Lymnaeid snails hosts of *Fasciola hepatica* and *Fasciola gigantica* (Trematoda: Digenea): a worldwide review

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Abstract

Fasciolosis is a snail-borne disease, causing serious public and veterinary health problems worldwide. This disease is produced by infection with *Fasciola hepatica* or *Fasciola gigantica* through the consumption of vegetables or water contaminated with the parasite's metacercarial cysts. Both species of liver flukes are transmitted worldwide by small freshwater snails of the family Lymnaeidae. A global account on the species that are actually or may act as potential hosts of *Fasciola* spp., compiling particular research on their geographical distribution and susceptibility, is needed as a helpful tool in the understanding of fasciolosis transmission, and therefore in the control and prevention programmes of the disease. We have gathered here a comprehensive review of those lymnaeid species that are known to transmit the parasites in the field or that have been experimentally tested. We aim to bring forward the main intermediate hosts by regions in order to facilitate the understanding of worldwide transmission.

Keywords: Lymnaeidae, *Fasciola hepatica*, *Fasciola gigantica*, Fasciolosis, Snail transmission

Review Methodology: We searched the following databases: Scopus, PubMed, Google Scholar, JSTOR, SciELO and SpringerLink. Most common keywords used in database search were: lymnaeid snails, *Fasciola hepatica*, *Fasciola gigantica*, natural prevalence, experimental infection, liver fluke transmission, fasciolosis. Relevant ancient and recent articles related to the snail species reported as hosts of *Fasciola hepatica* and/or *Fasciola gigantica* were included. We used articles written in English, French and Spanish. Up to 160 references were included from all continents. References of local studies that were included in larger scale studies were disregarded to avoid over citing. The names of species referenced in ancient studies are cited here using the latest nomenclature available for each species after recent molecular studies.

Background

One of the key aspects in the epidemiology of infectious diseases is acquiring a comprehensive view of their potential extension and their means of transmission. It is particularly complicated when a pathogen includes several organisms to complete its life cycle, making it more difficult to manage and prevent. This is especially the case of vector-borne diseases. The understanding of these diseases necessarily involves a knowledge of their chains of transmission and vector species or hosts. Usually, intermediate hosts and vectors are ultimately the target of control programmes because they represent the weakest link in the transmission chain. To accomplish this goal, having an up-to-date understanding of the distribution and actual role of the species involved in transmission is fundamental to prevent and control vector-borne diseases.

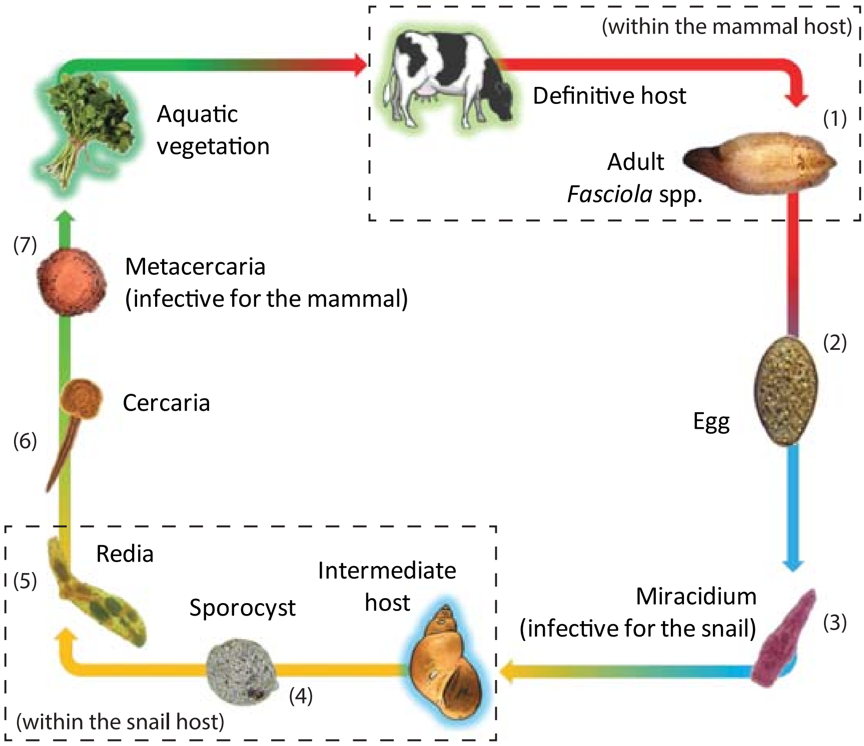

Figure 1 Life cycle of *Fasciola* spp. Adult parasites live in the bile ducts of mammals where sexual reproduction takes place (1). Approximately 40,000 eggs per individual are laid daily and carried out with the host faeces (2). If temperature and humidity conditions are favourable they hatch into miracidia. These larvae must find a susceptible lymnaeid snail in less than 24 h to which they are steered by means of chemotaxis and phototaxis (3). Once in the snail, the miracidium turns into a sporocyst (4) and then produces rediae (5) which, in time, can give place to other generations of daughter rediae. Inside each redia, several cercariae can be produced. These stages are part of the asexual reproduction of the parasite subjected to the compatibility with their host and can last between 30 and 80 days depending on the ecological conditions. When cercariae are mature, they leave the snail, usually producing fatal damages (6). In the water, they swim and encyst forming metacercariae in aquatic or semi-aquatic vegetation or any source of solid substratum (7). Floating metacercariae have also been reported and are a source of infection by contaminated water. Susceptible mammals may close the parasite cycle by eating vegetation with encysted metacercariae. When the parasite reaches the intestine, the juveniles excyst and migrate to the liver where they achieve the adult form. Later, they establish themselves in the bile ducts where sexual maturation takes place.

Fasciolosis: A Snail-Borne Disease

Fasciolosis is a snail-borne disease causing serious public health problems worldwide, especially in low-income nations [1]. However, it remains as an unsolved problem in both developing and developed countries at veterinary level [2, 3]. Additionally, fasciolosis is considered as one of the most globally spread parasitic diseases, which extends widely across a large variety of habitats in different geographic regions [4]. The disease is mostly caused by the hermaphroditic parasites *Fasciola hepatica* Linnaeus, 1758 and *Fasciola gigantica* Cobbold, 1855 (Platyhelminthes: Trematoda: Digenea). Fasciolosis affects more than 17 million people with nearly 180 million at risk of infection worldwide [5].

However, according to the World Health Organization (WHO), fasciolosis remains a neglected tropical disease [6]. Furthermore, *Fasciola* species are placed in a particular group known as the most 'neglected' among the neglected worms where all the main food-borne trematode infections also stand [7].

Both *Fasciola* species are capable of infecting a very wide spectrum of mammalian definitive hosts, including humans, [8] where parasites reproduce sexually producing thousands of eggs at a daily basis (see Figure 1 for a detailed description of the life cycle). Noteworthy, while ruminants are commonly described as the most infected definitive hosts (for which the disease asserts the highest economic losses), several smaller mammals (rodents, lagomorphs, etc.) may have an important role as reservoirs and disseminators of the parasite in the wild [9].

Lymnaeid snails (Gastropoda: Lymnaeidae) act as the intermediate hosts of *F. hepatica* where asexual reproduction of the parasite occurs and a clonal expansion from a single infective larva increases the probability of transmission. The family Lymnaeidae Rafinesque, 1815 is believed to comprise nearly 100 species of small aquatic and amphibious snails [10]. However, about 1200 species have been described worldwide [11]. Lymnaeid snails have a right coiled shell and are known to extend from tropical to temperate regions; some of them occur at very cold latitudes [12–14]. In general, the great ecological plasticity of lymnaeid snails allows them to inhabit a large range of ecosystems which is actually one of the key aspects of the successful extend of fasciolosis.

The family of Lymnaeidae has been the target of several taxonomic revisions in the last two decades due to its importance in the transmission of fasciolosis [15–17]. Vinarski [17] presents the Lymnaeidae divided into two subfamilies, Lymnaeinae (16 genera) and Radicinae (ten genera). Some genera are known to be best suited for a particular species of *Fasciola*, where *F. hepatica* appears to be mainly transmitted by the group of *Galba* whereas *F. gigantica* is commonly related with the *Radix* group [15]. However, different snail habitat preferences (e.g. ponds, ditches, flooded crops), rather than phylogenetic affinity, may better explain the patterns of host specificity by *Fasciola* spp. in different regions [18]. Interestingly, not all lymnaeid species act as intermediate hosts of *Fasciola* spp., and among those that host the parasites, there is a strong variation in the potential of transmission. Indeed, different patterns of susceptibility, host–parasite compatibility and even immunological resistance have been described in this host–parasite system [19–21].

The knowledge of which particular snail species inhabits a risk area for fasciolosis transmission can be used to trigger control campaigns or mapping risks [22]. The understanding of fasciolosis transmission worldwide requires a global account on the snail species that are vectors or that may act as potential hosts of *Fasciola* spp. The compilation of specific research on their geographical distribution and susceptibility is needed as a helpful tool that may serve in the control and prevention programmes of the disease. In the following sections, we present a review of the global distribution of lymnaeid snails with a known role in *Fasciola* spp. transmission according to the latest systematics published for this family. We will only consider those species which have experimentally proved to be susceptible to infection or that have been described as natural vectors of the parasite in the field (see Table 1).

Brief Overview of *Fasciola* spp. Distribution

Fasciola hepatica and *F. gigantica* (known as liver flukes), are the main aetiological agents of fasciolosis worldwide (Figure 2). The large diversity of hosts of *F. hepatica* (i.e. many lymnaeid snails and mammal species act as intermediate and definitive hosts, respectively) determine a major role for this species in the global burden of the disease. This species is reported in all continents except Antarctica and it is present in many oceanic islands. Contrastingly, given that *F. gigantica* is usually restricted to the tropical and subtropical region of Asia and Africa, it has a lesser global impact in public and veterinary health [4]. In any case, fasciolosis is a serious problem for public health in some endemic regions such as the Bolivian Altiplano, Peru, Egypt, Iran and southeast Asia where prevalence in the human populations is particularly high [4, 5]. From a veterinary point of view, there are reports of *F. hepatica* infecting over 300 million bovines and nearly 250 million ovine worldwide; together with *F. gigantica* the economic losses ascend up to 3000 million dollars [1, 5]. The localities where fasciolosis reaches the highest prevalence are known for having: (a) high infection rates and intensities in either human and livestock populations, (b) available surface water for compatible lymnaeid snail populations to settle in most of the year and (c) adequate temperature and humidity for the development and survival of each parasite stage in and out of the hosts [5].

Lymnaeid Distribution

The family of Lymnaeidae has a worldwide distribution [11] (Figure 3). Although this review focuses only in its role in fasciolosis transmission, it is important to note that several lymnaeid species also serve as hosts of a major number of trematode families, causing diseases in wildlife and domestic fauna as well as humans [68, 69].

Transmission in the Americas

The American lymnaeid species display a vast distribution ranging from north Canada to south of Patagonia as well as through the Caribbean Islands. However, the transmission is not as thoroughly reported in every region.

North American Lymnaeidae

In North America, studies depicting the diversity of Lymnaeidae accumulated in the past but have not been so abundant in the last decades. In the USA, *Galba cubensis* and *Pseudosuccinea columella* were identified as the main vectors of fasciolosis but only after a series of experimental infection trials [29]. However, in Florida (USA), Kaplan *et al.* [70] presented *G. cubensis* as the main host for *F. hepatica*, owing to its broad distribution and to its ability to transmit the parasite throughout the year after presented recovered field prevalence data. Still in the USA, *Galba bulimoides* from Wisconsin was experimentally infected with successful retrieval of metacercariae [46] and *Galba modicella* from Montana was found naturally infected in a goat farm with transmission occurring between spring and summer [33]. Also, in Montana, Knapp *et al.* [45] described the transmission of *F. hepatica* by *Hinkleyia caperata*, which is supposed to occur from the east to the west coasts of North America up north to Alberta [71, 72]. Another related species, *Stagnicola palustris* has been reported infected in eastern Washington [66] with a distribution range from south Alaska to New Mexico [73]. In Canada, although fasciolosis is recognized to occur within dairy cows in Quebec [74], the lymnaeid species implicated are not well studied. However, Hubendick [11] admitted *Galba truncatula*, *S. palustris* and probably *Galba humilis* to reach Canada. In Mexico, *G. humilis* and

Table 1 Summary of the main lymnaeid species host of the liver flukes worldwide with their type localities, main geographic distribution and records of infection with either *Fasciola hepatica* or *Fasciola gigantica* (EI: means that the lymnaeid species has been only experimentally infected)

Lymnaeid species	Type locality	Main geographic range	Liver fluke	Reference
Austropeplea tomentosa (Pfeiffer, 1855)	Auckland (New Zealand)	Australia	*F. hepatica*	[23]
Galba cousini (Jousseaume, 1887)	Chanchu-Yacu (Ecuador)	Ecuador, Colombia, Venezuela	*F. hepatica*	[24–26]
Galba cubensis (Pfeiffer, 1839)	Cuba	Cuba	*F. hepatica*	[27, 28]
		USA		[29]
		Lesser Antilles, Colombia		[30]
		Mexico, Uruguay, Venezuela		[31]
Galba humilis (Say, 1822)	South Carolina (USA)	Mexico	*F. hepatica*	[32]
Galba modicella (Say, 1825)	Owego, New York (USA)	USA	*F. hepatica*	[33]
Galba truncatula (Müller, 1774)	Thangelstedt (Germany)	Argentina, Bolivia, Chile, Peru, Venezuela	*F. hepatica,*	[34–36]
		Africa	*F. gigantica*	[37]
		Ireland, Europe		[38, 39]
Galba viator (d'Orbigny, 1835)	Río Negro (Argentina)	Argentina, Brazil, Peru, Uruguay	*F. hepatica*	[40–42]
Galba viridis (Quoy & Gaimard, 1832)	Guam	Hawaii	*F. hepatica*	[43]
		Micronesia	*F. gigantica*	[44]
		Australia		[23]
Hinkleyia caperata (Say, 1829)	Indiana, USA	North America	*F. hepatica*	[45]
Lymnaea bulimoides (Lea, 1841)	Oregon (USA)	USA	*F. hepatica*	[46]
Lymnaea diaphana (King, 1830)	San Gregorio (Chile)	Argentina, Chile	*F. hepatica*	[47, 48]
Lymnaea stagnalis (Linnaeus, 1758)	Europe	Europe, Asia	*F. hepatica*	[49]
Myxas glutinosa (Müller, 1774)	Fridrichsdal (Denmark)	Urals, Siberia	*F. hepatica* (EI)	[50]
Omphiscola glabra (Müller, 1774)	Fridrichsdal (Denmark)	France	*F. hepatica*	[51]
Pseudosuccinea columella (Say, 1817)	near Philadelphia (USA)	Cuba, USA, Central and South America	*F. hepatica*	[52–54]
		France		[55]
		Africa		[56]
		Australia, New Zealand		[23, 57]
Radix auricularia (Linnaeus, 1758)	Europe	Europe, Southeast Asia	*F. gigantica*	[58]
Radix balthica (Linnaeus, 1758)		Iceland, British Islands, Europe, western Siberia, Asia minor	*F. hepatica*	[12]
Radix gedrosiana (Annadale & Prashad, 1919)	Afghanistan	Afganistan, Iran	*F. gigantica*	[59]
Radix labiata (Rossmaessler, 1835)		Europe, Turkey, Urals	*F. hepatica* (EI)	[12, 60]
Radix lagotis (Schrank, 1803)	Danube river (Germany)	Europe (Danube Basin)		[61]
Radix luteola (Lamark, 1822)	Bengal (India)	Nepal	*F. gigantica*	[16]
Radix natalensis (Krauss, 1848)	Port Natal, Durban (South Africa)	Africa; Saudi Arabia	*F. gigantica*	[62]
Radix ovata (Draparnaud, 1805)	France	France	*F. hepatica*	[63]
Radix peregra (Mülller, 1774)	Fridrichsdal (Denmark)	Central Europe	*F. hepatica* (EI)	[12]
Radix rubiginosa (Michelin, 1831)		Eastern Asia, Malaysia	*F. gigantica*	[64]
Radix swinhoei (Adams, 1866)		South eastern Asia, Philippines	*F. gigantica*	[64]
Stagnicola corvus (Gmelin, 1791)	Thuringia (Germany)	Europe	*F. hepatica*	[65]
Stagnicola fuscus (Pfeiffer, 1821)	Füred, Tihany (Hungary)	Europe	*F. hepatica*	[63, 65]
Stagnicola palustris (Müller, 1774)	Oregon, USA	USA	*F. hepatica*	[66]
		Europe		[67]

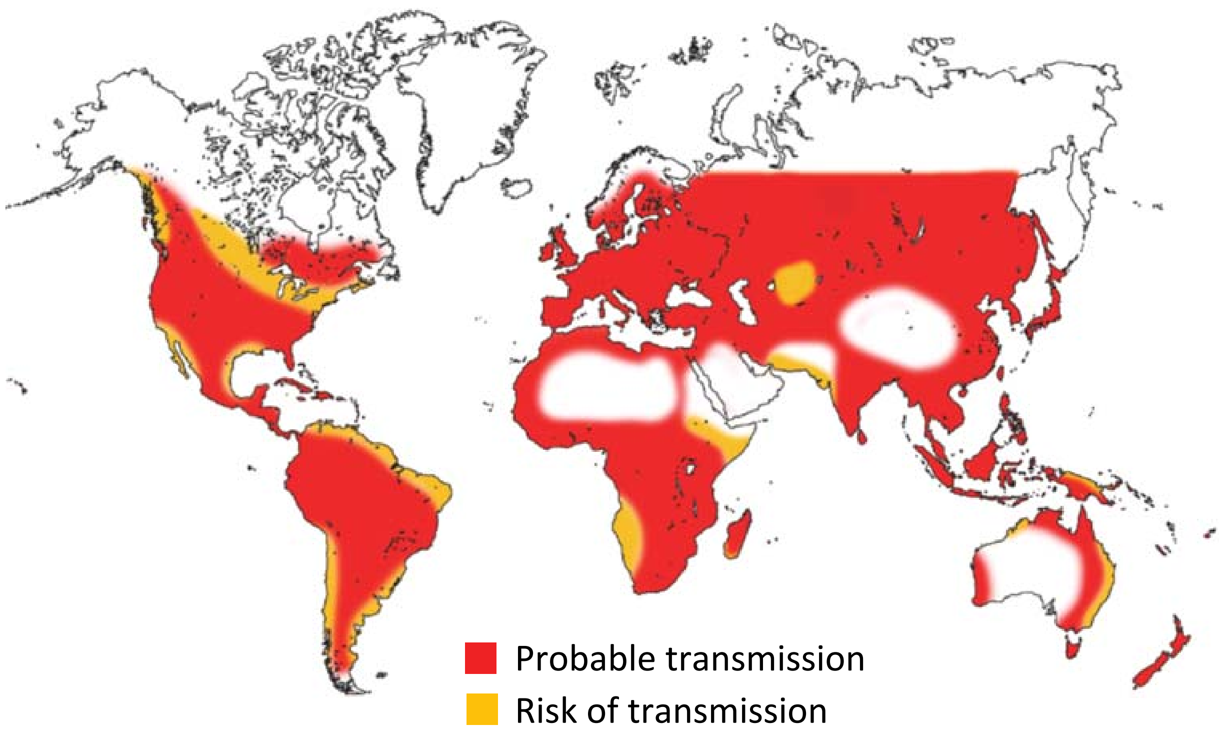

Figure 2 Worldwide transmission of fasciolosis. Map built using data gathered from different reports (Torgerson and Claxton, 1999; WHO, 2013, 2014).

G. bulimoides are known to transmit *F. hepatica* [32] from late summer to early winter mostly in warm and damp sites [75].

In any case, the actual distribution of the lymnaeid species, and particularly those able to transmit *F. hepatica*, in the northern region of North America is poorly known. An ancient species report made by Sterki [76] in eastern North America informed of 13 species of Lymnaeidae including *Lymnaea stagnalis*, *P. columella*, *G. modicella*, *G. humilis*, *Ladislavella elodes* and *Radix auricularia*. However, the systematics of this family in this region should be viewed cautiously due to the lack of molecular studies that would help to clarify the identity of the species described. Given that many lymnaeid species have a large phenotypic variability and are quite difficult to differentiate by shell morphology, the numbers might be overestimated. A more recent list made by Johnson *et al.* [77] on the freshwater snails from Canada and the USA includes 61 species of Lymnaeidae. Among them, 21 correspond to the group of the small-shelled *Galba*. Here again, these numbers are perhaps overestimated due to possible systematic confusions in the absence of molecular studies. In the arctic region, lymnaeid snails are known to occur but are related to the transmission of *Fascioloides magna* parasitizing caribou populations as it has been demonstrated by the observation of parasite stages overwintering in the snails. However, the snail species are not outlined [78]. A recent study carried out by Vinarski *et al.* [79] suggests that the endemic lymnaeid from Greenland, former *Lymnaea vahlii* should be considered as a form of the North American *Ladislavella catascopium* which is known to transmit the liver fluke [15]. In any case, transmission of *F. hepatica* in these high latitudes remains unknown.

Caribbean Lymnaeidae

In the Caribbean basin, the situation is much less complicated with three species occurring. In Cuba, Vázquez *et al.* [21] infected several populations of *G. cubensis* and *P. columella* with different isolates of *F. hepatica* and reported, according to the levels of susceptibility and compatibility, the former as the main host in the island. *Galba cubensis* is described from Cuba and has an extended distribution in the country while *P. columella* is found only from the west to the central region [80]. Field studies have reported natural prevalences in *G. cubensis* ranging from 0 to 11% [27] and 0 to 34% [28] in localities reported as transmission foci. In Cuba, *P. columella* might play a secondary role in the transmission [21] and has been only recently reported naturally infected by for the first time in the Caribbean region with a prevalence of 1% [52]. Transmission in Cuba is therefore supposed to occur by both species with several human outbreaks and important economic losses due to high cattle infection [3]. Interestingly, at least six natural populations of *P. columella* from Cuba have been found to display an active resistance against *F. hepatica* miracidia infection [20, 21]. Resistant populations can be phenotypically distinguished by a

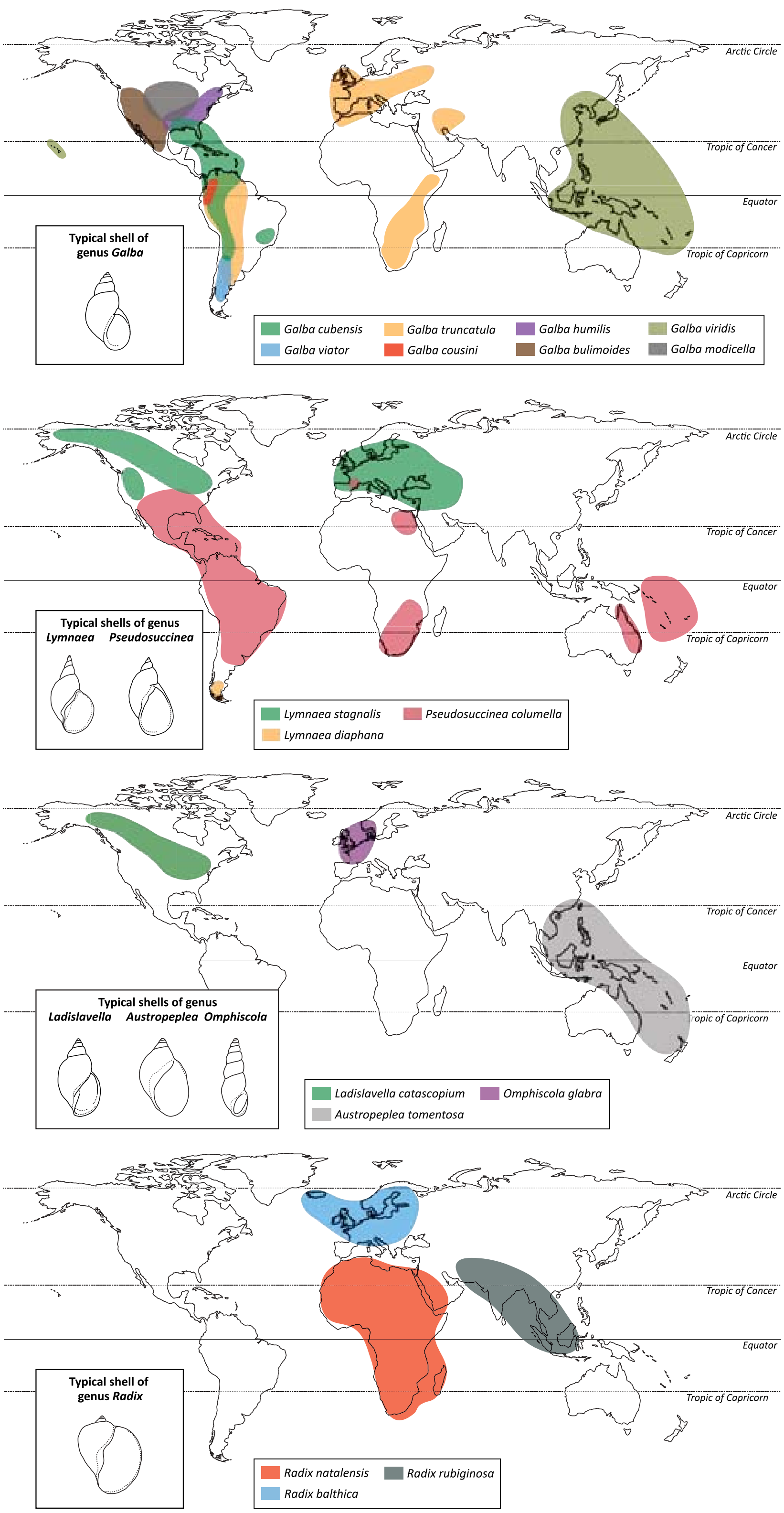

Figure 3 Most common ranges of the main lymnaeid species hosts of *Fasciola* spp.

different mantle pigmentation pattern consisting of a number of small well-defined spots in a belt-like shape in the centre [81]. These resistant populations, although frequently rare, are an interesting model to tackle fasciolosis transmission. The mechanisms of resistance are not yet well known.

Both *G. cubensis* and *P. columella* are also described in some Lesser Antilles where transmission of *F. hepatica* had never been reported, like Martinique [82] and Guadeloupe [83]. Both lymnaeid species are also reported in some other Caribbean countries such as the Dominican Republic [84]. In Puerto Rico [85] and Jamaica [86], *G. cubensis* is responsible for *F. hepatica* transmission. Recently, a third species, *Galba schirazensis*, has been reported in the Dominican Republic [87] but it seems that it does not act in fasciolosis transmission. There is a previous report of *Galba viator* from the Dominican Republic [88] but its identification is questionable given the lack of molecular tools at that time. The fact that it is rather the distribution range of *G. cubensis* and that both species are very difficult to separate morphologically, it would probably correspond to the latter.

South American Lymnaeidae

As in North America, the South American scenario becomes again ravelled with a diversity of very morphologically similar species able to transmit the liver fluke. In northern South America, the genus *Galba* is probably mainly responsible for transmission. Several species such as *Galba cousini*, *G. cubensis*, *G. schirazensis* and *G. truncatula* are all reported in this region and most have been found regularly infected with *F. hepatica* [34, 89]. The species *G. cousini* has been found in Venezuela, Colombia and Ecuador [24, 90, 91]. Its role in the transmission in these countries seems restricted to altitudes lying between 2000 and 4000 m [90]. In the last years, *G. schirazensis* was discovered in many types of habitats from Venezuela, Colombia and Ecuador [92] and its role in the transmission of *F. hepatica* remains under discussion. In Venezuela and Colombia, this snail was the only species of lymnaeid found in several active foci, and although not found infected during sampling, it is highly probable that it is responsible for the transmission of *F. hepatica*. In any case, experimental infections carried out with an isolate of *F. hepatica* and a strain of *G. schirazensis* from Colombia showed that seven snails out of 400 harboured several rediae and two contained free cercariae on day 50 post-exposure [19]. In addition, in Ecuador, a 6% natural prevalence was detected in *G. schirazensis* using molecular techniques [93]. However, the actual role of this snail species in a sustained transmission should be confirmed with cercarial shedding and effective metacercarial infectivity. Apart from *Galba* spp., *P. columella* is also reported in Venezuela [34], Colombia [94] and Ecuador [40], and also extends down through Brazil [95, 96] and Argentina [97]. In the Andean countries, particularly the Bolivian Altiplano, *G. truncatula* plays a prominent role in *F. hepatica* transmission [13, 35, 98, 99]. This species may also be a key player in Chile [99] and Argentina [100]. *Galba viator* is also a very important intermediate host of *F. hepatica* in the southern region of Chile and Argentina [41, 101], although current reports of natural prevalence are lacking. According to Kleiman *et al.* [102], this species occurs as far south as beyond parallel 42°S in the Chubut province in the Patagonian region, where a 0.67% natural prevalence of *F. hepatica* was recorded [41]. There were in fact reports of natural infection in *G. viator* and *P. columella* from Argentina as assessed by mean of PCR amplification of the cytochrome *c* oxidase subunit I of *F. hepatica* [103]. Other South American Lymnaeidae are *Lymnaea diaphana* and *Lymnaea rupestris*. The former species is described to serve as a host of *F. hepatica* in the southern part of the Chilean and Argentinean Patagonia [47]. The role of the second species *L. rupestris* in the transmission of *F. hepatica* is not known [104].

Transmission in Eurasia

Transmission in this region has been fairly frequently recorded in several studies except where climatic conditions are probably too harsh for the parasite life cycle, such as in Iceland [105] and probably Siberia. However, several lymnaeid species have been reported from these regions [14, 50, 106] that could eventually act as hosts.

European Lymnaeidae

In Britain and Ireland, there are at least eight lymnaeid species reported by Anderson [107]. However, transmission has been mainly linked to the widespread *G. truncatula* and to the local *Radix balthica* [108]. In continental Europe, several species such as *Radix peregra* have a broad distribution ranging from Nordic countries to southern regions and east to Ukraine. According to Schniebs *et al.* [60], *R. peregra* occurs also in Turkey and the Urals. Although there is no record of this species being naturally infected with *F. hepatica*, its role as well as that of *R. balthica* as incidental hosts in Belgium was demonstrated by Caron *et al.* [12] through series of experimental infections. More recently, the field prevalence of *F. hepatica* was confirmed in *R. balthica* (0.16%) and *G. truncatula* (1.31%) from Belgium and Luxembourg using a multiplex PCR [109]. Another species, *Stagnicola fuscus*, was experimentally tested with *F. hepatica* miracidia originating from France and proved to be partially refractory to infection although the snails have shed cercariae [63]. According to Novobilsky *et al.* [67], *S. fuscus* and *S. palustris* are also potential intermediate hosts of *F. hepatica* in Sweden. Overall, transmission in the field is commonly attributed to *G. truncatula* and *Omphiscola glabra* particularly in France [51, 110, 111]. Recorded prevalences for *G. truncatula* range between 5 and 33% in France and a mean of 11% in Spain [112], and 1.4–1.8% for French *O. glabra* [110]. *Galba truncatula* has been also found naturally infected in several districts of Moscow [113] and up to 85% prevalence was detected in Poland [114]. Although there are no much field data on prevalence on the snail populations, *G. truncatula* is presumed to be a key vector in dairy farms from south Germany and Austria [115] and natural prevalence of 7% is reported from Switzerland through real-time PCR [116]. Recently, some small-scale risk mapping of *F. hepatica* in farms from Belgium has been based on the spatial distribution of *G. truncatula* [22]. From central Europe, several species have been described as potential hosts such as *Catascopia terebra*, *Stagnicola corvus* and *S. fuscus* in the Czech Republic [65]. Several introductions, probably through the aquarium plant trade, have occurred in the past few years and may increase the risk of transmission in some countries. Such introductions include *P. columella* in France [55] and *Austropeplea viridis*, *G. schirazensis* and *G. cubensis* in Spain [92, 117, 118].

Asian Lymnaeidae

There are several species of lymnaeid snails described or reported in northern Asia from the Urals to eastern Russia [14, 50, 106, 119–121]. However, there are no significant reports on *F. hepatica* infection neither in natural nor under experimental conditions. In many other areas of Asia (particularly in the south), fasciolosis is caused by both *F. hepatica* and *F. gigantica* with some regions reporting the existence of hybrid forms of the parasite such as in South Korea and Vietnam [122, 123].

As in many other regions where it has been introduced, *G. truncatula* is held responsible for transmission of *F. hepatica* in some areas in Iran together with *L. stagnalis* [49]. Also, from southwest Asia, transmission of *F. gigantica* is generally linked to the presence of *Radix natalensis* (syn. *Lymnaea arabica*) and *S. palustris* in Saudi Arabia [62, 124], and *Radix gedrosiana* in Iran [59].

Southeast Asia is known to be heavily hit with both species of *Fasciola.* In Thailand, at least three species of lymnaeid snails have been recorded infected with *F. gigantica*: *Radix rubiginosa*, *Radix swinhoei* and *Galba viridis* [64]. Similarly, *G. viridis*, *R. auricularia* and *R. rubiginosa* are the main lymnaeid species recorded in Vietnam with the latter being reported infected in the field [125]. Unfortunately, not all field reports from fasciolosis outbreaks define the snail species responsible for the transmission. In southwest China, for example, after an outbreak of fasciolosis, the transmitting snails in the area were only identified as *Galba* spp. [126]. From Japan, several lymnaeids were experimentally infected using Australian strains of *F. hepatica* by Itagaki *et al.* [127]. Only the species *Austropeplea ollula* and *R. auricularia* resulted infected while *G. truncatula* proved to be refractory.

Transmission in Africa

Fasciolosis in Africa may occur either by infection of *F. hepatica* or *F. gigantica*. One of the most affected regions is the Nile basin in Egypt [128]. In east Africa, both species are also responsible for infections in countries such as Kenya, Uganda, Ethiopia and Sudan [129].

The African Lymnaeidae

One of the lymnaeid species with broader distribution in the continent is *R. natalensis* described from South Africa [56], usually living in steady shallow waters, and considered as a very suitable host for *F. gigantica* [18]. Based on field and experimental studies, this species has been recognized as the main responsible for transmission of *F. gigantica* in Egypt [130]. However, *R. natalensis* is presumed to be also a potential host of *F. hepatica* after a successful experimental infection with French strains of this parasite [131]. It has also been found infected in other countries like Benin [132], Nigeria [133], Ghana [56] and is presumed to be the main transmitter in Ethiopia [134] and Uganda [135]. The distribution range reaches Tanzania and Cameroon but the transmission of either *Fasciola* spp. is not well assessed [136]. In western Africa, *R. natalensis* has been pointed as the main host for *F. gigantica* transmission in Senegal [137]. Outside African mainland, *R. natalensis* is also found in the island of Madagascar [138] where it is the main host of *F. gigantica* [139], and in Reunion Island [140]. The distribution of this species in other African countries includes Somalia and Gambia and is less common along the east and southwestern coasts [56]. According to Brown [56], the similar species *R. peregra* is also found in northwest Africa (Morocco and Algeria) with a single report from Ethiopia.

Moreover, *F. hepatica* transmission in Africa does not follow the same epidemiology than that of *F. gigantica*, with different hosts and distribution. In South Africa, *F. hepatica* is known to be transmitted by *G. truncatula* which inhabits preferably ecosystems of low-flowing water like borders of irrigation channels [141]. This species is also responsible for transmission in Lesotho [142] and Tunisia [143] where horses have been found infected with the parasite [144]. In northeastern Algeria, natural infected *G. truncatula* have been also recorded [145]. Susceptibility to Algerian strains of *F. hepatica* miracidia was experimentally tested showing that the number of obtained metacercariae did not vary regardless the origin of the parasite in that country [146]. Into the west, *G. truncatula* has been also found responsible for transmission of *F. hepatica* infecting sheep in the Middle-Atlas Mountains of Morocco [147]. Studies regarding the compatibility between Moroccan populations of *G. truncatula* and sympatric *F. hepatica* have been done by Belfaiza *et al.* [148] showing that snails may impose a bottleneck on the development of mother rediae which grows more and have a higher production of daughter rediae and cercariae. According to Rondelaud *et al.* [38], a prevalence of 3% has been recorded in field-collected Moroccan *G. truncatula*. In the east, *G. truncatula* is known to maintain *F. hepatica* life cycle in the highlands of Ethiopia [149]. Moreover, *G. truncatula* has been experimentally infected with Egyptian strains of *F. gigantica* with a frequency of 80% of cercariae-shedding snails proving that it may serve as a natural host for this parasite in Egypt [150]. *Galba truncatula* has also been reported from Zaire, Kenya and Tanzania [56].

Another lymnaeid host of *F. hepatica* in Africa is the invasive species *P. columella*. This species has been reported as widely distributed in South Africa [56] but its contribution to fasciolosis transmission in this country is yet to be evaluated [141]. After the discovery of its introduction in South Africa in 1944, it has also been found in Mozambique, Zimbabwe, Zambia and Egypt [56]. However, populations of *P. columella* might be easily mistaken with *R. natalensis* and thus ancient distribution data should be re-evaluated. More recently, Grabner *et al.* [151] molecularly detected the natural infection of Egyptian populations of *P. columella* with several trematodes among which is *F. gigantica*.

Other lymnaeid species occurring in Africa are *L. stagnalis* and *S. palustris*, both recorded from Morocco and Algeria [56]. Transmission of *F. hepatica* by any of these lymnaeids is supposed but not assessed. Finally, it has been recently studied the introduction of *R. rubiginosa* into South Africa which could exacerbate the transmission of *F. gigantica* in this country and whose spread might go unnoticed due to similar shell morphology with the native *R. natalensis* [152].

Transmission in Australia and the Pacific islands

Transmission of *F. hepatica* in this region has been usually linked to the native lymnaeid *Austropeplea tomentosa*, particularly in Australia, Tasmania and New Zealand [23, 153]. The role of this species as the main host of *F. hepatica* in Australia was confirmed by Boray [154]. However, in this study, the author also confirms the introduction of three invasive lymnaeid species: *P. columella*, *G. viridis* and *R. auricularia*. Subsequent infection assays were carried out proving that both *P. columella* and *G. viridis* are highly susceptible, whereas *A. tomentosa* remains the most suited host [154]. Later, Molloy and Anderson [23] concluded that although the introduced species may not yet have had an important impact in fasciolosis transmission, the adaptability of *P. columella* to tropical habitats could result in the expansion of *F. hepatica* in the north. Another species was described from Tasmania by Ponder and Waterhouse [153] named as *Kutikina hispida* but transmission capacity has yet to be assessed. Fasciolosis in mainland Australia not only affects bovines but also native marsupial hosts [155]. In the Indonesian archipelago, *R. rubiginosa* has been found infected with *F. gigantica* in irrigated rice fields of West Java [156]. From the Micronesia, particularly the Mariana Islands, the only lymnaeid species reported is *G. viridis* ranked as a native species but no transmission of *Fasciola* spp. has been described so far [44]. *Galba viridis* is also known to occur in Guam, Indonesia, Papua New Guinea and Thailand [157]. However, far northern in the Hawaiian archipelago the species *G. viridis* is a major intermediate host of the liver fluke *F. gigantica* [43]. This species has also been experimentally infected with *F. hepatica* and cercarial shedding was successfully verified [158]. Also, the invasive *P. columella* has been found in Hawaii [157]. In some other Pacific islands, *P. columella* has been reported from Tahiti, Rapa, Tubuai and Rurutu, but its role in the transmission of *F. hepatica* has not been established [159].

Concluding Remarks on Lymnaeidae–*Fasciola* spp. Transmission

As illustrated in this review, although many species may actually serve as intermediate hosts of *Fasciola* spp. in the field, there are a lesser number posing major threats at both regional or world scales. These threats can be due to several factors among which we may highlight: (a) the species is widely distributed and adapted to the circulating strains of liver fluke (shows higher compatibility in terms of surviving infection and redial burden, e.g.), (b) the species is capable of establishing itself in areas of cattle-related human activities (even very anthropized habitats) with ecological preferences that match those of the definitive hosts or (c) the species has a high invasive ability and the lack of genetic diversity of introduced individuals that may facilitate the transmission. Worldwide, the introductions of *G. truncatula* and *P. columella* may have played a key role in the spread of fasciolosis. Both species have a proved susceptibility to *F. hepatica* infection, but more important, a recognized invasive ability allowing both to succeed in new environments [35, 160]. As an attempt to highlight particular species by regions, major threats may be summarized for (a) the Americas: *G. truncatula*, *G. cubensis*, *G. viator* and *P. columella*; (b) Europe: *G. truncatula* and *R. balthica*; (c) Asia (particularly the southern regions): *R. rubiginosa* and *R. auricularia*; (d) Africa: *R. natalensis* and *G. truncatula*; and (e) Oceania: *A. tomentosa* and *G. viridis*.

Although we have reviewed only the main actors in the *Fasciola*–Lymnaeidae interplay by region, we should note that the huge number of described lymnaeid snails in ancient and recent literature may lead to an annoying scenario of who transmit who in many regions. The absence of reliable morphological traits has led to confusion regarding specific identities of lymnaeid populations worldwide. Some species cannot be accurately distinguished because their shell morphology and anatomy are very similar. Even species relatively easy to identify such as *P. columella* or *G. cousini* could have been misidentified in the past due to, for instance, lack of experience in snail identification or the status of the individuals used for the identification (juveniles, worn or broken shells). Thus, studying lymnaeid species often requires an accurate molecular tool. The species identification of fasciolid larval stages found in nature also needs to be always verified, usually by experimental infections or by molecular markers. It is therefore necessary to review in the near future all reported names using the latest molecular tools and data available to reach a more plausible scenario in which, though probably complicated enough, we can picture the world transmission of liver flukes in a more reduced and comprehensible way.

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