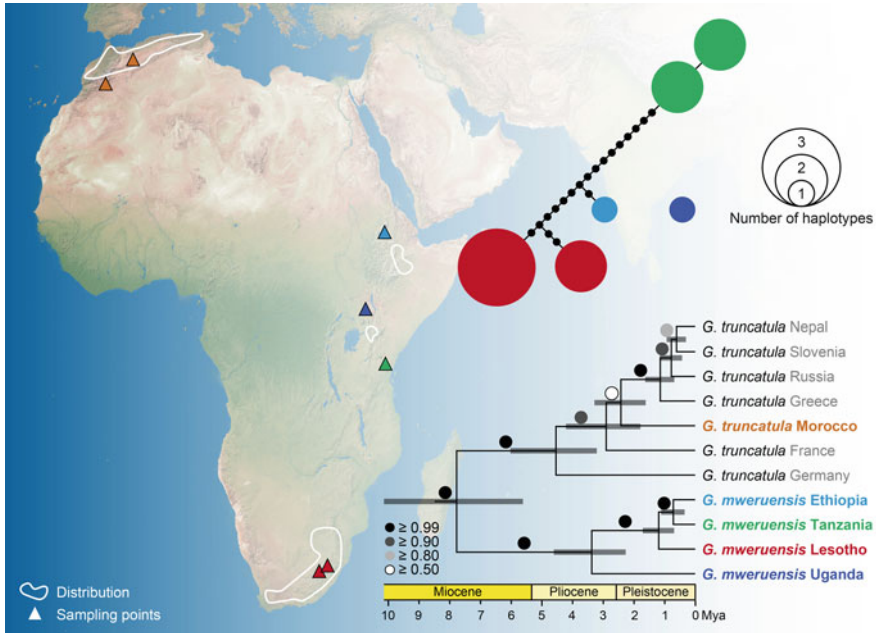


Fig. 8.4 Diversification of *Galba* on the African continent. The time-calibrated molecular phylogeny and the respective sampling (triangles in map) were redrawn after Mahulu et al. (2019). Both the phylogenetic relationships and the haplotype network (top-right) show that all African mountain populations (except those from Morocco) belong to a different species other than *G. truncatula* and that their genetic distinctiveness is probably a result of their Plio-Pleistocene origin

Plio-Pleistocene and is probably ongoing, leading to potentially even more cryptic species in high-altitude areas of Africa as exemplified by the genetic distinctness of the population from Mt. Elgon, Uganda (Fig. 8.4). The widely disjunct populations of *G. mweruensis* are indicative of allopatric speciation. However, it remains unclear whether allopatry or an “evolutionary trap” scenario as proposed for *Tibetoradix* or competitive exclusion by the widespread *Radix natalensis*, which actually represents a species complex (C. Albrecht & C. Clewing, unpubl. data), is responsible for the quite restricted distribution of that species.

Cryptic species have been found in several other lymnaeid genera, namely in *Tibetoradix* (Vinarski et al. 2022) and *Galba* (Bargues et al. 1997, 2013; Standley et al. 2013; Mahulu et al. 2019). Originally, cryptic species were assumed to be less common among Lymnaeidae (Vinarski et al. 2019). However, more recent studies on smaller geographical scales continue to reveal more diversity that is either morphostatic (Schniebs et al. 2013) or obscured by phenotypic plasticity (Vinarski et al. 2020). In a recent comprehensive and geographically large-scale study, American representatives of the genus *Galba* were studied with respect to the presence of cryptic species (Fig. 8.5). It was concluded that morphostatic speciation in widely distributed and genetically diverse populations accounted for at least six cryptic

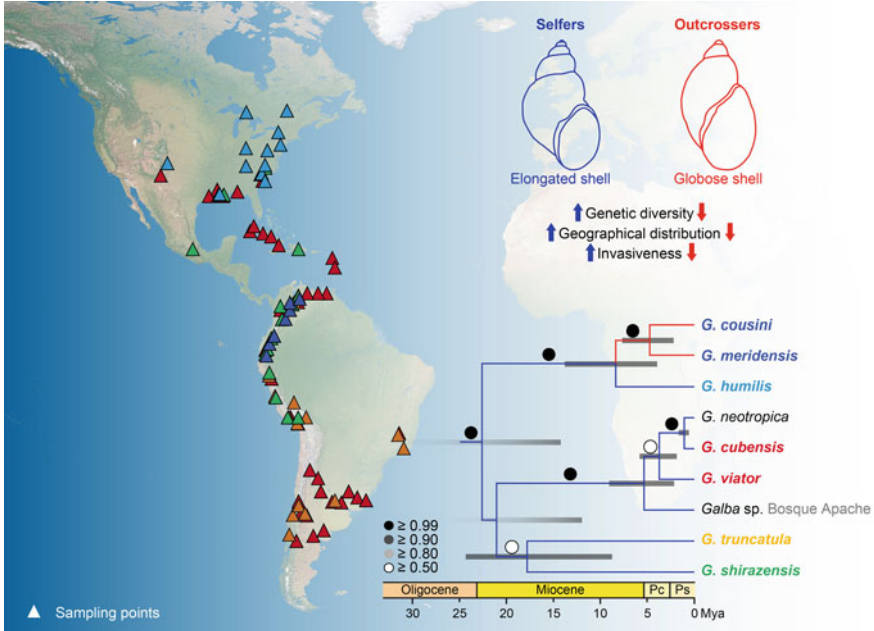


Fig. 8.5 Diversification of *Galba* on the American continent. The time-calibrated molecular phylogeny and the respective sampling (triangles in map) were redrawn after Alda et al. (2021). In selfing lineages (blue branches), shells are elongated, while genetic diversity, geographical distribution, and invasiveness are high (scheme on top-right). In contrast, outcrossing species (red branches) possess a globose shell and are less diverse and invasive and only occupy small ranges

species and that more detailed studies are needed to understand the roles of both ecology and mating system evolution (Alda et al. 2021).

8.2.2 Small-Scale Patterns

Surprisingly, only few studies addressed speciation in lymnaeids directly at smaller scales, i.e., in field studies from natural populations. However, some observational evidence for diversification patterns of sister species or diverging populations within a single species in *Radix* s.l., i.e., encompassing all radicine species, exists from confined areas. Isolated ecosystems, and specifically ancient lakes, can serve here again. Allopatric speciation has often been proposed, but should involve strict geographical barriers, preventing or reducing gene flow considerably (see, e.g., Bolnick and Fitzpatrick 2007).

A study on *Radix* including *R. relicta* and *R. pinteri* from lakes Ohrid and Prespa on the Balkans showed the difficulty in elucidating what (geographical) type of speciation is present in these sister lakes. The two species are geographically

separated by a mountain ridge and, although still closely related, can be distinguished by shell morphology and genetics (Albrecht et al. 2008, but see Vinarski et al. 2020). Here, allopatry is the most likely mode of speciation, which may also act in the lake proper itself, with barriers that are intralacustrine, both vertically and horizontally, and thus difficult to assess. A parapatric speciation process (see Coyne and Orr 2004) is often discussed in the context of ancient lakes (Schön and Martens 2004) and is assumed to occur along ecological or geographical clines or habitat fragmentation settings in Lake Ohrid (discussed in Albrecht and Wilke 2008). However, less clear is the situation within the lake basin, where small peripheral populations in feeder springs led to founder events and strong genetic drift, i.e., peripatric speciation (see Albrecht and Wilke 2008). Regardless of the different modes presented, for the invertebrate fauna of Lake Ohrid (and possibly other ancient lakes), ecological opportunity appears to have been an important factor for the onset of diversification, when suitable lake conditions were reached (Stelbrink et al. 2020).

Lakes have been among the few examples where the highly debated sympatric mode of speciation has been proposed (e.g., Martin et al. 2015; Foote 2018; Richards et al. 2019; Sutra et al. 2019). Lake Lugu in the Chinese province of Yunnan is an interesting example in this context. Here, a species flock of potentially four endemic lymnaeid species experiencing ongoing speciation was proposed (Fig. 8.6). The lake's specific environment gave rise to neritid-like *Radix* shells three times independently (Wiese et al. 2020). However, syntopic occurrence, i.e., living in the same lake, is not synonymous with sympatric speciation (Bolnick and Fitzpatrick 2007). This type of speciation involves hybridization and reproductive barriers within a single, initially randomly mating population (Futuyma 2013). However, such processes have not been studied for any lymnaeid species assemblage and thus render a discussion premature. To date, microallopatry seems more likely responsible for population divergences at the intralacustrine scale. Moreover, either ecophenotypic shell-shape changes or morphostasis makes the detection and delimitation of diversification and speciation events challenging (see discussion on cryptic species above).

8.2.3 *Adaptation in Extreme and Isolated Habitats: The Role of Ecology*

Ecophenotypy in Lymnaeidae has been discussed for decades, and it is undoubted that the immediate environmental conditions of these gastropods play a role in shell size and shape parameters (Vinarski & Pointier, 2023, this book, Chap. 2). However, to what extent such plasticity is manifested through selective forces is less well-known. A look at the adaptations to extreme environments can serve here to identify potential cases, where ecological speciation (see Rundle and Nosil 2005; Nosil 2012) might be involved in species formation. Occurrence in extreme altitudes

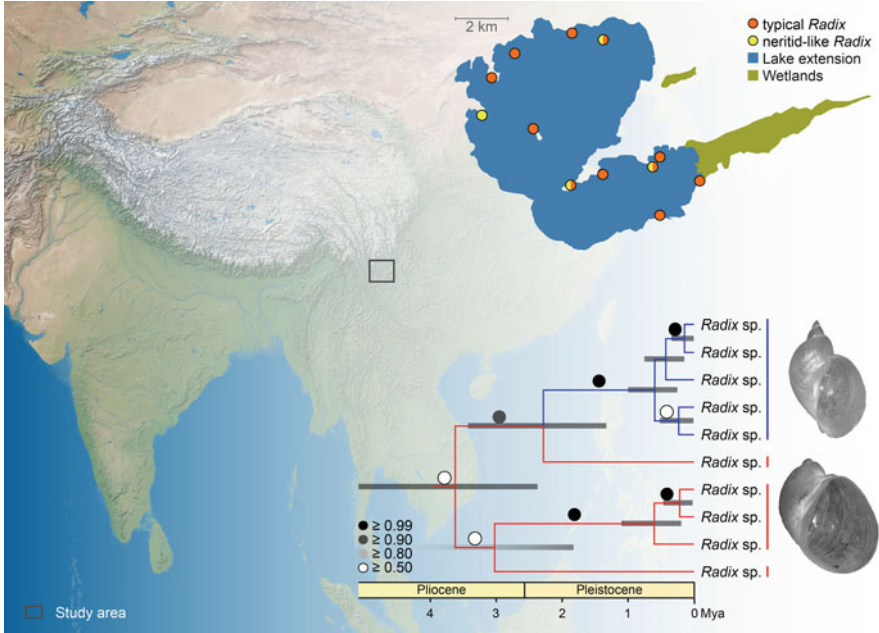


Fig. 8.6 *Radix* diversification in Lake Lugu (Yunnan, China). The time-calibrated molecular phylogeny was redrawn after Wiese et al. (2020). The phylogenetic relationships together with the genetic distances between the lineages suggest that neritid-like forms (lower shell in the phylogeny) evolved at least three times independently (red lineages) together with regular shell forms (blue lineages and upper shell in the phylogeny)

(up to and sometimes above 4000 m a.s.l.) have been reported for several *Galba* species across the Altiplano in South America (e.g., Alda et al. 2021) and for *G. mweruensis* in Afro-montane regions (Mahulu et al. 2019). Although high-altitude freshwater habitats provided unexplored niches, adaptations to these harsh conditions (freezing over extended periods of time, scarcity of food, etc.) are hypothesized to have led to “evolutionary dead ends” for the high-mountain fauna (Vinarski et al. 2022). On the other hand, such extreme habitats may also have acted as evolutionary reservoirs during severe environmental conditions. Populations of *Radix* from the Lake Donggi Cona drainage system (north-eastern Tibetan Plateau) were examined in order to study the impact of glaciation-related changes on the demographic history of this group (Clewing et al. 2016). Phylogenetic, phylogeographical, and demographic analyses suggested that not only a single refugium was present but also that isolated sub-refugia in and outside the lake proper existed and provided suitable habitats for ancestral *Radix* populations during the Last Glacial Maximum (Fig. 8.7).

Ancient lakes are known to host an extraordinary range of biodiversity and endemics (e.g., Brooks 1950; Martens 1997; Albrecht et al. 2020). Lymnaeidae are only showing moderate endemism in such lakes, which is apparently restricted to

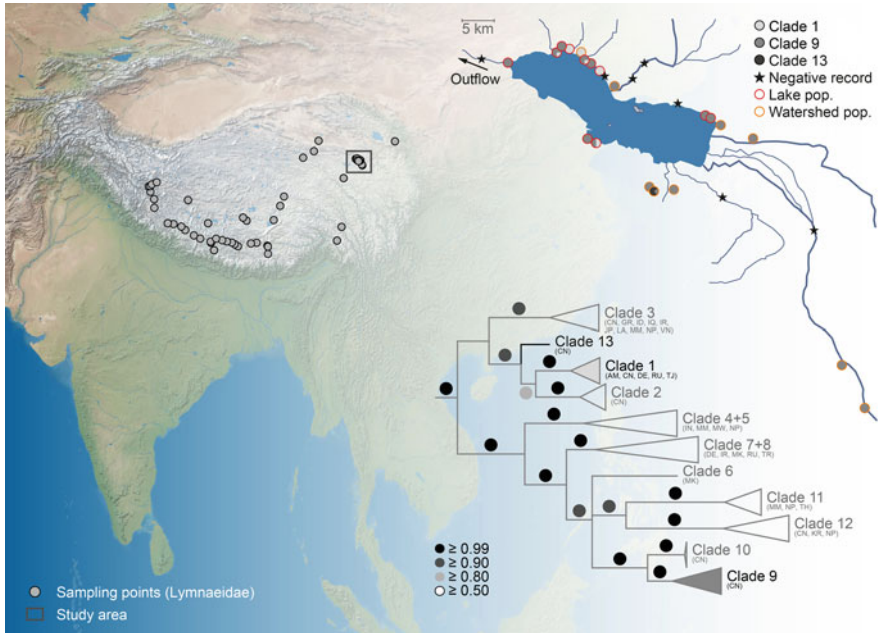


Fig. 8.7 Radicine lymnaeids on the eastern Tibetan Plateau. The molecular phylogeny and the Lake Donggi Cona and watershed sampling were adopted from Clewing et al. (2016). The remaining lymnaeid sampling points (grey circles in map) were compiled from the literature (von Oheimb et al. 2011; Clewing et al. 2016). The occurrence of genetically distinct lineages suggests the presence of sub-refugia during the Last Glacial Maximum that served as suitable habitats for ancestral populations

the radicine clade *Radix* s.l. (Vinarski et al. 2017, but see Neubauer, 2023, this book). A key ecological feature is the adaptation to sublittoral and even profundal habitats in these often very deep lakes. An impressive example is *Radix relicta* (Polinski, 1929) that occurs in depths up to 30 m owing to special physiological modifications related to respiration and tissue vascularization (Kaiser 1959; see Albrecht et al. 2008). Similar to isolated insular-like ecosystems such as ancient lakes, true islands sometimes host endemic forms of Lymnaeidae that are distinguished on the genus level, for example *Pseudisidora* and *Erinna* from the Hawaiian Islands. Species of these genera are only scarcely explored, and in addition, potentially cryptic forms exist (Christensen et al. 2021). These lymnaeids live in special habitats such as waterfalls and seeps, a situation also existent at La Reunion Island in the Indian Ocean, where a single limpet-shaped species, *Lantzia carinata*, is known only from very few waterfalls. Although these island taxa have not yet been included in lymnaeid phylogenetic studies, convergent evolution has potentially led to the limpet or neritid-like shell forms in the particular environment these gastropods are confined to.

Another factor presumably driving ecological speciation in lymnaeids is temperature. Here, both cold and warm-stenotherm forms have been described (von Oheimb et al. 2016; Vinarski et al. 2021), and in some cases, a closer examination revealed that supposedly endemic forms are rather ecotypes of widespread species (Vinarski et al. 2017; Vinarski et al. 2020).

8.3 Speciation Processes

Given the patterns observed at different geographical, temporal, and taxonomic scales, the actual underlying processes leading to the morphospace disparity and generally to diversification in Lymnaeidae should also be discussed. Following the mechanisms of initial divergence proposed by Schluter (2001), all four suggested categories can be discussed for the Lymnaeidae. (1) Polyploid speciation due to chromosomal rearrangements does not play a major role, unlike in other Hygrophila, especially the Planorbidae and Bulinidae (see Albrecht et al. 2019a, 2019b). In Lymnaeidae, chromosome numbers are rather uniform and range from the plesiomorphic haploid $N = 18$ to $N = 16$ and $N = 17$ in derived clades (Inaba 1969; Correa et al. 2010). To what extent hybridization is involved in species formation in Lymnaeidae is currently not well understood. (2) Speciation by genetic drift requires effective long-time isolation and dispersal barriers to allow for drift-based speciation in allopatry. Whereas long-term isolation is very plausible in insular systems as described above, it is more difficult to assume dispersal limitations given the colonization potential of most lymnaeids (Hubendick 1951). (3) Maybe more likely is ecological speciation due to adaptations to different selective regimes. This idea has been proposed earlier for lymnaeid taxa (Pfenninger et al. 2006) and is now supported by a recent study, which suggests that niche conservatism and varying climatic conditions (mainly temperature) most likely act as different selective regimes to *Radix* lineages (Saito et al. 2021). (4) Another category encompasses cases where differential adaptation to a similar selective regime occurs (divergence under uniform selection). However, such an initial cause of speciation is not easy to prove and might not be very common among lymnaeids.

Despite environmental factors driving speciation, biotic interactions can also lead to adaptations and even co-evolution. The best-studied system in this context is the interaction of lymnaeid intermediate hosts with trematode parasites (see, e.g., Vázquez et al. 2023 this book). More and more genomic approaches help to disentangle host–parasite relationships on the organismic level through simultaneous genotyping of gastropods and infecting trematode parasites using high-throughput amplicon sequencing (Hammoud et al. 2021). Moreover, the immunobiological interplay between gastropod and parasite (Alba et al. 2019, 2020) are starting to be understood on the molecular level (Juhász and Lawton 2022). Here, transcriptomes of the model species *Lymnaea stagnalis* revealed highly varying factors that may be the key determinants of differences in parasite resistance among individuals both within and between natural host populations (Seppälä et al. 2021).

The steadily growing number of mitogenomes, (annotated) genomes, and transcriptomes of lymnaeid species (e.g., Feldmeyer et al. 2010; Tills et al. 2015; Schell et al. 2017; Qin et al. 2019) will revolutionize our abilities to study genetic mechanisms involved in important life-history traits such as developmental time, age and size at maturity, chirality (Kuroda and Abe 2020; Davison and Neiman 2021), and even reproductive systems as a whole. For example, left–right asymmetry has been extensively studied (Davison 2020), but mainly in *L. stagnalis* (e.g., Davison et al. 2016; Kuroda et al. 2016). Chirality is a topic of general interest in developmental biology and has implications to speciation (Abe and Kuroda 2019). A debate around chirality-determining single genes in *L. stagnalis* has arisen, suggesting that chirality is maternally inherited by the actin-related gene *Lsdial* (Kuroda and Abe 2020). To what extent this is directly related to speciation remains a question, with a “single-gene speciation”—though possible in theory—considered unlikely (Davison 2020). Other developmental traits relate to the reproductive system and the mode of reproduction. The evolution of hermaphroditism and its consequences for sexual selection is of particular interest here. Most recently, sexual selection has been shown to exist in *L. stagnalis*, something that used to be considered less important in hermaphroditic animals (Fodor et al. 2020). Moreover, selfing or outcrossing as the predominant mode of hermaphroditic reproduction has been supposed to be a key factor in diversification of American *Galba* (e.g., Alda et al. 2021; Fig. 8.5).

Radix balthica (= *Ampullaceana balthica*) emerges as a new model system to study developmental plasticity of functional traits that are partly genetically based (Tills et al. 2013a, 2013b). The relative importance of genetic drift vs. selective processes during the embryonic development can now be evaluated on the transcriptome level for both juvenile (Tills et al. 2015) and adult stages (Feldmeyer et al. 2011). Given the fast progress in the “omics” era, that is not reflected yet in mollusc and specifically gastropod studies (see Klein et al. 2019; Gomes-dos-Santos et al. 2020; Yang et al. 2020), very few studies have set such datasets in a specific speciation framework studying life-history traits directly related to fitness. An exception is the study by Feldmeyer et al. (2015) on European *Radix*, showing that species divergence is driven by positive selection on life-history traits such as development and growth-rate regulated genes, which are thought to be advantageous under contemporary climates with distinct climate niches occupied by the different species. Preadaptation to persisting climate regimes is also thought to be a key component in the invasion success of alien species. The North American *Pseudosuccinea columella* is a self-fertilizing global invader, in which new genotypes are found in many of the colonized regions, despite an otherwise very low genetic variability (Lounnas et al. 2017). Such cases provide ideal models for studying potentially rapid speciation in its initial stages (Fig. 8.8).

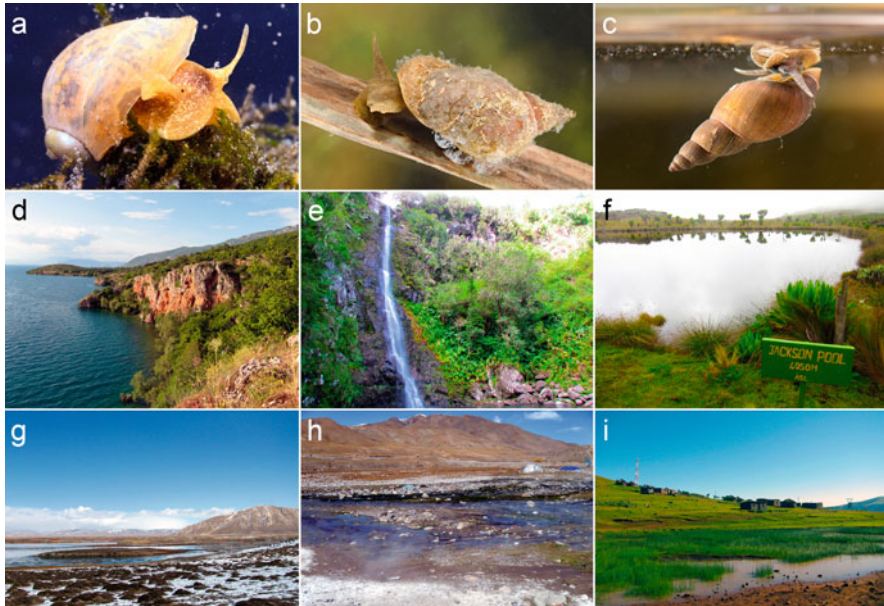


Fig. 8.8 Examples of live specimens of Lymnaeidae and selected extreme and isolated habitats. (a) *Radix relicta*, Lake Ohrid, North Macedonia; (b) *Lymnaea stagnalis*; (c) *Stagnicola* sp.; (d) Ancient Lake Ohrid, North Macedonia and Albania; (e) Cascade Maniquet, La Réunion, type locality of *Lantzia carinata*; (f) Jackson Pool on Mt. Elgon Uganda, highest known occurrence of *Galba mweruensis*; (g) High-altitude habitat at Lake Donggi Cona (Tibetan Plateau); (h) Hot spring on the eastern Tibetan Plateau where radicine specimens were found; (i) Wetland in the highlands of Lesotho, habitat of *Galba mweruensis*. Photo credit (Christian Albrecht: d, e, i; Catharina Clewing: g; Daniel Engelhard: f; Jan Hamrsky: b, c; Parm Viktor von Oheimb: h; Thomas Wilke: a)

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