Chapter 4
Intermediate Hosts of *Fascioloides magna*

Abstract The complexity of the life cycle of *Fascioloides magna* and its ability to invade new region is ensured by the presence of suitable intermediate hosts, in particular aquatic pulmonate mollusks, in which larval development of the parasite takes place. This Chapter summarizes intermediate snail hosts of giant liver fluke specific in North America and Europe. In North America, six species of the family Lymnaeidae were found to be naturally infected with *F. magna* (*Lymnaea caperata*, *Lymnaea modicella*, *Stagnicola palustris nuttalliana*, *Pseudosuccinea columella*, *Galba bulimoides techella* and *Fossaria parva*). In Europe, *Galba* (syn. *Lymnaea*) *truncatula*, *Radix labiata* and *Radix peregra* were found to be naturally infected. Besides natural infections, number of snail species were experimentally infected with *F. magna* in order to determine their potential to serve as the intermediate hosts of giant liver fluke. The mature cercariae able to develop into infective metacercariae stages, were detected in snails of the genera *Lymnaea* and *Pseudosuccinea* (family Lymnaeidae) in North America and in lymnaeid genera *Galba*, *Lymnaea*, *Omphiscola, Pseudosuccinea* and *Stagnicola* in Europe. It is evident, that broader spectrum of aquatic mollusks is susceptible to *F. magna* infection and may serve as its potential intermediate hosts.

Keywords Giant liver fluke · Intermediate hosts · Freshwater snail · Lymnaeidae · *Lymnaea* · *Galba* · *Radix* · Experimental infection · Natural infection

4.1 General Characterization of Intermediate Snail Hosts

The complex life cycle of *F. magna* requires suitable intermediate hosts, pulmonate freshwater gastropod mollusks, in which larval development of the parasite takes place (see Sect. 1.3; Fig. 1.2). In North America and Europe, specific spectrum of snail species of the family Lymnaeidae was detected to be naturally infected with *F. magna* (see Tables 4.1, 4.2 and references therein).

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Table 4.1 Spectrum of naturally infected intermediate snail hosts (Lymnaeidae) with *F. magna* in North America

Snail species	CA province US state	Enzootic region	References
Lymnaea caperata	USA/Minnesota	GLR	Griffiths (1959)
	USA/Minnesota	GLR	Laursen and Stromberg (1993)
	USA/Montana	RMT	Knapp et al. (1992)
Lymnaea modicella	USA/n.i.	n.i.	Krull (1933, 1934) c.i. Swales (1935)
	USA/Minnesota	GLR	Laursen and Stromberg (1993)
Stagnicola palustris nuttalliana	USA/Montana	RMT	Swales (1935)
Pseudosuccinea columella	USA/Montana	RMT	Krull (1933, 1934) c.i. Swales (1935)
Galba bulimoides techella	USA/Texas	SAS	Sinitsin (1930) c.i. Swales (1935)
Fossaria parva	CA/Alberta	RMT	Swales (1935)

CA Canada, *US* United States, *GLR* Great Lakes region, *RMT* Rocky Mountain trench, *SAS* Gulf coast, lower Mississippi, and southern Atlantic seaboard, *n.i.* not indicated in the respective literature, *c.i.* cited in

Table 4.2 Spectrum of naturally infected intermediate snail hosts (Lymnaeidae) with *F. magna* in Europe

Snail species	Country	Natural focus	References
Galba (syn. *Lymnaea*) *truncatula*	Czech Republic	CZ-PL	Erhardová (1961)
	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
	Czech Republic	CZ-PL	Chroust and Chroustová (2004)
	Czech Republic	CZ-PL	Faltýnková et al. (2006)
	Czech Republic	CZ-PL	Kašný et al. (2012)
	Czech Republic	CZ-PL	Leontovyč et al. (2014)
	Austria	DFF	Hörweg et al. (2011)
	Austria	DFF	Haider et al. (2012)
	Slovakia	DFF	Rajský et al. (1996)
	Hungary	DFF	Majoros and Sztojkov (1994)
Radix labiata	Czech Republic	CZ-PL	Leontovyč et al. (2014)
Radix peregra	Czech Republic	CZ-PL	Faltýnková et al. (2006)

CZ-PL Czech Republic and southwestern Poland, *DFF* Danube floodplain forests

Taxonomic classification and systematics of the family Lymnaeidae, and snails in general, is rather complicated and underwent several revisions. As generally accepted in current modern taxonomy and systematics, the most effective strategy for an accurate classification of the species is traditional alfa-taxonomy based on morphological descriptions with the combination of DNA-based methods. The

morphology of reproductive system and shell morphometry are crucial markers for identification of snails; however, they are not generally applicable markers for all taxa (e.g. shell morphology is not suitable for delimitation of species of the genus *Radix*; Pfenninger et al. 2006). Therefore, molecular tools, in particular internal transcribed spacer 2 of the ribosomal DNA (ITS2 rDNA), were applied in the family Lymnaeidae as effective marker of molecular taxonomy (Mas-Coma et al. 2009; Huňová et al. 2012; Leontovyč et al. 2014).

Recently, many snail species have underwent taxonomic revisions (e.g. *Stagnicola palustris* and *Omphiscola glabra* were transferred to the genus *Lymnaea*; Correa et al. 2010; Novobilský et al. 2012); different scientific names of some snail species were simultaneously used by several authors. We summarized the data on naturally and experimentally infected intermediate snail hosts of *F. magna* indicating the original scientific name of the snail, as provided in the reference literature.

Apart from natural infections, several attempts to infect different mollusks under experimental conditions were performed by researchers on both continents. Sporocysts, mother rediae and daughter rediae represent non-infectious larval intramolluscan stages. On the other hand, mature cercariae released from snails are able to encyst in exogenous environment on aquatic vegetation, and may develop to metacercariae, the stage infective for final host. Therefore, full development of *F. magna* intramolluscan stages and production of mature cercariae were the main criteria for an assessment of the potential of snail species to serve as an intermediate host.

The successful infection of intermediate host by *F. magna* depends mainly on the susceptibility of selected snail, the infectivity of miracidia (Smyth and Halton 1983), and favourable environmental, ecological and physical factors (e.g. temperature, humidity etc.) (Rapsch et al. 2008). The optimal temperature range for infections is 15–30 °C, when a sufficiently moist environment assists the development of the first larval stage, miracidium. Changes in temperature and moisture may also considerably influence the complete embryonation process during summer field conditions (Pybus 2001). Besides suitable hydrological conditions may determine the population density of intermediate hosts (Rajský et al. 2002).

One of the key factors influencing susceptibility of snail is epidermal mucus covering the surface of snail host. It may serve as an important barrier for an attempt of *F. magna* miracidium to penetrate into snails. *Fascioloides magna*-incompatible snails possess a potent cytotoxic protein-like factor in the mucus, which is absent in *F. magna*-compatible snails. This factor could play a significant role in mediating larval trematode-snail compatibility (Coyne et al. 2015).

4.2 Natural Infections

North America Different larval stages of giant liver fluke were found in six snail species of the family Lymnaeidae, in particular *Lymnaea caperata*, *L. modicella*, *Stagnicola palustris nuttalliana*, *Pseudosuccinea columella*, *Galba bulimoides*

techella and *Fossaria parva* in three enzootic regions (GLR, RMT and SAS) (see Table 4.1 and references therein). In natural conditions, co-existence of different snail species susceptible to *F. magna* can significantly increase the risk of infection and its further spread to final hosts. For example in Alberta (RMT), the Canadian province with one of the highest prevalence of fascioloidosis in free-living ruminants, four species of lymnaeid snails are known to be suitable intermediate hosts for *F. magna* either in natural or in experimental conditions (Kennedy et al. 1999).

Europe Comparing with North America, lower number of intermediate snail hosts has been detected in Europe (Table 4.2). The most frequent and the only confirmed intermediate host is air-breathing freshwater snail *Galba* (syn. *Lymnaea) truncatula* (Fig. 4.1), in which the larval development of the parasite can be completed. *Galba truncatula* was proved to produce mature cercariae and can significantly contribute to successful transmission of infective stages to final hosts (Erhardová-Kotrlá 1971). The snail requires a moderate climate and moisture for its survival and reproduction. *Galba truncatula* is dominant intermediate host of *F. magna* in Europe, what is probably closely related to the adaptation of this snail species to a wide range of ecological conditions and biotops (running waters, backwater systems, river banks, ponds, marsh areas, flooded meadows etc.) (Hörweg et al. 2011; Haider et al. 2012).

Natural infections of *G. truncatula* with *F. magna* were mainly detected in the Czech Republic (Erhardová 1961; Erhardová-Kotrlá 1971; Chroust and Chroustová 2004; Faltýnková et al. 2006; Kašný et al. 2012; Leontovyč et al. 2014), also reported in Danube floodplain forests, including Slovakia (Rajský et al. 1996), Hungary (Majoros and Sztojkov 1994) and Austria (Hörweg et al. 2011; Haider et al. 2012). The mean prevalence of fascioloidosis in *G. truncatula* varied from 0.03–0.23 % in Austria (Hörweg et al. 2011; Haider et al. 2012) up to 30–60 % in Czech Republic (Faltýnková et al. 2006; Kašný et al. 2012; Leontovyč et al. 2014). It is interesting that in Austria, almost 8-fold increase of infection rate in

Fig. 4.1 *Galba* (syn. *Lymnaea*) *truncatula* from Danube floodplain forests, Slovakia (*Photo* M. Špakulová)

G. truncatula was observed despite an ongoing triclabendazole treatment programme of final hosts (Haider et al. 2012).

Galba truncatula was considered to be the only intermediate host of *F. magna* in Europe for a long time (Erhardová-Kotrlá 1971), until Faltýnková et al. (2006) described naturally infected *R. peregra* in Czech Republic (prevalence 0.08 %). Despite the fact, that *R. peregra* is dominant snail species over *G. truncatula* in Czech Republic, *R. peregra* can produce only immature cercariae of *F. magna* (Erhardová-Kotrlá 1971; Faltýnková et al. 2006).

Radix labiata is another species, in which natural infection of *F. magna* was detected (Leontovyč et al. 2014). Similarly to *R. peregra*, also *R. labiata* produced cercariae unable to encyst. However, *R. labiata* might represent a potential intermediate host of *F. magna* in localities ecologically unsuitable for *G. truncatula* (e.g. localities with acid soils) (Leontovyč et al. 2014). The determination of natural infections of *F. magna* in other snail hosts in Europe indicates that the parasite undergoes a process of adaptation to other mollusks (Faltýnková et al. 2006). There is a threat that a broader spectrum of competent intermediate hosts will be detected in the future.

4.3 Experimental Infections

Experimental *F. magna* infections of different snail species were primarily focused on determination of (i) susceptibility of snails to be infected with *F. magna* miracidia; (ii) development of larval stages (sporocysts and rediae) of the parasite within the infected snail hosts; (iii) the potential of snails to produce mature cercariae able to develop into metacercariae (Foreyt and Todd 1978; Sanabria et al. 2013).

North America A spectrum of experimentally infected snails of families Lymnaeidae and Planorbidae is summarized in Table 4.3. Out of 12 tested species, cercariae and infective stages (metacercariae) were detected in seven lymnaeids; *Lymnaea bulimoides*, *Lymnaea caperata*, *Lymnaea humilis*, *Lymnaea palustris*, *Lymnaea stagnalis*, *Lymnaea umbrosa* and *Pseudosuccinea columella* (see Table 4.3 and references therein). In North America, namely *L. caperata* and *P. columella* represent intermediate hosts with previously determined natural *F. magna* infection (Krull 1933, 1934 c.i. Swales 1935; Griffiths 1959; Knapp et al. 1992; Laursen and Stromberg 1993), so they ability to produce infective stages in experimental conditions was anticipated. The remaining five mollusks represent very probably intermediate hosts with a potential to be infected also naturally. Production of rediae was determined but further development into cercariae and metacercariae was not detected in *Ferrissia fragilis*, the only experimentally infected snail of the family Planorbidae (Flowers 1996). The development and production of infective stages in four remaining lymnaeids (*Fossaria modicella rustica*, *Lymnaea ferruginea*, *Lymnaea modicella* and *Stagnicola palustris*) were

Table 4.3 Spectrum of experimentally infected intermediate snail hosts (Lymnaeidae and Planorbidae*) with *F. magna* in North America

Snail species	Detected stage of parasite	Infective stage	US state	Enzootic region	References
Lymnaea bulimoides	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
Lymnaea caperata	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
	n.i.	n.i.	Montana	RMT	Dunkel et al. (1996)
Lymnaea humilis	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
Lymnaea palustris	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
Lymnaea stagnalis	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
	Cercariae	n.i.	Minnesota	GLR	Wu and Kingscote (1954)
	Cercariae	n.i.	Minnesota	GLR	Griffiths (1973)
	Rediae	n.i.	Minnesota	GLR	Friedl (1961)
Lymnaea umbrosa	Metacercariae	yes	Wisconsin	GLR	Foreyt and Todd (1978)
Pseudosuccinea columella	Metacercariae	yes	North Carolina	SAS	Flowers (1996)
	n.i.	n.i.	USA/n.i.	n.i.	Krull (1933) c.i. Swales (1935)
*Ferrissia fragilis**	Rediae	no	North Carolina	SAS	Flowers (1996)
Fossaria modicella rustica	n.i.	n.i.	USA/n.i.	n.i.	Krull (1933) c.i. Swales (1935)
Lymnaea ferruginea	n.i.	n.i.	Oregon	NPC	Dutson et al. (1967)
	n.i.	n.i.	Washington	NPC	Dutson et al. (1967)
Lymnaea modicella	n.i.	n.i.	n.i.	n.i.	Krull (1934) c.i. Swales (1935)
Stagnicola palustris	n.i.	n.i.	Minnesota	GLR	Griffiths (1962)

GLR Great Lakes region, *RMT* Rocky Mountain trench, *SAS* Gulf coast, lower Mississippi, and southern Atlantic seaboard, *NPC* northern Pacific coast, *n.i.* not indicated in the respective literature, *c.i.* cited in

either not determined during the experimental infections, or not indicated in the respective literature (see Table 4.3 and references therein).

Europe Adaptation of *F. magna* to different spectrum of intermediate snail hosts in European natural conditions has been one of the crucial factors for successful establishment of natural foci of giant liver fluke outside North America. Experimental infections, focused on detection of susceptibility of various snail species to *F. magna* infection and determination of a spectrum of potential intermediate hosts of *F. magna*, were carried out mainly by the Czech researchers (Erhardová 1961; Erhardová-Kotrlá 1971; Chroustová 1979; Faltýnková et al. 2006; Novobilský et al. 2007, 2012; Huňová et al. 2012), or under international cooperation with Czech parasitologists (Vignoles et al. 2006, 2014; Rondelaud et al. 2006, 2014; Sanabria et al. 2013).

Spectrum of experimentally infected intermediate snail hosts in Europe is summarized in Table 4.4. Despite the fact that development of *F. magna* in snail species other than *Galba* (syn. *Lymnaea*) *truncatula* is much slower (Erhardová 1961) and the prepatent period is longer (Swales 1935; Erhardová-Kotrlá 1971; Rondelaud et al. 2006), infective stages of mature cercariae were developed in several experimentally tested snails. The majority of experimental infections were carried out using *G. truncatula* (Erhardová 1961; Erhardová-Kotrlá 1971; Faltýnková et al. 2006; Vignoles et al. 2006, 2014; Novobilský et al. 2007; Rondelaud et al. 2006, 2014; Sanabria et al. 2013). The experiments confirmed completion of larval development and production of infective stages in this most frequent naturally infected mollusk in Europe. Mature cercariae/metacercariae were detected also after experimental infection of several other species of family Lymnaeidae, in particular *Lymnaea fuscus* (Novobilský et al. 2012), *Lymnaea palustris* (Chroustová 1979), *Omphiscola glabra* (Rondelaud et al. 2006), *Pseudosuccinea columella* (Novobilský et al. 2007), *Stagnicolla palustris* (Chroustová 1979) and *Radix peregra* (Faltýnková et al. 2006).

In some experimental infections, *G. truncatula*, *L. fuscus*, *O. glabra* and *R. peregra* snails originated from France (or Sweden), while *F. magna* eggs were obtained from Czech Republic (see Table 4.4 and references therein). It was assumed, that allopatry/sympatry of snails and *F. magna* miracidia might influence the larval development of the parasite during the experimental infection and modify the intensity of infection and production of cercariae.

Indeed, the larval development of giant liver fluke was more intense, when both, *G. truncatula* and eggs/miracidia of *F. magna* originated from the Czech Republic (Erhardová-Kotrlá 1971). In contrast, *G. truncatula* from France experimentally infected with eggs/miracidia from Czech Republic showed lower or even absent production of cercariae (Rondelaud et al. 2006).

Development of *F. magna* into non-infective stage of sporocysts (mother and daughter rediae, young cercariae) was determined in lymnaeid species of genera *Lymnaea* (*L. peregra ovata*, *L. peregra peregra* and *L. stagnalis*) and *Radix* (*R. lagotis*, *R. labiata*, *R. peregra peregra* and *R. peregra ovata*) (Erhardová 1961; Erhardová-Kotrlá 1971; Faltýnková et al. 2006; Huňová et al. 2012). Since mature cercariae were not produced by these snail species, they would probably not

Table 4.4 Spectrum of experimentally infected intermediate snail hosts (Lymnaeidae, Physidae* and Succinidae$^{\Delta}$) with *F. magna* in Europe

Snail species	Detected stage of parasite	Infective stage	Country	Enzootic region	References
Galba (syn. *Lymnaea*) *truncatula*	Cercariae, metacercariae	yes	Czech Republic	CZ-PL	Erhardová (1961)
	Metacercariae	yes	Czech Republic	CZ-PL	Novobilský et al. (2007)
	Cercariae, metacercariae	yes	France/CZ[a]	n.r.	Vignoles et al. (2006)
	Cercariae, metacercariae	yes	France/CZ[a]	n.r.	Rondelaud et al. (2006)
	Cercariae, metacercariae	yes	France/CZ[a]	n.r.	Vignoles et al. (2014)
	Cercariae, metacercariae	yes	France/CZ[a]	n.r.	Sanabria et al. (2013)
	Rediae, cercariae	n.i.	France/CZ[a]	n.r.	Rondelaud et al. (2014)
	Rediae, cercariae	no	Czech Republic	CZ-PL	Faltýnková et al. (2006)
	Rediae, cercariae	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
Lymnaea fuscus	Cercariae, metacercariae	yes	France/Sweden/CZ[b]	n.r.	Novobilský et al. (2012)
Lymnaea palustris	Cercariae, metacercariae	yes	Czech Republic	CZ-PL	Chroustová (1979)
	n.i.	n.i.	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
Omphiscola glabra	Cercariae, metacercariae	yes	France/CZ[a]	n.r.	Rondelaud et al. (2006)
Pseudosuccinea columella	Metacercariae	yes	Czech Republic	CZ-PL	Novobilský et al. (2007)
Stagnicola palustris	Encysting cercariae, metacercariae	yes	Czech Republic	CZ-PL	Chroustová (1979)
Radix peregra	Mother and daughter rediae, mature cercariae	no	France/CZ[c]	n.r.	Faltýnková et al. (2006)
	n.i.	n.i.	Czech Republic	CZ-PL	Huňová et al. (2012)
Lymnaea peregra ovata	Mother rediae	no	Czech Republic	CZ-PL	Erhardová (1961)
Lymnaea peregra peregra	Mother rediae	no	Czech Republic	CZ-PL	Erhardová (1961)
Lymnaea stagnalis	Sporocysts	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
	n.i.	no	Czech Republic	CZ-PL	Faltýnková et al. (2006)

(continued)

Table 4.4 (continued)

Snail species	Detected stage of parasite	Infective stage	Country	Enzootic region	References
Radix lagotis	Rediae	no	Czech Republic	CZ-PL	Huňová et al. (2012)
Radix labiata	Rediae, young cercariae	no	Czech Republic	CZ-PL	Huňová et al. (2012)
Radix peregra peregra	Mother rediae	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
Radix peregra ovata	Sporocysts, mother rediae	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
*Physa acuta**	n.i.	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
Succinea oblonga$^{\Delta}$	n.i.	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)
Succinea putris$^{\Delta}$	n.i.	no	Czech Republic	CZ-PL	Erhardová-Kotrlá (1971)

CZ-PL Czech Republic and southwestern Poland, *CZ* Czech Republic, *n.i.* not indicated in the respective literature, *n.r.* not relevant
[a]eggs/miracidia of *F. magna* originated from Czech Republic and snails from France
[b]eggs/miracidia of *F. magna* originated from Czech Republic and snails from France and Sweden,
[c]eggs/miracidia of *F. magna* originated from Czech Republic and snails from France and Czech Republic

contribute to completion of the life cycle of *F. magna* in natural conditions. The findings on experimental infections in *R. labiata* and *R. peregra* (Erhardová-Kotrlá 1971; Huňová et al. 2012) corroborate data on natural infections in these snail species (Faltýnková et al. 2006; Leontovyč et al. 2014).

Besides family Lymnaeidae, experimental infections were carried out also in species of the families Physidae (*Physa acuta*) and Succinidae (*Succinea oblonga* and *S. putris*) (Erhardová-Kotrlá 1971). However, their potential to serve as intermediate hosts of *F. magna* in Europe was excluded, since miracidia of *F. magna* did not enter these snails. In conclusion, the only declared or potential hosts of giant liver fluke in Europe are species of the family Lymnaeidae.

Experimental infections revealed also very interesting phenomena, such as "age-related resistance" and "parasitic gigantism". The first one was observed in *L. fuscus* infection, when only juvenile snails (measuring less than 3 mm; 1–3 weeks of age) were successfully infected with *F. magna* and produced viable cercariae (Novobilský et al. 2012). Success of *F. magna* infection decreased with age of a snail, as documented by increased shell height. Age-related resistence is probably associated with the progressive development of snails' immune system (Novobilský et al. 2012). "Parasitic gigantism" is explained as intensive growth stimulation of snails during redial and cercarial development (Thompson 1997). This general phenomenom was observed also for *F. magna* infections (Vignoles et al. 2006); contrary, reduced snail growth was detected in *L. fuscus* infected with *F. magna* (Novobilský et al. 2012).

4.4 Intermediate Snail Hosts in Other Continents

Apart from North America and Europe, experimental infections were performed also in snails of family Lymnaeidae from South America (Fig. 4.2). In all these experiments, eggs/miracidia of *F. magna* originated from Czech Republic. The relatively high prevalence of infection of two South American snails, *Lymnaea neotropica* (57.4 %; Argentina) and *Lymnaea viatrix* var. *ventricosa* (45.9 %; Uruguay), and successful development of *F. magna* cercariae and metacercariae in these mollusks indicated, that *F. magna* has the high potential to spread to new territories and adapt to local snail species (Sanabria et al. 2013). Similarly, *Lymnaea cubensis* (Guadeloupe) was able to sustain complete larval development of the parasite (prevalence 28 %), including the shedding of cercariae under experimental conditions (Vignoles et al. 2014). All three South American lymnaeids, as well as *Austropeplea (Lymnaea) tomentosa* in Australia (Foreyt and Todd 1974) can be potential new intermediate hosts of *F. magna*, even though the fascioloidosis has not been recorded in these countries (Sanabria et al. 2013).

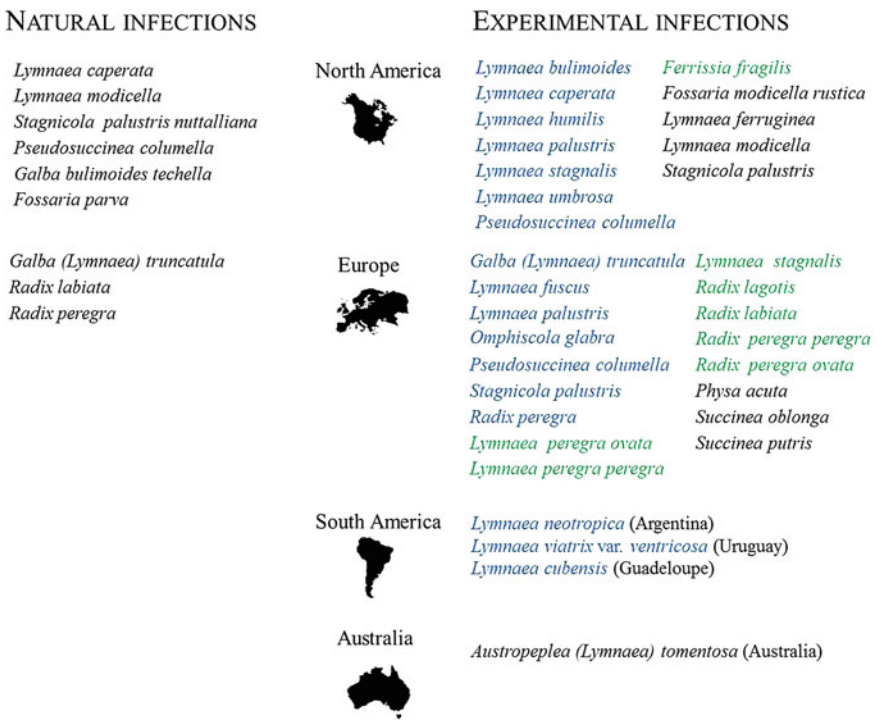

Fig. 4.2 The worldwide spectrum of naturally and experimentally infected intermediate snail hosts of *F. magna*. Experimental infections: *in blue* snails with developed mature cercariae or infective stages metacercariae; *in green* snails with developed non-infective larval stages (sporocysts, mother and daughter rediae, immature or young cercariae); *in black* production of infective stages either not determined during the experimental infections, or not indicated in the respective literature

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