Chapter

Zoonotic Trematode Infections; Their Biology, Intermediate Hosts and Control

Henry Madsen and Jay R. Stauffer, Jr.

Abstract

Many diseases linked with trematodes are zoonotic, including liver flukes (*Fasciola* spp., *Clonorchis*, and *Opistorchis* are the most common), intestinal flukes (some species of the Heterophyidae), lung flukes (*Paragonimus* spp.) and the blood flukes (schistosome species). A characteristic for all these species is that they have a vertebrate as final host and have freshwater snail species as the first intermediate host, and for the food-borne trematodes, also a second intermediate host where their infective stage (metacercariae) lodge or in case of the Fasciolidae, cercariae encyst on aquatic or semi-aquatic plants. We describe the biology of transmission with emphasis on the intermediate snail hosts, and the control of these.

Keywords: schistosomiasis, liver flukes, intestinal flukes, snail intermediate host

1. Introduction

Diseases resulting from zoonotic transmission of parasites are common [1]. Most parasitic zoonoses are neglected diseases despite causing a considerable global burden of ill health in humans and have a substantial financial burden on livestock industries [1]. Zoonotic trematodiasis are found worldwide and are responsible for some serious and debilitating helminthic diseases in people, particularly in rural and poor urban areas of low and middle-income countries [2, 3]. Many of the trematodes that infect humans are zoonotic or have zoonotic potential. Here we briefly discuss the most important zoonotic trematodes and focus on their first intermediate hosts, snails, and their control. Trematodes (Trematoda) belong to the phylum Platyhelminthes which also contains Turbellaria (mostly non-parasitic animals such as planarians), and three entirely parasitic groups: Cestoda, Trematoda, and Monogenea. Trematoda includes two subclasses of parasitic flatworms, also known as flukes, i.e., Aspidogastrea and Digenea. Here we focus on Digenea, which as adults are internal parasites of vertebrates. Trematodes have both sexual and asexual reproduction in different host species. Sexual reproduction occurs in the final vertebrate host, while asexual reproduction occurs in the first intermediate host, usually certain species freshwater or marine snails. Most trematodes have a second intermediate host where their infective stage (metacercariae) lodge. For the food-borne trematodes, various fish species, crustaceans, or

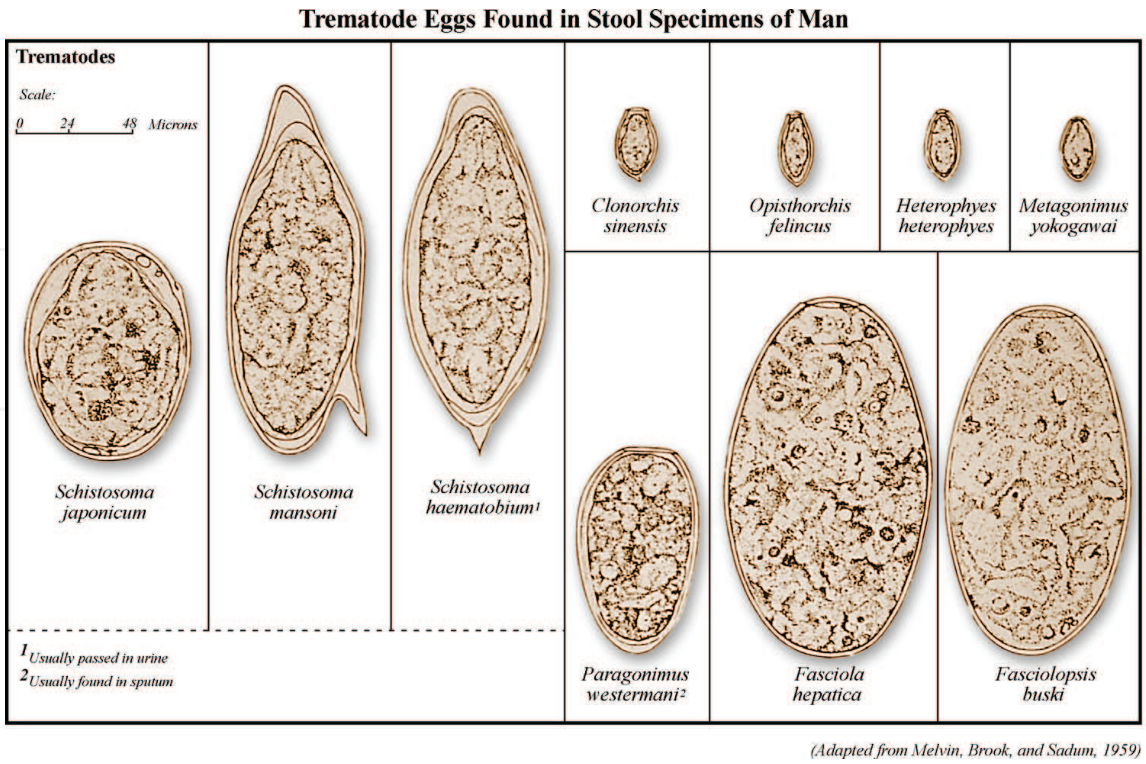

Figure 1.
Eggs of various trematodes found in human feces or urine (source: Mae Melvin, public health image library (PHIL); Centers for Disease Control and Prevention).

snails may serve as second intermediate host or in case of the Fasciolidae, cercariae encyst on aquatic or semi-aquatic plants (see more details below).

The Digenea contains about 20,000 species, within two orders, Diplostomida and Plagiorchiida. Only a few of these species infect humans, and some of the diseases they cause are briefly discussed below, i.e., schistosomiasis and several species of food-borne zoonotic trematodes (paragonimiasis, fascioliasis, clonorchiasis, opisthorchiasis, and others). Examples of eggs from these trematodes are shown in **Figure 1**. Some species of trematodes have a relatively narrow range of snail species that serve as intermediate hosts, while others have an apparently wide range (**Table 1**).

2. The diseases

2.1 Schistosomiasis

Schistosomiasis is native in many countries in Africa, South America, and Asia with an estimated number of 200 million infected people and with 800 million being at risk according to Doumenge et al. [4], but considering the population increase since then, the number of humans currently at risk must be well over a billion [5]. According to latest available information somewhere between 230 and 250 million people are actually infected [6, 7]. People become infected by contact with water harboring schistosome-infected intermediate host snails (**Figure 2**). The snails release cercariae into the water that contact and penetrate human skin.

The schistosomes belong to the trematode order Diplostomida, superfamily Schistosomatoidea and Schistosomatidae. The genus *Schistosoma* contains 23 recognized species and at least 7 of these are of medical and veterinary importance [8].

Digenean order	**Diplostomida**		**Plagiorchiida**						
				Opisthorchioidea			**Echinostomatoidea**		**Paramphistomoidea**
	Schistosomatidae		**Paragonimidae**	**Opisthorchiidae**		**Heterophyidae**	**Echino-stomatidae**	**Fasciolidae**	**Paramphistomidae**
	Schistosoma	**Other schistosomes**	***Paragonimus***	***Clonorchis***	***Opistorchis***	**Intestinal flukes**	***Echinostoma***	***Fasciola***	***Paramphistomum***
Neritomorpha									
Neritidae									
Caenogastropoda									
Viviparidae									
Ampullaridae									
Cerithiidae		x				x			
Melanopsidae									
Pachychilidae		x	x	x			x		
Paludomidae									
Potamididae									
Semisulcospiridae									
Thiaridae		x	x	x			x		
Littorinidae		x				x			
Planaxidae		x							
Amnicolidae			x			x			
Cochliopidae			x						
Bithyniidae				x	x	x			
Pomatiopsidae	x		x			x			
Stenothyridae						x			

Digenean order	Diplostomida		Plagiorchiida						
				Opisthorchioidea			Echinostomatoidea		Paramphistomoidea
	Schistosomatidae		Paragonimidae	Opisthorchiidae		Heterophyidae	Echino-stomatidae	Fasciolidae	Paramphistomidae
	Schistosoma	Other schistosomes	*Paragonimus*	*Clonorchis*	*Opistorchis*	Intestinal flukes	*Echinostoma*	*Fasciola*	*Paramphistomum*
Assimineidae			x	x					
Hydrobiidae			x			x			
Panpulmonata									
Valvatidae									
Ellobiidae									
Planorbidae	x	x					x	x	x
Bulinidae	x	x							
Physidae		x					x		x
Ancylidae									
Lymnaeidae		x					x		x
Acroloxidae									

Table 1.
Snail families involved as intermediate hosts for trematodes (flukes) causing disease in humans or domestic animals. Only certain species within a family are intermediate hosts for a given parasite.

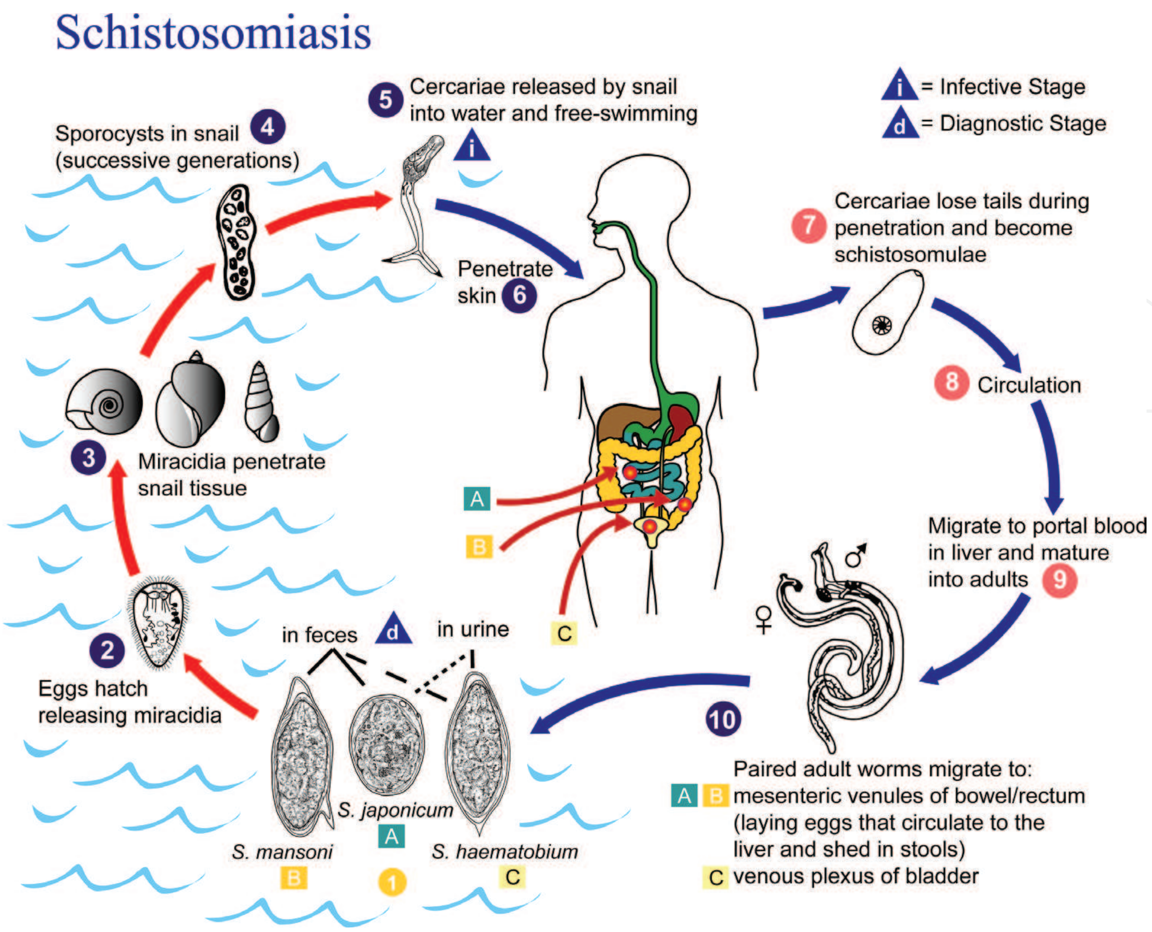

Figure 2.
Life cycle of schistosomes infecting humans (source: Alexander J. da Silva & Melanie Moser, public health image library (PHIL), Centers for Disease Control and Prevention).

The species are divided into four groups, i.e., the *S. japonicum* group, the *Schistosoma mansoni* group, the *S. indicum* group and the *S. haematobium* group [8]. Some species primarily infect humans while others primarily infect non-human animals, but infections with the former group may be found in non-human vertebrates and infections with the latter group may be found in humans [9, 10].

Species within the group of *S. japonicum* use as intermediate hosts, species of the Pomatiopsidae. *Schistosoma japonicum* is the major species of medical importance in South-East Asia and the species has many definitive hosts [6]. *Schistosoma mekongi* is found in parts of the Mekong River basin region in Cambodia, Laos, and Thailand [11]. The other species of the *S. japonicum* group are mainly parasites of rats [12] although human infection by *Schistosoma malayanum* are found [11].

The group of *Schistosoma mansoni* has 2 species, *S. mansoni* and *Schistosoma rodhaini* both using *Biomphalaria* spp. (**Figure 3**) as an intermediate host. *S. mansoni* is found throughout sub-Saharan Africa, parts of the Arabian Peninsula and it is the only *Schistosoma* spp. found in South America [8]. The two species hybridize in the wild [12]. Species of the group *S. indicum* occur in the western and southern Asian regions and are commonly found in animals, i.e., ungulates, horses, pigs, and possibly dogs [8]. The species use *Indoplanorbis exustus* as intermediate host [8]. The group associated with *S. haematobium* includes nine species that are the most widespread, i.e., Africa, Indian Ocean Islands, Arabian Peninsula, and Mediterranean regions [8]. *Schistosoma haematobium* causes urogenital schistosomiasis, while other species, *S. intercalatum* and *S. guineensis* infecting humans in this group cause intestinal

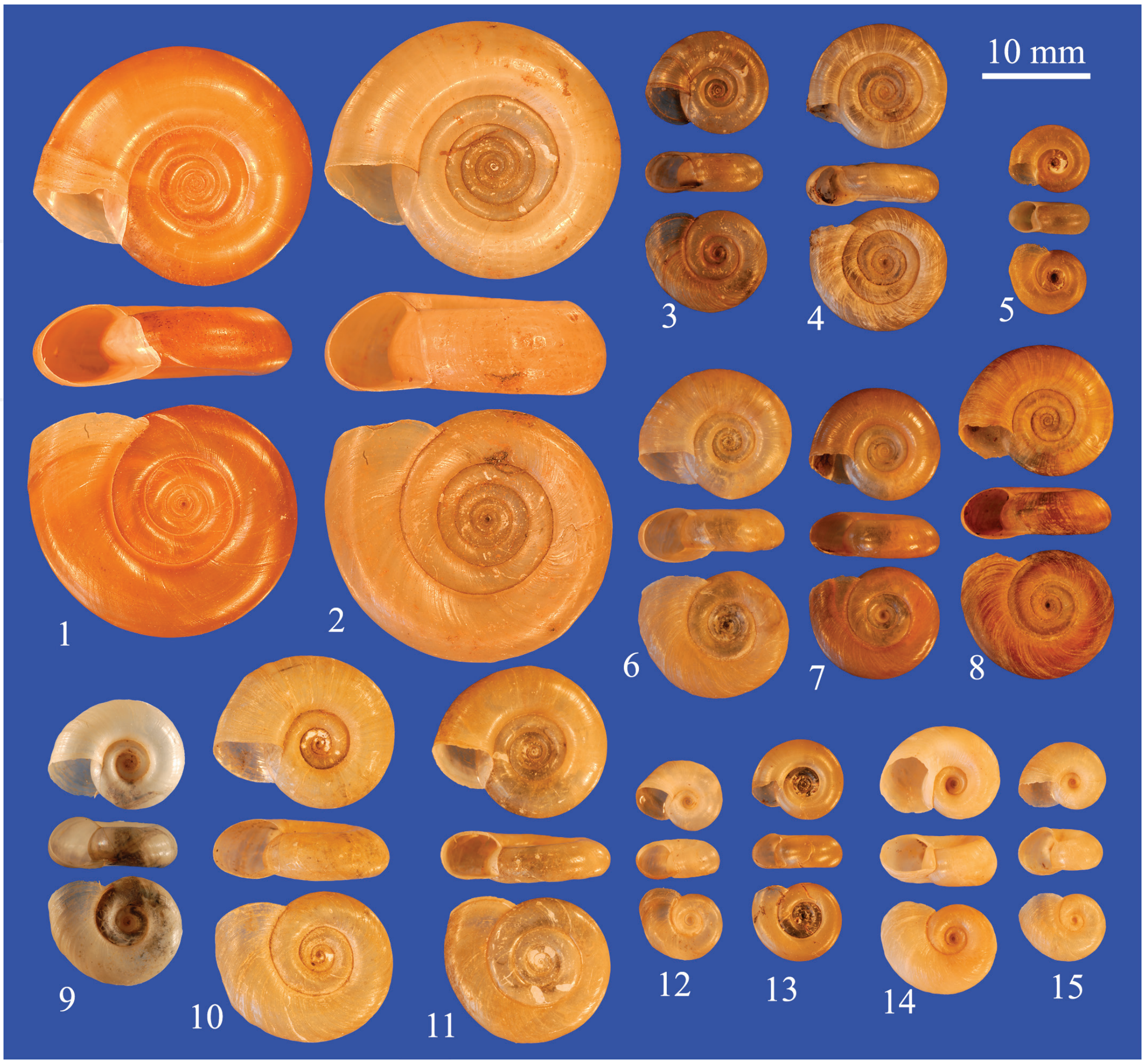

Figure 3.
Neotropical (1–5) and African (6–15) Biomphalaria species, B. glabrata (1), B. tenagophila (2), B. straminea (3), B. havanensis (4), B. helophila (5), B. alexandrina (6), B. angulosa (7), B. camerunensis (8), B. pfeifferi (9), B. salinarum (10), B. sudanica (11), B. choanomphala (12), B. rhodesiensis (13), B. smithi (14), B. stanleyi (15).

schistosomiasis [8]. Natural interactions and introgressive hybridisation between these species are common [8, 13, 14].

Each of the species of schistosomes infecting humans has a characteristic and limited intermediate snail-host spectrum. The intermediate hosts of *S. mansoni*, *S. haematobium*, *S. intercalatum*, and *S. guineensis* belong to the family Planorbidae or Bulinidae (previously a subfamily of the Planorbidae) while those of *S. japonicum*, *S. mekongi*, and *S. malayensis* are caenogastropods that belong to the Pomatiopsidae [15]. Various species of *Biomphalaria* serve as intermediate hosts for *S. mansoni* (**Figure 3**) and certain *Bulinus* spp. (**Figure 4**) are intermediate hosts for *S. haematobium*, *S. guineensis*, and *S. intercalatum*. For *S. japonicum*, species of the genus *Oncomelania* are the intermediate hosts (**Figure 4**). Species-level relationships within *Oncomelania* are not fully resolved but there seems to be four species that currently transmit *S. japonicum*, i.e., subspecies of *O. hupensis* in eastern China, *O. robertsoni* in western China, *O. quadrasi* in the Philippines and *O. lindoensis* on Sulawesi [16]. For *S. mekongi* and *S. malayensis*, the intermediate host is from the subfamily Triculinae, tribe Pachydrobiini, i.e., *Neotricula aperta* and *Robertsiella kaporensis*, respectively [17, 18] (**Figure 4**). More species can

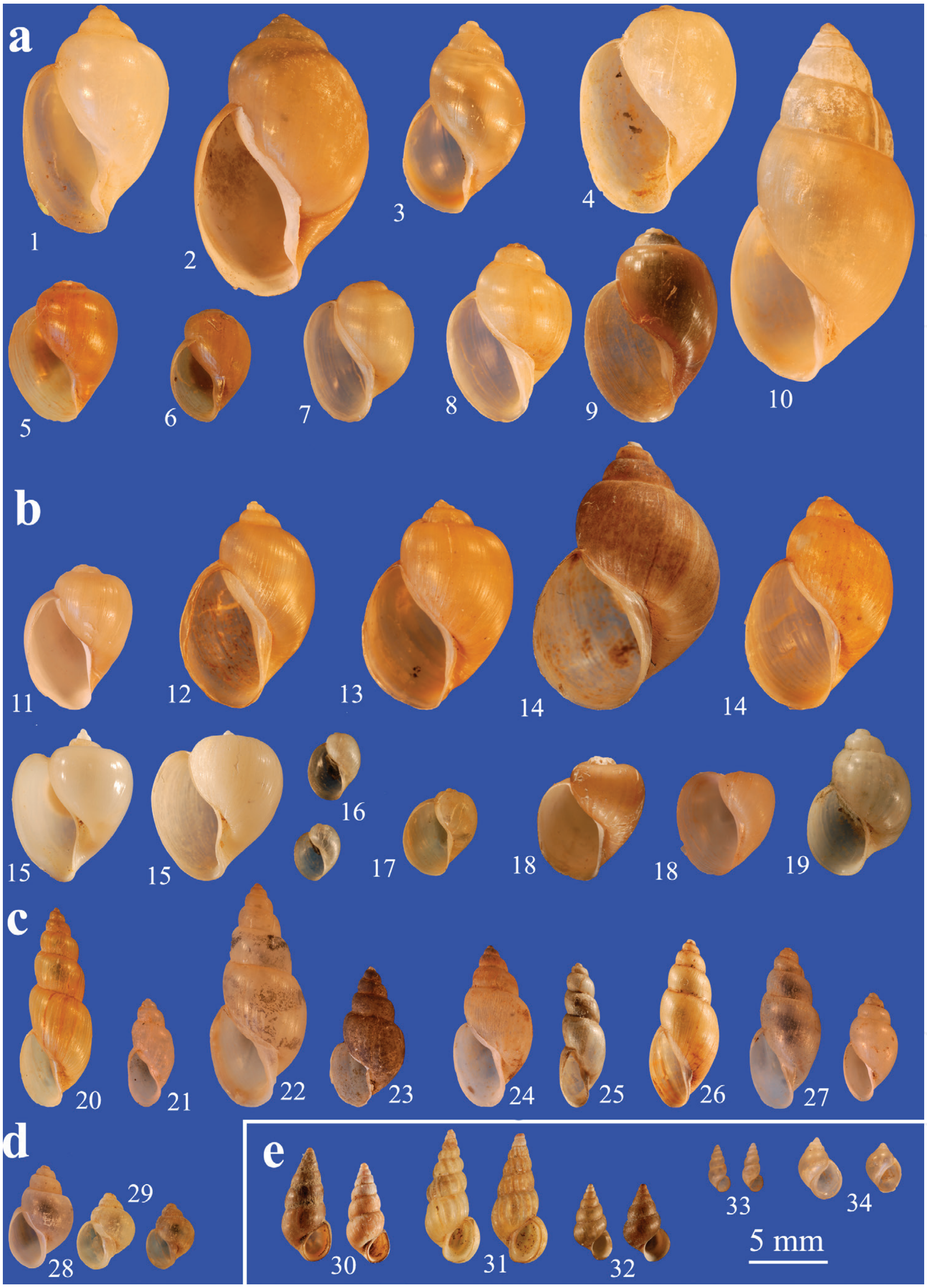

Figure 4.
Representative species of Bulinus, Oncomelania, Robertsiella and Neotricula. The B. africanus group (a): Bulinus abyssinicus (1), B. africanus (2), B. nasutus (3), B. ugandae (4), B. jousseaumei (5), B. obtusus (6), B. obtusispira (7), B. umbilicatus (8), B. globosus (9), B. productus (10). B. truncatus/tropicus complex (b): Bulinus angolensis (11), B. liratus (12), B. natalensis (13), B. tropicus (14), B. nyassanus (15), B. succinoides (16), B. transversalis (17), B. trigonus (18), B. truncatus (19). The B. forskalii group (c): Bulinus bavayi (20), B. beccarii (21), B. canescens (22), B. cernicus (23), B. crystallinus (24), B. forskalii (25), B. scalaris (26), B. senegalensis (28). The B. reticulatus group (d): B. reticulatus (28), B. wrighti (29). Asian species (e): Oncomelania hupensis smooth (30) form and ribbed form (31), O. quadrasi (32), Robertsiella kaporensis (33), Neotricula aperta (34).

be infected experimentally but they may not transmit the parasite in nature [19]. For example, there have been reports that *S. haematobium* was transmitted by *Ferrissia* in India; at least three endemic foci of human schistosomiasis have been described in India previously and sporadic autochthonous cases and cercarial dermatitis are also common (see references in [20]). Experimental exposure of *Ferrissia tenuis* to miracidia of *S. haematobium* showed that this snail could be infected and shed cercariae [21]. In the north-western extremity of Africa, *Planorbarius metidjensis* is common and although it is an experimental host for *S. mansoni* and *S. haematobium* [22, 23] there is no evidence that it is a natural host [23].

Snails may be widely distributed in an area, but there is a tendency for infected snails with *Schistosoma* spp. to be focally distributed in particular areas where infected people contaminate the water with their wastes. In some cases, human infections may be facilitated by prior contamination of habitats by reservoir hosts especially for *S. japonicum*, but also possibly for *Schistosoma mansoni* and *S. haematobium*. Snail populations undergo great seasonal variations in density and infection rates. Rainfall and/or temperature are the main causative factors. This results in the pattern of transmission commonly being of a focal and seasonal nature. Although prevalence of infection in the intermediate hosts may be low, this can result in a high percentage of human infections, e.g., in Lake Malawi [24].

2.2 Avian schistosome

Swimmer's itch or cercarial dermatitis is a short-term immune reaction occurring in the skin of humans that have been penetrated by cercariae of schistosomes (Schistosomatidae) that normally develop in birds or in mammalian hosts other than humans. Genera often associated with swimmer's itch in humans are *Trichobilharzia* and *Gigantobilharzia*, but species such as *Schistosomatium douthitti*, a parasite of rodents, may also cause swimmer's itch. In marine habitats, especially along the coasts, swimmer's itch can occur as well. Symptoms, which include itchy, raised papules, commonly occur within hours of infection and do not generally last more than a week. It is common in freshwater, brackish, and marine habitats worldwide and application of molecular diagnostic techniques has begun to unravel the many schistosome species that can be responsible [25]. Various species of Lymnaeidae, Physidae, Planorbidae, Bulinidae (see some species in **Figures 5** and **6**) and other taxa are intermediate hosts [25–28].

In Thailand, *Indoplanorbis exustus* together with *Lymnaea rubiginosa* are referred to as the "itchy snail" by rural people [29]. These snail species are hosts for a number of schistosomes including *Schistosoma spindale*, *S. indicum*, and *S. nasale*. Though these species do not develop to maturity in humans, they may cause cercarial dermatitis.

2.3 Paragonimus

Paragonimiasis, also known as pulmonary distomiasis, is a parasitic disease of humans and animals in various parts of the world, but principally in the Orient (Far East). Its etiological agents are species of the trematode genus *Paragonimus* which utilize caenogastropods (specifically superfamilies Cerithiodea and Truncatelloidea) as first intermediate hosts (see examples in **Figures 7** and **8**) and decapod crustaceans, primarily freshwater crabs and crayfish, as second intermediate hosts.

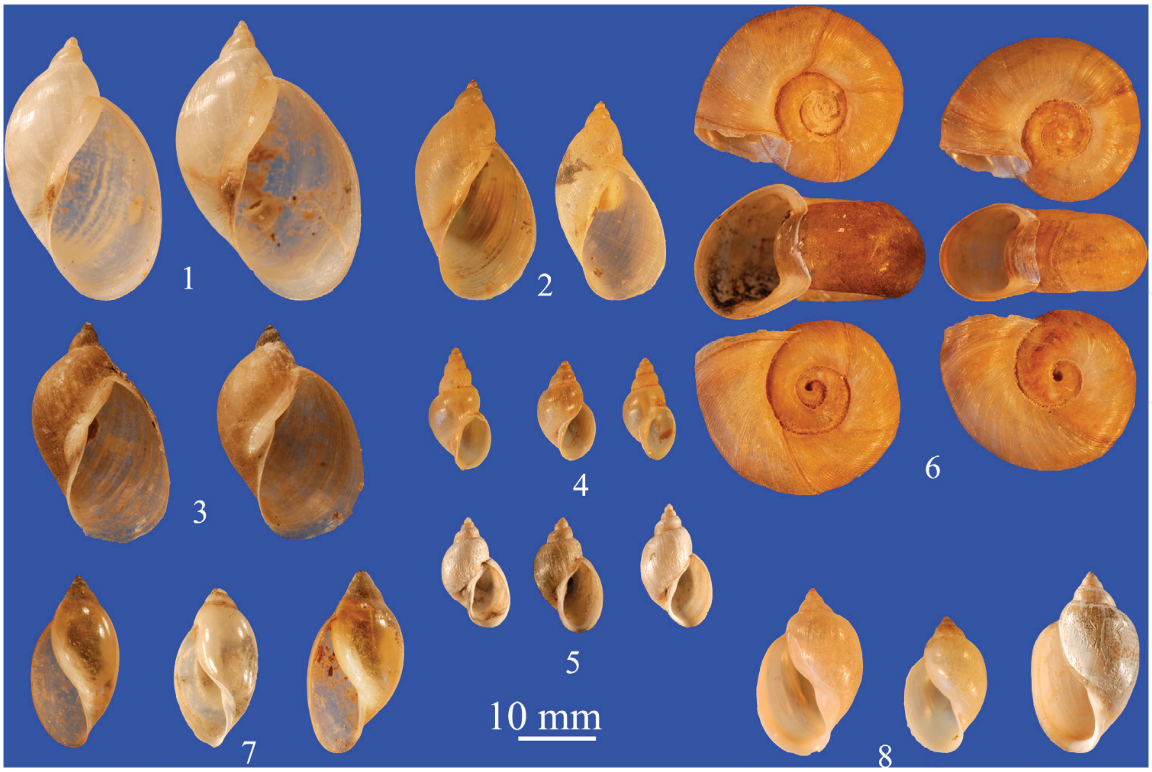

Figure 5.
Some species of the Lymnaeidae, Physidae and Bulinidae. Lymnaeidae: Radix natalensis (1), Pseudosuccinea columella (2), Radix auricularia (3), Galba truncatula (4), Austropeplea viridis (6). Bulinidae: Indoplanorbis exustus (6). Physidae: Aplexa waterloti (7), Physa acuta (8).

The genus *Paragonimus* contains several species that infect a variety of mammals and birds and some of these species affect other vertebrates. Lung fluke infections are distributed in certain parts of the World where food habits include eating raw crabs, and crayfish, which contain the infective metacercarial cysts. Several million people are thought to be infected with paragonomiasis and almost 300 million are at risk of infection [30, 31]. In Africa, *Paragonimus africanus* is important [32], while in Mexico and Central America *Paragonimus mexicanus* causes occasional human infections [30]. Similarly, in the Midwest states of the USA, a number of human infections with *Paragonimus kellicotti* have been reported. The main endemic areas are in the Orient and Southeast Asia. In these areas, the etiological agent in humans is mainly *Paragonimus westermani* [31].

The cercariae penetrate the soft body parts of the crustacean host and then invade the viscera and muscles of this host, where they usually become encysted in specific organs depending on the species of lung fluke and the species of the crustacean host (**Figure 9**). When the mammalian host, human or reservoir host ingests infected crab or crayfish meat or viscera (raw, soaked in rice wine, or salted), the metacercaria excyst in the duodenum and migrates through the intestinal wall in about an hour, reaching the abdominal cavity in 3–6 h. The larvae of various lung flukes enter and remain in the abdominal wall for several days (up to 3 weeks), then migrate through the diaphragm to the pleural cavity, where they penetrate the serosal layers of the lungs. Finally, they arrive near the bronchioles, where they develop to adult worms in pairs, and exist in tissue capsules laid down by the host, about 6–8 weeks after ingestion of the parasitized crustacean host. The lung capsules containing the worms connect with the respiratory passages of the lung, and the eggs of the parasite are moved along with lung exudates [33].

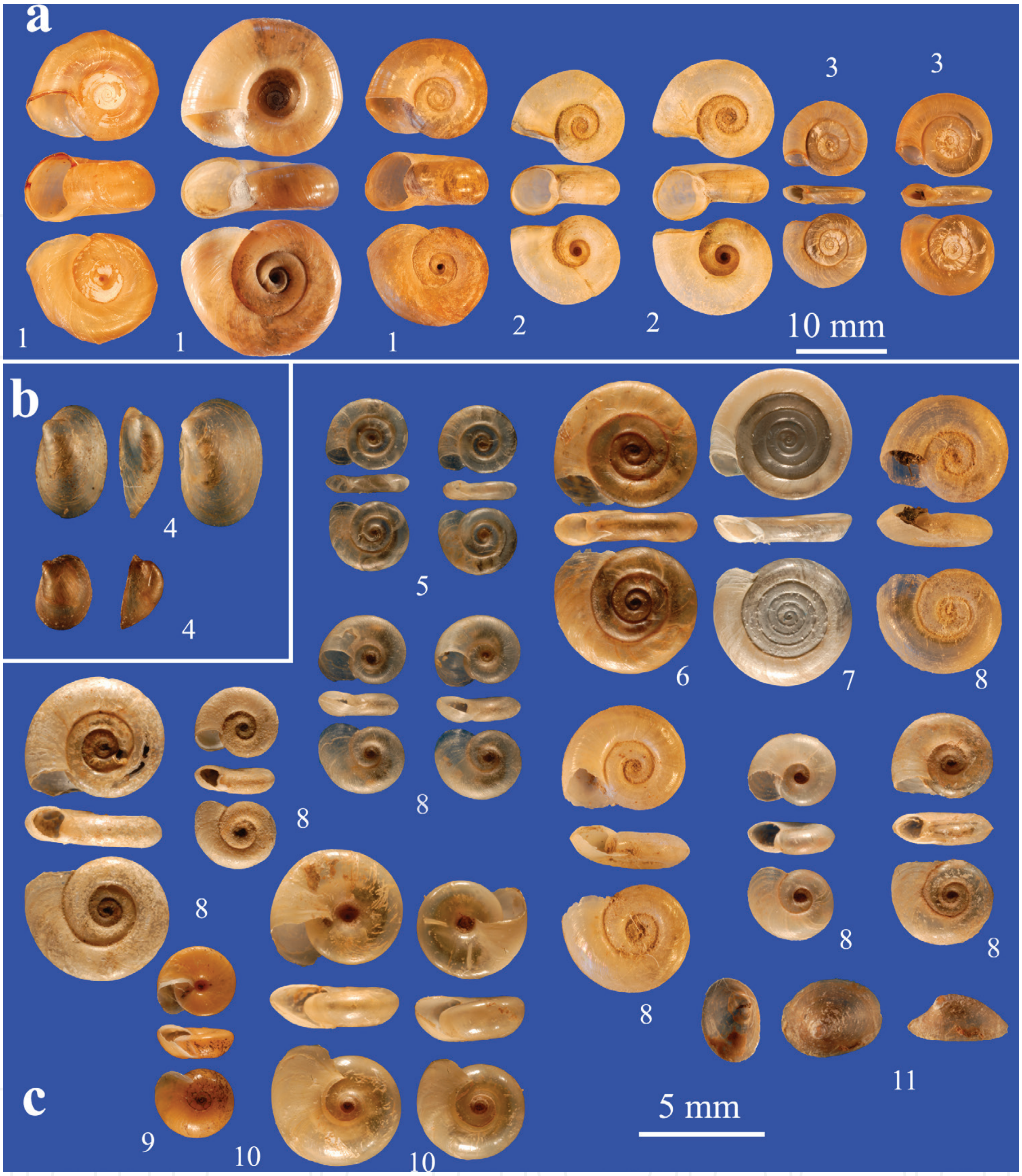

Figure 6.
Species of the Planorbidae (a and c) and Burnupiidae (b). Planorbidae: Planorbella (Helisoma) duryi (1), Planorbarius metidjensis (2), Planorbis planorbis (3), Africanogyrus coretus (5), Ceratophallus natalensis (6), Drepanotrema sp. (7), Gyraulus spp. (8), Polypylis hemisphaerula (9), Segmentorbis spp. (10), Ferrissia sp. (11). Burnupidae: Burnupia sp. (4). The scale shown in part c is also used for part b.

2.4 Fish-borne zoonotic trematodes (Clonorchiasis, Opistorchiasis, and Heterophyidiasis)

Fish-borne zoonotic trematodes utilize fish as their second intermediate host and comprise about 12 families, and five of these, Clinostomatidae, Echinostomatidae, Heterophyidae, Opisthorchiidae, and Troglotrematidae have been reported to infect humans. Among those, the opisthorchid flukes have the most public health importance [34]. It has been recognized as a Type I carcinogen, and chronic infection by this liver fluke leads to cholangiocarcinoma development. The heterophyid intestinal

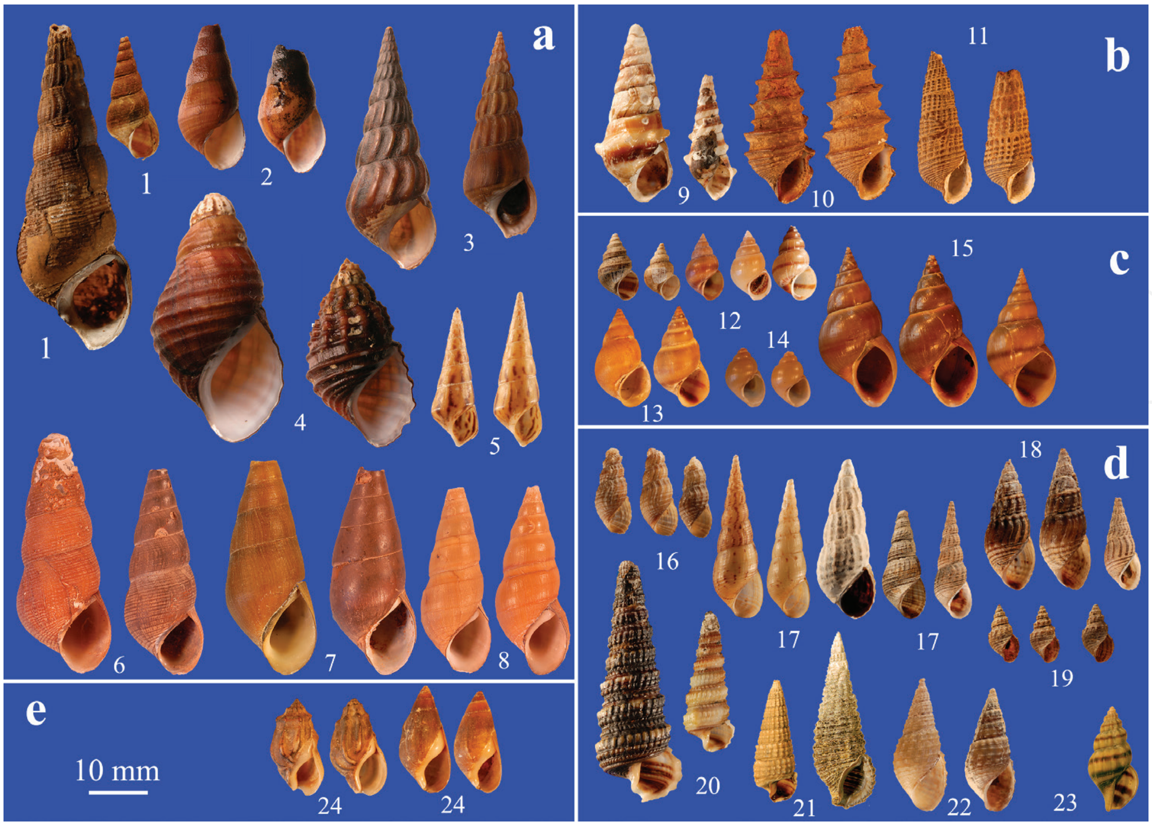

Figure 7.
Selected species of Pachychilidae (a), Heminiscidae (b), Paludomidae (c), Thiaridae (d) Potamididae (d), Melanopsidae (e) and other (d). Pachychilidae: Brotia sp. (1); Brotia costula (2); Brotia swinhoei (3); Sulcospira aubryana (4); S. housei (5); Potadoma moerchi (6); P. freethi (7); P. liricincta (8). Heminiscidae: Pachymelania aurita (9); Pachymelania fusca (10, 11). Paludomidae: Cleopatra bulimoides (12); C. nsedwensis (13), C. ferruginea (15) Pseudocleopatra togoensis (14). Thiaridae: Melanoides jugicosta (16), M. tuberculata (17), Sermyla riqueti (18), Thiara scabra (19), Tarebia granifera (22), Potamididae: Tympanotonus fuscatus (20), Cerithidea sp. (21). Melanopsidae: Melanopsis spp. (24). Other: Anentome helena (23).

fluke sometimes coexists in the endemic region of the liver fluke and can cause confusion in diagnosis and prevalence since eggs of both the opisthorchid and heterophyid flukes are similar. An overview of the various species is given in Waikagul and Thaenkham [34] and Hung et al. [35].

Fully embryonated small eggs of *C. sinensis* are found in the stools of infected humans and other mammalian hosts (e.g., dogs and cats). These eggs do not hatch until they are eaten by the snail, the first intermediate host [36]. For *C. sinensis*, the snail hosts are species of caenogastropods of the family Bithyniidae (*Parafossarulus*, *Bithynia*) or Semisulcospiridae (*Semisulcospira*). In addition, species of the Thiaridae, especially *Melanoides tuberculata* have been reported as hosts for *C. sinensis* [37] but experimental infection of this species failed [38]. The miracidia hatch in the esophagus, intestine, or rectum of the snail, and then penetrate the wall of these organs to become sporocysts developing in the hemolymph spaces of the snail (**Figure 10**). Rediae develop and migrate to the digestive gland area and form cercariae, which soon leave the snail and swim in the adjacent water [36]. They then penetrate the skin of the fish second intermediate host and become encysted metacercariae in the muscles. The metacercariae become infective within a month, and when the infected fish is ingested raw, or slightly cooked or pickled, by man or eaten by other mammalian hosts, the metacercariae excyst and make their way to the liver, which they reach in about a day or less. After reaching the bile passages, the young worms mature. The

Figure 8.
Selected species of the Truncatelloidea. Bithynia fuchsiana (1), Bithynia sp. (2), Digoniostoma siamensis (3), Alocinma longicornis (4), Parafossarulus manchouricus (7), Gabbiella stanleyi (5), Gabbiella senaariensis (6), Assiminea sp. (8), Hubendickia sp. (9), Pachydrobia spp. (10, 11), Fairbankia sp. (12), Julienia sp. (13), Stenothyra spp. (14), Neotricula aperta (15), Robertsiella kaporensis (16).

first eggs are laid about 4 weeks after infection, but the worms continue to grow for some additional months. In addition to humans, dogs, cats, pigs, and rats have been found naturally infected and constitute effective reservoir hosts. In some regions where prevalence of infection among humans is very low or lacking, as in some parts of China and Vietnam, prevalence of infection is usually high among other mammals. Cats, rabbits, and guinea pigs are good experimental hosts.

Clonorchiasis is caused by the fluke *Clonorchis sinensis* (China, Japan, Korea, Russia, Thailand, and North Vietnam), and human opisthorciasis is caused by primarily *Opisthorchis viverrini* (Cambodia, Lao PDR, Thailand, Central and South Vietnam) or *O. felineus* (The Baltic States, eastern Germany, Italy, Kazakhstan, Poland, Russia, Eastern Siberia, and Ukraine) and is contracted through eating raw infected fish [34]. These trematodes have very similar life cycles.

Heterophyidae comprises several genera and species of trematodes of almost worldwide distribution. More than 25 species have been found parasitizing humans around the World [34, 35]. The heterophyid is a small-sized fluke, about 1 mm in length, and is parasitic mostly in the small intestine of birds and mammals and rarely in fish and reptiles.

The worms are usually found lodging in intestinal mucosa between villi, however, they have invaded the submucosal level in experimental immunosuppressive mice. Within a week after the metacercaria is ingested by the definitive host, metacercaria develop to mature adults in the intestine. Heterophyid adults have a short life; the reported life spans varied among different host species [34, 39].

Fish-borne zoonotic trematodes (FZT) are an important problem and fish produced in aquaculture may present a food safety risk in some areas of

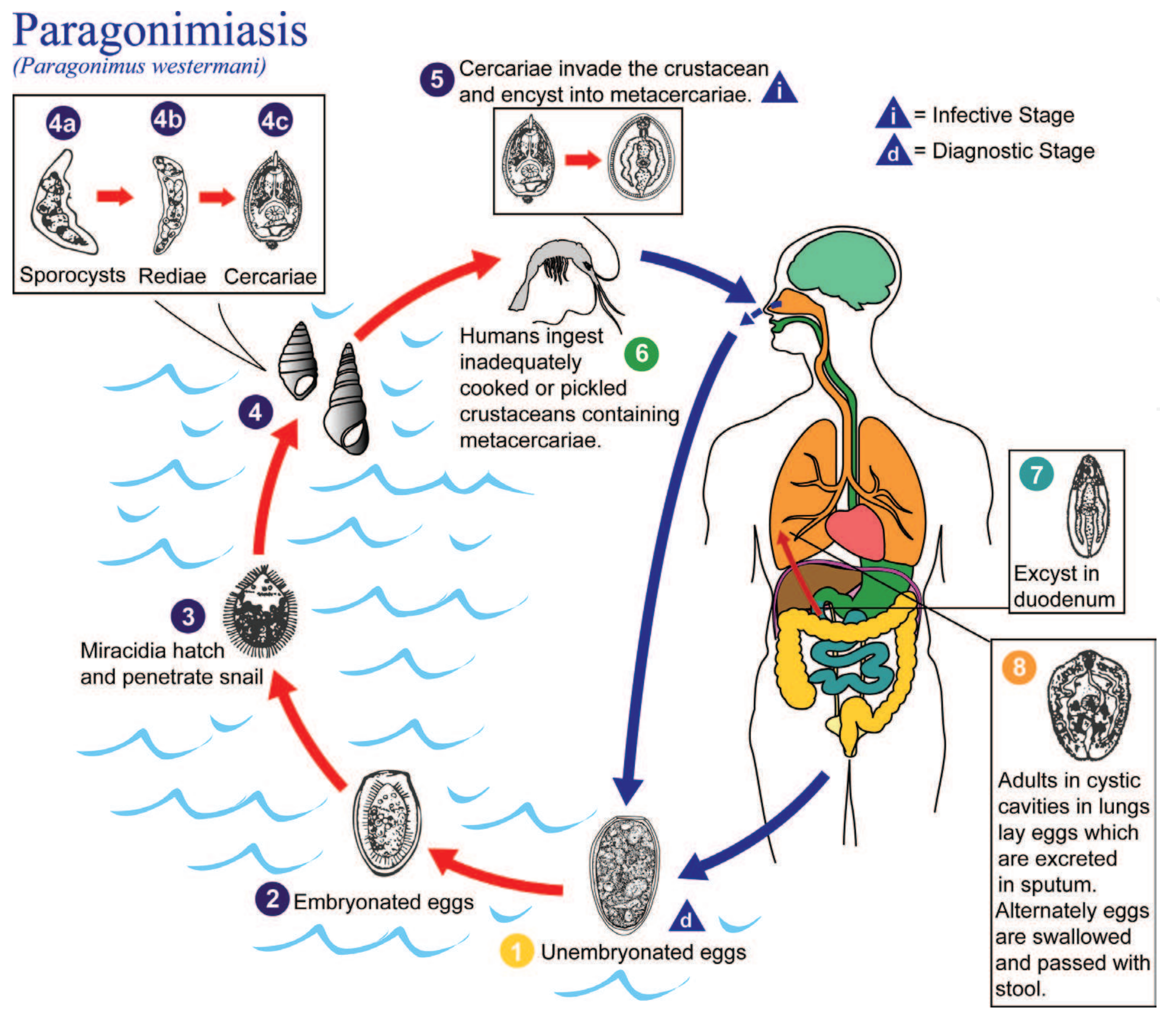

Figure 9.
Life cycle of Paragonimus westermani (source: Alexander J. da Silva & Melanie Moser, public health image library (PHIL), Centers for Disease Control and Prevention).

Southeast Asia where aquaculture is very important [36]. In at least parts of Vietnam, however, transmission of *C. sinensis* is not common in aquaculture ponds and usually occurs in natural habitats [40]. On the other hand, heterophyid trematodes are very common in aquaculture ponds. The fish culture industry may have aggravated the situation in some areas, although *C. sinensis* and *O. viverrini* mainly are transmitted in natural waterbodies. Large and small lakes and ponds are used for culturing fish, and these bodies of water are usually polluted with human and animal excreta containing eggs of FZT. Because raw fish are mainly eaten by adults, infections with clonorchiasis are, in general, more prevalent in the higher age groups (30–50 years); this is usually consistent in all endemic areas.

2.5 Echinostomatidiasis

The superfamily Echinostomatoidea is a large, cosmopolitan group of digeneans currently including nine families and 105 genera, with the vast majority parasitic, as adults, in birds with relatively few taxa parasitizing mammals, reptiles, and exceptionally, fishes [41]. Recent studies on the phylogeny of the group combining morphology and molecular data have resulted in several changes [41].

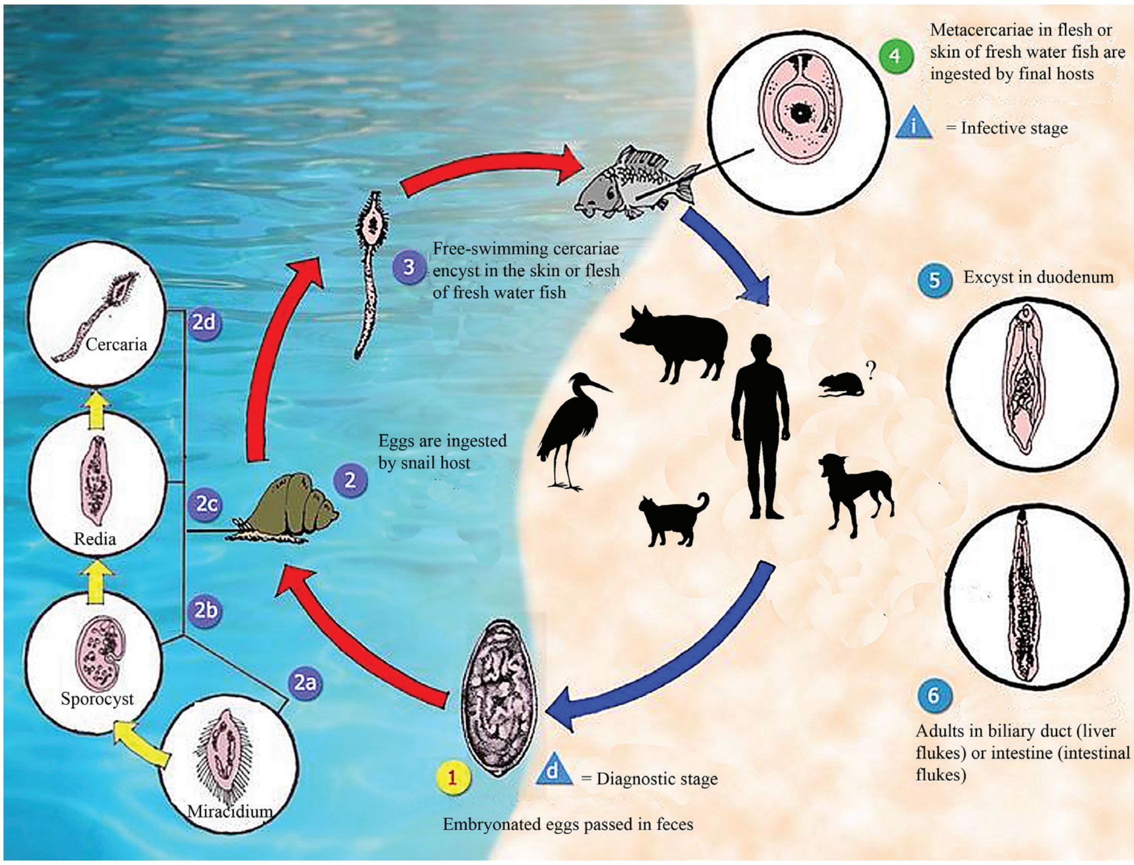

Figure 10.
Life cycle of fish-borne zoonotic trematodes (Opistchorchidae and Heterophyidae) (source Clausen et al. [36]).

Echinostomatidiasis is caused by a number of fluke species, belonging to the Echinostomatidae, which share certain morphological features, among which are the presence of a head collar surrounding the oral sucker, provided with a single or double crown of large spines which are larger than those covering the body surface. They are usually stout, fleshy, medium-sized flukes parasitizing birds and mammals in various parts of the world [42]. Several birds, during their migration, carry the infection with several echinostome species along their migratory routes. Various life cycle patterns are exhibited by echinostomes. Usually they are less specific than schistosomes as to their first or second intermediate hosts or their definitive hosts. The first intermediate hosts are several species of aquatic Hygrophila or Caenogastropods and the second intermediate hosts are the same or other species of snails, bivalves, tadpoles, or fish. The cercariae of certain species do not require a second intermediate host but, instead, encyst in the open.

Echinostomes are usually harmless flukes in the intestine of their hosts. Certain species, however, and heavy infections of the harmless species, produce some pathology and pronounced symptoms in poultry and small mammals. They are, therefore, of significance in veterinary medicine.

Transmission of the echinostome to humans is either through eating raw or undercooked fish, snails, or amphibians. Human cases have been reported mostly in Asia. Duodenum mucosal bleeding and ulceration are the main clinical findings due to mechanical damages caused by the worms. The common symptoms are abdominal pain and diarrhea followed by weakness and weight loss [42].

2.6 Fascioliasis

Fascioliasis, a disease caused by the liver flukes *Fasciola hepatica* and *Fasciola gigantica*, is cosmopolitan in distribution and occurs in sheep- and cattle-raising countries of the world, parasitizing these animals and other herbivores on almost every continent and on several islands. In Europe, diseases of sheep and cattle are found in every country, and they manifest in the form of epidemics among humans, especially in England, France, and Italy. Human fascioliasis has also been reported from Mexico, South and Central America, Asia, Africa, and Australia and is believed to be more common than has been thought. This could be ascertained if there were more accurate diagnostic methods and better reporting [43].

Fascioliasis due to *F. hepatica* generally occurs in temperate climates, and thus the disease is prevalent in Europe, North America, northern Asia, Australia, and northern Africa [44]. It is also present in the highlands of Kenya, in South Africa, and in Central and South America. *F. gigantica*, on the other hand, is the common liver fluke in widespread areas of Africa and Asia. In some parts of the world, the geographical distribution of *F. gigantica* overlaps that of *F. hepatica*.

The life cycle of *F. hepatica* is illustrated in **Figure 11**. Adults reside in the intrahepatic biliary ducts of the mammalian host. The eggs are laid in the bile

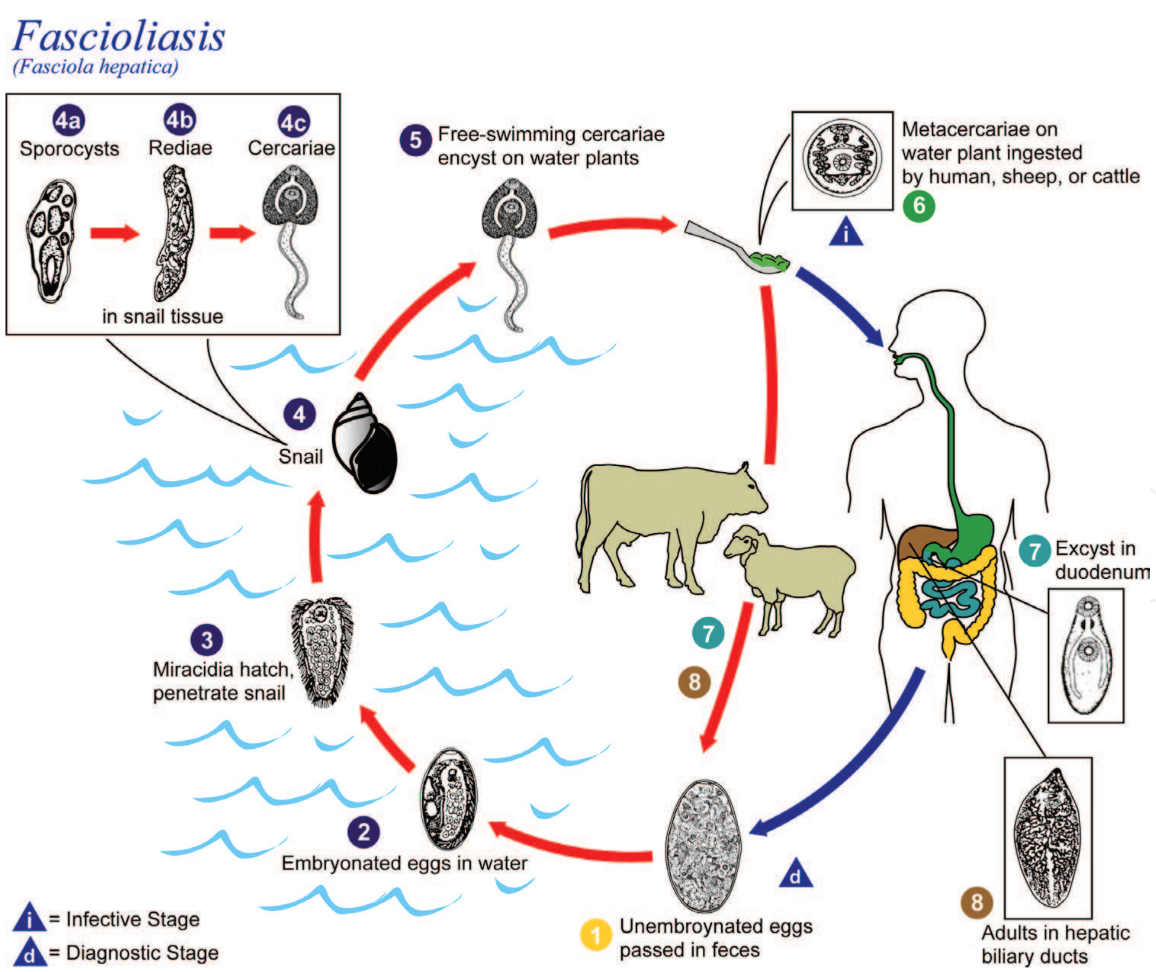

Figure 11.
Life cycle of Fasciola hepatica (source: Alexander J. da Silva & Melanie Moser, public health image library (PHIL), Centers for Disease Control and Prevention).

ducts, proceed to the intestine with the bile, and are evacuated with the feces. The development of the eggs in the water takes from 10 to 15 days at an optimal temperature of 23–25°C. The fully developed miracidium escapes from the egg. The miracidium swims actively in the water and tries to invade various snail species of the Lymnaeidae (**Figure 5**) in different geographic areas of the world. The sporocyst developing from each miracidium near the site of penetration, usually in the mantle edge, the kidney and the esophageal area, produces rediae in about 2–3 weeks. The latter move actively and migrate to the distal area of the snail, containing mainly the digestive gland. Within the body of rediae, cercariae are produced which exit the snail and actively swim in the water. Development of *Fasciola* in the snail host is affected by the environment, in particular temperature. Cercariae encyst rapidly on aquatic vegetation, grass, bark, or any floating debris, or encyst free in the water, and may either float or settle to the bottom of the water. The metacercarial cysts are resistant and remain viable for a long period but are killed by excessive heat and dryness.

Mammalian hosts, including humans, consuming aquatic vegetation with metacercariae or drinking water from contaminated snail habitats containing the metacercariae, contract the infection. The metacercariae, soon after ingestion, excyst in the small intestine. After excystment, they penetrate the wall of the small intestine to the abdominal cavity. They have been found in the latter cavity 1–3 days from the time that they have been ingested, depending on the species of the host. They wander around in the viscera and may settle and become established in ectopic sites other than the liver.

2.7 Paramphistomatidiasis

The paramphistome flukes are represented by many species throughout the world, and they are parasites of the alimentary tract (stomach and intestine) of humans, nonhuman primates, ruminants, equines, and other herbivores; only about two species occur in birds [45]. These flukes are large fleshy parasites, measuring up to 20 mm in length and 15 mm in width. Some of these flukes cause gastrodisciasis or paramphistomiasis. Whereas gastrodisciasis is restricted to Africa and Asia, paramphistomiasis occurs throughout the world [46].

Three important intestinal parasites cause gastrodisciasis: *Gastrodiscoides hominis*; *Gastrodiscus aegyptiacus*, and *Gastrodiscus secundus*. High prevalence rates have been reported from humans in various parts of India, but the parasite was also found in the Philippines, Kazakhstan, Vietnam, and from Indian immigrants in Guyana. In some countries, *G. hominis* infecting humans is a different strain from that infecting pig. *Gastrodiscus aegyptiacus* and *G. secundus* are common parasites of equines in Africa and Asia, and several pathological cases are on record in horses in Africa.

Infections with all the paramphistomatids (including the gastrodiscids) are acquired from the same habitats where the animals also contract fascioliasis, bovine schistosomiasis, and others, where various species of snails live together. The life cycle, though differing in minute details, is similar to that of *Fasciola* spp.

Like the fasciolid flukes, the paramphistomatids utilize freshwater pulmonate snails as intermediate hosts. Whereas *Fasciola* spp. utilize only lymnaeid snails throughout their wide geographical area, some rumen paramphistomes, such as those in the U.S., use lymnaeid snails, while other paramphistomes, and also gastrodiscids, utilize planorbid snails in other parts of the world.

3. The first intermediate hosts (overview of major clades of the Gastropoda)

Trematodes require one or two intermediate hosts to complete their life cycle. The first intermediate host is specific species of freshwater water (and for some trematode species brackish or marine) gastropods. Due to the necessity of passing through the gastropods, control of these snails could, at least for some of zoonotic trematodes, be an important way to reduce their transmission (see later).

The class includes the snails, which are superficially asymmetrical and possess a spirally coiled shell; the limpets, which possess a low, conical un-spiraled shell; and the slugs, which possess a concealed shell or no shell at all. A recent paper [47] estimates the number of named and valid recent species as about 63,000 in 476 families. There is a great diversity among the freshwater gastropods. Gastropod taxonomy has undergone considerable revision and still undergoes revision as new DNA data become available. Here we use the classification as described in Bouchet et al. [47].

The class, Gastropoda, contains the following subclasses: Patellogastropoda, Neomphaliones, Vetigastropoda, Neritimorpha, Caenogastropoda, and Heterobranchia of which the last three are represented in freshwater. Many of the existing identification keys to freshwater gastropods follow the classification of Thiele [48] where Gastropoda was divided into three sub-classes Prosobranchia (Streptoneura, i.e. crossed nerve system), Pulmonata and Opisthobranchia (Euthyneura). Using the existing keys for species identification of freshwater snails, however, does not pose a real problem. Thus, Prosobranchia (often called prosobranchs) equates Caenogastropoda plus Neritidae and Pulmonata (often referred to as pulmonates) equates Hygrophila within the Panpulmonata. We shall restrict our discussion to primarily the freshwater gastropods.

3.1 Subclass: Neritomorpha

3.1.1 Neritidae and Neritilidae

The Neritidae are one of the most abundant groups of freshwater snails in the coastal streams of tropical and subtropical regions worldwide, as well as in the inland waters of the European continent [49]. The Neritiliidae, previously a subfamily in the Neritidae, include 23 described species in seven genera from low latitude areas of the World. Species of *Neritilia* occur in freshwater streams to brackish estuaries [50]. These are species of medium-sized snails with a characteristic shell, radula and operculum. Neritids require hard substrata for their grazing and locomotion, and some species of *Dostia* and *Septaria* can exclusively be found on branches and drift logs in estuaries and mangrove swamps [49]. These markedly euryhaline neritids have the potential to survive in fully marine conditions for some extended period of time and to disperse as benthic adults and eggs on drift logs [49]. The families are not known as intermediate hosts for medical or veterinary important trematodes, but some species may harbor other trematode or nematode infections. Examples of species are shown in **Figure 12**.

3.2 Subclass: Caenogastropoda

3.2.1 Viviparidae

The family (**Figure 12**) has a global distribution and moderate diversity [51] in the extant fauna (125–150 valid, described species). Viviparids are distributed primarily in

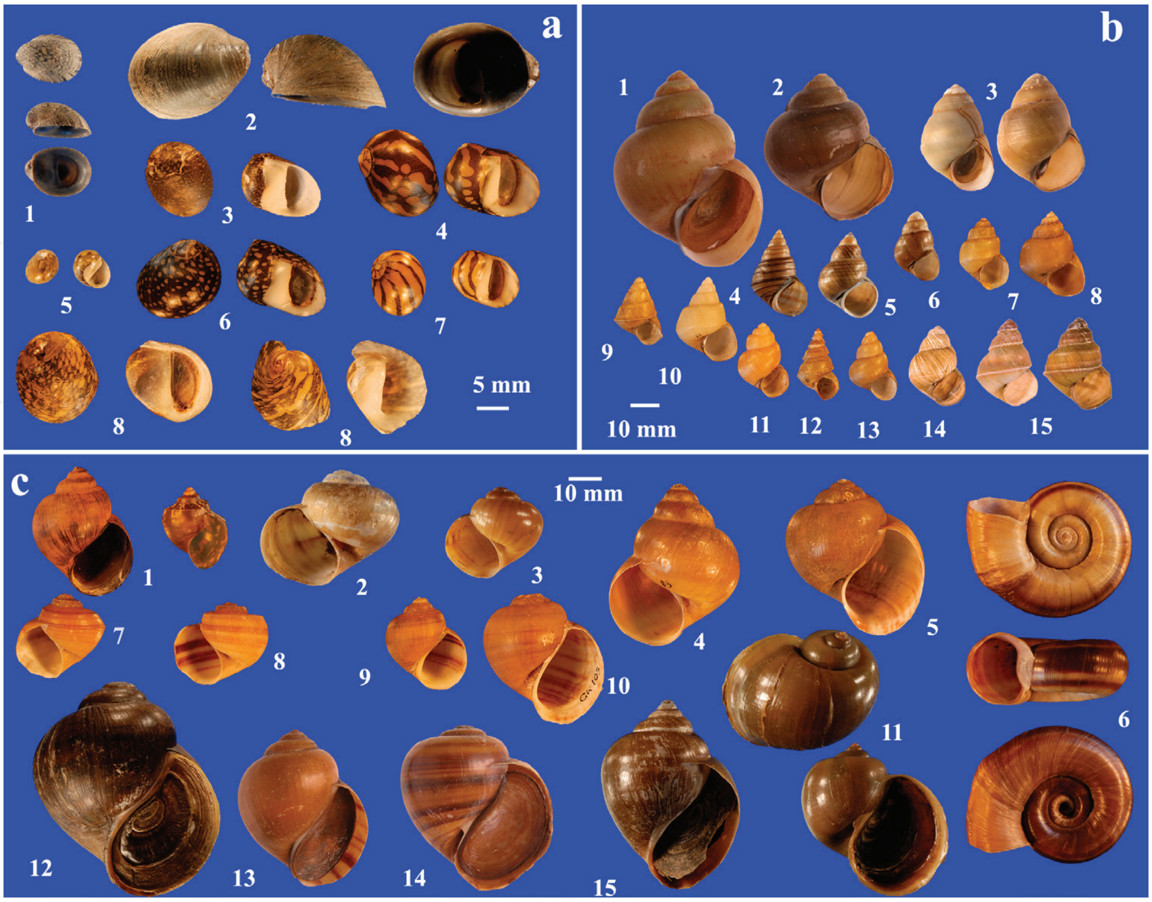

Figure 12.
Selected species of Neritidae (a), Viviparidae (b) and Ampullariidae (c). Neritidae: Dostia violacea (1, 2), Neritina afra (3, 5), N. natalensis (4, 6, 7), N. oweniana (8). Viviparidae: Cipangopaludina chinensis (1), C. lecythoides (2), Mekongia lithophaga (3), Angulyagra polyzonata (4), Filopaludina sumatrensis (5), Sinotaia aeruginosa (6), various African Bellamya spp. (7–15). Ampullariidae: Saulea vitrea (1), Lanistes spp. (2–4, 7, 8), Marisa cornuarietis (6), Pila ovata (5), Afropomus balanoidea (9), Pila africana (10), Pomacea canaliculata (11), Pila sp. (12), P. conica (13), P. ampullacea (14), P. polita (15).

lakes, rivers, and streams in temperate to tropical regions. Although they can be found in freshwater of all kinds, many species prefer, or are restricted, to one habitat type only. Their greatest diversity occurs in tropical and subtropical regions of Asia, where some 60–85 species occur. These species are medium to large snails usually with a conical shell. Tentacles are short and pointed and the right tentacle of males is transformed into a copulatory organ. The females are ovoviviparous with a uterine brood-pouch. Size and number of mature embryos may be of help to taxonomists [29]. The family is quite diverse in Asia where representatives are commonly consumed by humans. Metacercariae of the Echinostomatidae and possibly other trematodes are commonly found in viviparid snails and since many species are eaten by local people they could serve as intermediate hosts for human trematode infections if consumed insufficiently cooked. Species within the family are also reported as first intermediate hosts of some species of echinostome [51]. Some if not all species within the family are suspension feeders giving them a competitive advantage over species that only graze.

3.2.2 Ampullariidae

Ampullariidae (**Figure 12**) are predominately distributed in humid tropical and subtropical habitats in Africa, South and Central America, and Asia. The family includes 186 recent species with the majority in the three genera *Pomacea* (96 species), *Lanistes* (43 species), and *Pila* (29 species) [52]. These are large or very large species (some species can reach shell height or diameter of about 10 cm). The animal has a short rostrum that carries a tentacle-like process (pseudopodia) on either side. Tentacles are very long and thin, the eyes are placed on separate stalks beside the tentacles. The mantle cavity is separated into two parts by a septum; the right side contains the gill, the left side serves as a lung. The male has a copulatory organ formed by part of the mantle edge. Some species may harbor metacercariae of trematode species, i.e., *Echinostoma* spp. and it may also serve as first intermediate host for some avian schistosomes or echinostome species. *Pila* spp. deposit egg masses in damp soil, *Pomacea* deposit their egg masses on various objects above the water while *Lanistes* spp. deposit gelatinous egg masses in water. Only one genus, *Pila*, is represented in Asia but *Pomacea* spp., which were introduced into Asia for commercial purposes have become a very prominent element of the gastropod fauna in Asia. *Pomacea* spp. were originally introduced to Taiwan and later to other Asian countries and has become pests of wetland rice and other crops causing massive economic losses. Especially, *P. canaliculata*, the Golden Apple Snail, is effective in spreading and has become a major pest in the area. Apple snails have highly diverse feeding mechanisms (shredding, scraping and collecting) to exploit diverse food sources. *M. cornuarietis*, which has a discoid shell (**Figure 12**), has potential in biological control of schistosome intermediate hosts and it has been introduced in Africa [53–55]. Due to the unforeseeable potential impact of such introductions, further introduction or propagation of the species outside its original area of distribution should be discouraged.

3.2.3 Superfamily: Cerithioidea

The Cerithioidea (**Figure 7**) is a superfamily within the Sorbeoconcha and comprised of marine, brackish water, and freshwater gastropods containing more than 200 genera. The freshwater species are found on all continents, except Antarctica. They are dominant members of mangrove forests, estuarine mudflats, fast-flowing rivers, and placid lakes. The shell is generally turreted, sometimes ovoidal-conic, rarely subglobose. It can be smooth or with spiral and/or axial sculpture, sometimes with spiral microsculpture. The operculum is corneous, generally spiral, rarely concentric; it is retractable into the shell. The male reproductive organs are without a verge. Female reproductive organs often have a brood pouch, generally with an egg transfer groove. Many species seem to be parthenogenetic.

The superfamily contains the Hemisinidae [56], Melanopsidae [57], Pachychilidae [58], Paludomidae [59], Pleuroceridae [60], Semisulcospiridae [61], and Thiaridae [62]. Only some of these families are described further below. Some of these species are important as intermediate hosts for medically important trematodes, e.g., Semisulcospiridae is an important host for *Paragonimus westermani* and some species for *C. sinensis*.

3.2.4 Potamididae

The family has a circumtropical, distribution but is also found in moderate climates. The Potamididae (mudwhelks or mud creepers) are small to large brackish water snails that live on mud flats, mangroves, and similar habitats. The trees provide the snails with shelter, protection from predators, a solid substrate, and sometimes food [63]. Some species are intermediate hosts for some fish-borne zoonotic trematodes.

3.2.5 Pachychilidae

Pachychilidae are a group of freshwater gastropods only recently recognized as an independent freshwater radiation within the diverse and predominantly marine gastropod superfamily Cerithioidea [58]. Pachychilids were previously assigned to other cerithioidean freshwater families, such as Thiaridae or Pleuroceridae. Pachychilidae has a circumtropical distribution with the freshwater inhabiting *Pachychilus* and *Doryssa* from South and Central America, *Potadoma*, from tropical western Africa and the Congo River drainage system, and *Madagasikara* from Madagascar [58]. Asian taxa include *Paracrostoma*, *Sulcospira* and *Brotia* from Southeast Asia [58].

Pachychilid gastropods are a conspicuous element of the freshwater macroinvertebrate fauna of Southeast Asia. In this region, three spatially separated groups of pachychilids can be differentiated mostly by means of their brooding strategy [64]. Pachychilids have rather heavy, thick shells and are not eaten by molluscivores in experimental studies [65]. They often occur at very high density [66]. Some species have rather specialized habitat requirements, and this may make them more vulnerable to habitat degradation, modification, and pollution [67].

3.2.6 Thiaridae

The Thiaridae form a monophyletic group with its constituent species being probably autochthonous in Southeast and South Asia, Australia, and some Pacific Islands, as well as sub-Saharan Africa, both in lotic and lentic freshwater environments, with some species also tolerating brackish conditions in the lower courses and estuaries of rivers [62]. Some species, such as *Melanoides tuberculata*, have an extraordinarily high invasive potential and today have an almost circumglobal distribution in tropical and subtropical biomes [62]. This spread apparently has assisted in the elimination of schistosomiasis from the Caribbean [68]. The females are ovoviviparous and the young are brooded within a non-uterine subhaemocoelic brood pouch situated in the right headfoot and extending deep into the neck region above the columellar muscle. Functional males have been found in a few species.

Some populations of *M. tuberculata* are comprised of only females reproducing parthenogenetically, while males may appear only during periods of environmental stress, for example high level of infection. Relatively few studies have been done on population dynamics of thiarid snails. Dudgeon [69] found that there was a single peak in juvenile recruitment coinciding with the warmer months; hatchlings grew quickly and were sexually mature before the next breeding season. Thiarid snail species, but in particular *M. tuberculata*, are very abundant in fishponds in Vietnam and Thailand [70, 71].

The family is very important as intermediate hosts for heterophyid intestinal trematodes and possibly *Paragonimus westermani*. Some papers mention that selected species also are intermediate hosts for liver flukes [37], but this has been questioned by others [70].

3.2.7 Paludomidae

The genera and species suggested to be included in the Paludomidae have hitherto been classified as Thiaridae, especially the endemic thalassoid species from Lake Tanganyika [59]. Generic diversity of African paludomids is concentrated in the Lake Tanganyika basin and adjacent water bodies, with only two genera, *Cleopatra* and *Pseudocleopatra* recorded from outside of this region. The genus *Cleopatra* is widespread in rivers, lakes, and even temporary water bodies of sub-Saharan Africa reaching North Africa through the Nile River system and in Madagascar, while *Pseudocleopatra* is reported from Ghana and the Congo River basin [59].

3.2.8 Superfamily: Truncatelloidea

Families within this superfamily were earlier included in the Rissooidea which was one of the largest and most diverse molluscan superfamilies, with about 23 recognized recent families, including marine, freshwater, and terrestrial members. The freshwater, brackish water, and semiterrestrial families and genera were moved to Truncatelloidea [47]. Most families contain small-sized species (**Figure 8**) and several species have medical and/or veterinary importance. The following families belong to this superfamily: Amnicolidae, Assimineidae, Bithyniidae, Cochliopidae, Helicostoidae, Hydrobiidae, Lithoglyphidae, Moitessieriidae, Stenothyridae, and Tateidae. Detailed reviews of these families are found in Refs. [16, 72–79]. Here, we present a brief overview of selected families.

3.2.9 Assimineidae

The species are mostly amphibious, spending most of the time outside the water on wet mudflats under stones, on decaying wood or in the stumps of palms [29]. Some species, however, are fully aquatic [29]. They are found in drainage creeks, in the estuaries of rivers, and in trenches and ponds in freshwater within the tidal zone [29]. The animals are oviparous with free-swimming larvae. *Assiminea lutea* was reported to harbor microcercous cercariae of *Paragonimus*, probably a species infecting non-human final hosts [29]. Brandt [29] checked several thousand specimens of *A. brevicula* and *A. obtuse* from Thailand for cercariae but no infected snails were found.

3.2.10 Bithyniidae

The family (**Figure 8**) is very important in Asia because some species are intermediate hosts of liver and intestinal trematodes. Species identification based on only morphological characters may be difficult. Species are commonly found in shallow reservoirs and wetlands including rice fields and may often be exposed to desiccation. Although some snails die during desiccation, some survive through aestivation to recolonize the habitat when water returns. Species within this family may feed both by grazing and by filter feeding. Bithynid snails are often found in aquaculture ponds in the Red River and Mekong deltas and occasionally at high density but they are more commonly found in small canals and rice fields. During the spring planting of rice fields, density of *Bithynia* spp. can be extremely high in newly planted fields.

3.2.11 Pomatiopsidae

With approximately 170 species, the Pomatiopsidae is among the most species-rich freshwater gastropod families. The highest diversity can be found in Southeast Asia and the Japanese archipelago (>140 species), followed by sub-Saharan Africa with approximately 10–11 species, southern Australia with ca. 9 species, the north-western Palearctic with 1–8 species, North America with 5–6 species, and South America with ca. 2 species [80]. The Pomatiopsidae comprise two subfamilies, the

Pomatiopsinae Stimpson, 1865 and the Jullieniinae. The Asian intermediate hosts for *Schistosoma* species belong to this family.

The Triculinae in Asia is very diverse with an endemic fauna that includes over 90 species occurring along a 300 km stretch of the lower Mekong River in Thailand and Laos [29, 80–82]. Relatively few species are reported from Vietnam [83], but this is likely because relatively little work has been done on the Vietnamese part of the Mekong River. Within the Triculinae, several species have been described from Vietnam [83], i.e., *Tricula ovata*, *T. similunaris* and 11 species of a new genus *Vietricula*. Liu et al. [82], however, believed these snails to be *Pachydrobia*. Some of the pomatopsid species are intermediate host for *Paragonimus westermani* [18, 84]. Doanh et al. [85] found two *Vietricula* spp. (originally identified as *Oncomelania*) infected with *Paragonimus heterotremus* and Doanh [86] experimentally infected the two species with *P. heterotremus*.

3.2.12 Hydrobiidae

Hydrobiidae, commonly known as mud snails, is a large cosmopolitan taxonomic family of very small freshwater snails and brackish water snails. These are small snails, with a shell height of less than 8 mm. The dextrally coiled shells are smooth and renders few robust characteristics to the systematist. Furthermore, there is considerable intraspecific variation in shell characteistics. Description is mostly based on the characteristics of the operculum, radula, and penis.

3.2.13 Stenothyridae

The Stenothyridae is comprised of small-sized gastropods found in intertidal and shallow-water aquatic habitats in Asia and Australia. Also, this family is very diverse in the Mekong River. The species live in fresh or brackish water on sandy ground, on stones and decaying wood or buried in the mud where they feed on decaying organic matter. Dung et al. [70] reported, however, pleurolophocercous cercariae were shed by *Stenothyra messageri* in the Red River Delta; these cercariae were not identified to species but they could potentially be zoonotic.

3.2.14 Other caenogastropod species

Some predominantly marine species may enter rivers. For example, the neogastopod *Anentome helena* (**Figure 7**) is found in the Mekong River in Vietnam and Thailand. The species is common in the Mekong River and is exported to Europe and Americas where it is used to control snails in hobbyist's aquaria. In the wild, it probably primarily feeds on carrion rather than seeking live prey.

3.3 Heterobranchia

3.3.1 Valvatidae

Small wide-spired operculate snails, commonly referred to as valve snails. They are egg-laying and hermaphroditic [87]. Burch [88] lists 11 North American species. According to Strong et al. [89] there are 60 species in the Palaearctic region, 10 in the Nearctic, and 1 for the Afrotropical region. They have a featherlike gill, visible on the left side outside the shell when the snail is active, and a ciliated pallial tentacle extending out to the right.

3.3.2 Lymnaeidae

Lymnaeidae (**Figure 5**) is a large and diverse family of freshwater pulmonates widely distributed on all continents except Antarctica. Lymnaeidae exhibit a great diversity in shell morphology which is linked to substantial eco-phenotypic plasticity [90]. Conchological and anatomical traits cannot be taken as reliable diagnostic characters to discriminate species of Lymnaeidae as they vary largely within species [91]. At the supraspecific (genus, subgenus) level there is confusion [92], with some researchers considering numerous genera and subgenera and others only accepting the large genus *Lymnaea*, following the old classification of Hubendick [93]. Phylogenetic analyses, however, show the presence of four well defined subgenera among the genus *Lymnaea* sensu lato, *Radix*, *Galba*, *Leptolimnaea*, and *Lymnaea* [94]. For further details refer to Vinarski et al. [94].

The family is of great parasitological importance as it includes several intermediate hosts of trematodes which infect man and mammals e.g., *Fasciola* spp., and schistosomes infecting both domestic livestock, wild mammals, and birds, the cercariae of all of which can cause swimmer's itch or cercarial dermatitis.

3.3.3 Physidae

The Physidae has a Holarctic distribution, extending into Central and South America [95]. Physids have been introduced around the world and are common, particularly in lentic habitats. Physid diversity is centered in North America, where they are the most abundant and widespread freshwater gastropods [88]. Physidae are hermaphrodites and can be distinguished from other pulmonates by a high-spired sinistral shell, radula with teeth in V-shaped rows, simple jaw with no lateral processes, and lack of both hemoglobin and a pseudobranch [29]. Other unique characteristics of many species of Physidae are an extended mantle edge that can partly cover the shell, as well as the presence of a preputial gland [29]. Six major clades were uncovered in an analysis of the penial morphology [96], while four major clades, *Physa acuta*, *Physa gyrina*, *Physa fontinalis*, and *Physa pomilia* were recognized by Pip & Franck [97]. They are common hosts of avian schistosomes responsible for causing swimmer's itch. *P. acuta* which is thought to be native to North America has spread throughout the world, and this may pose some difficulties for snail identification (e.g., with confusion with *Bulinus* species) and it may cause displacement of native, disease-transmitting species.

3.3.4 Burnupiidae

The monogeneric Burnupiidae are a limpetlike group of freshwater pulmonate snails predominantly occurring in Africa. The genus *Burnupia* has traditionally been seen as member of either a freshwater limpet family Ancylidae or as a member of the Planorbidae [98]. The majority of species of *Burnupia* occur in sub-Saharan Africa, particularly in eastern and southern parts, from the isolated Ethiopian highlands down to the Cape region [98].

3.3.5 Bulinidae

Bulinidae (**Figures 4** and **5**) comprise small to medium-sized planorboid gastropods, reaching up to 25 mm in height or diameter. They are sinistral and either high-spired (e.g. *Bulinus*) or discoid (e.g. *Indoplanorbis*) and possess a large pseudobranch that is deeply folded and vascularized [99]. Buliniforme pulmonate gastropods have traditionally been a subfamily of the Planorbidae. Recent molecular phylogenetic analyses, however, have suggested a very different scenario for planorboid gastropods, in which the bulinine forms would be reduced to be represented by *Bulinus* and *Indoplanorbis* only [100, 101]. These phylogenetic suggestions were followed in the most recent classification of the worldwide gastropods [47], in which the family Bulinidae is proposed, comprising the subfamilies Bulininae and Plesiophysinae.

The classification still largely relies on the early accounts of Mandahl-Barth [102, 103], and the system is based on both shell and anatomical characters; however, the definition of the majority of the more than 30 species currently recognized is still unsatisfactory [104]. A variety of taxonomic characters have been employed in *Bulinus*, ranging from (shell) morphology to genital anatomy and radulae, chromosome numbers, and data from electrophoresis and immunodiffusion [104]. Conchological characters are of restricted value in a planorboid snail genus such as *Bulinus* that is characterized by a rather uniform shell shape largely lacking specific characters such as keels [99]. The four species groups have been basically confirmed by phylogenetic studies based on mitochondrial and nuclear markers, but all, unfortunately, suffer from unresolved or poorly supported relationships within and between the proposed species groups [99]. Clearly, many more genetic studies are needed to identify cryptic species (complexes) and to study the role of hybridization of *Bulinus* spp. [99].

Indoplanorbis exustus is an intermediate host for the *Schistosoma indicum* species group, and the role of this snail in the transmission of several other medically and veterinary important parasites has been emphasized repeatedly [99]. The species is rather ecologically flexible and thrives in unspecific freshwater habitats that are not flowing, but it requires warm climates. The species is found in Africa, and it is widespread in southern Asia.

3.3.6 Planorbidae

Planorbidae (**Figures 3** and **6**) represent the most diverse taxon of freshwater pulmonate gastropods on earth that has an almost cosmopolitan distribution [105]. After excluding the Bulinidae and Burnupiidae there are approximately 150 species globally [105]. Following the most recent classification of freshwater gastropods [47], based on various phylogenetic analyses conducted during the past two decades, the Planorbidae consist of three subfamilies, namely Planorbinae Rafinesque, 1815, Ancylinae Rafinesque, 1815, and Miratestinae P. Sarasin & F. Sarasin, 1897 [105].

Planorbidae occur in all kinds of freshwater habitats, ranging from temporary and permanent ponds, streams, rivers, and large lakes [89]. The cosmopolitan distribution of Planorbidae has been the result of a high dispersal capacity and ecological flexibility, including desiccation resistance that is particularly important for the successful passive transport via (aerial) vectors.

The snails are small to medium-sized with long slender tentacles and blood containing hemoglobin [106]. The shell is discoid, lens-shaped, or higher ovate to turreted and the animals are sinistral, that is, the genital openings and the anus are situated on the left side, but in most of the discoid forms the shell appears to be dextral, because it is carried inverted, so that the side representing the spire (apical side) in other families is the lower side of the planorbid shell and the upper side is umbilical [106].

In the Planorbinae, there are several tribes, i.e., Planorbini (almost global distribution); Segmentinini (comprise Palearctic, Oriental, and Afrotropical species); Drepanotrematini (Central and South America); Neoplanorbini (represent a likely extinct taxon endemic to river systems in the southeasten United States); Helisomatini (includes Afrotropical and American taxa); Coretini (primarily European); and Camptoceratini (southern and eastern Asia) (see references in [105]). Several species are intermediate hosts for medically or veterinary important trematodes including schistosomes.

Freshwater limpets of the subfamily Ancylinae occur on all continents. They are small species with cap- or shield-shaped shell [29]. These animals have a pallial lung, as do all pulmonate snails, but they also have a pseudobranch which serve as a gill in situations where the limpet is unable to reach the surface for air.

The subfamily Miratestinae comprises Australian high-spired planorbid species the buliniform species *Amerianna carinata* that spread widely from its Australian origin [107]. Other species of planorbid snails are global invaders as well [105].

4. Control

4.1 Changing transmission patterns

Distribution and transmission patterns for some of the zoonotic trematodes may be changing for various reason. Climate plays an important role in the transmission of many infectious diseases; it not only determines spatial and seasonal distributions, but influences inter-annual variability, including epidemics, and long-term trends [108]. Evidence of climate change includes the instrumental temperature record, rising sea levels, and decreased snow cover in the Northern Hemisphere [109]. One of the most conspicuous effects of climate is an increased frequency of extreme weather conditions, which can have devastating effects on the snail fauna in some vulnerable habitats and at least temporarily affect schistosome transmission [110]. Obviously, one of the key factors for changing transmission patterns would be temperature changes [111].

Another possibility for changing transmission patterns is introduction of intermediate hosts into new areas. There are numerous examples of snails spreading over long distances and becoming invasive. Although snails may be spread over short distances attached to other animals, in mud on feet of birds or over somewhat longer distances passing alive through the digestive channel of migratory birds, the major mean of transport is the global trade in aquatic animals and plants [108]. Asian species such as *Tarebia granifera* have spread to South Africa, *Biomphalaria straminea* from South America to Asia, *Indoplanorbis exustus* to sub-Saharan Africa, and many other examples. Apple snails were introduced to Asia for food production. Invasive species could have major impact on local biodiversity. Another reason could be parasite introduction with imported final hosts or parasites change genetically and thereby perhaps be able to use new species as intermediate hosts. Gibbs [112] listed six interconnected parameters that have increased the rate of emerging diseases including: (1) global trade and tourism; (2) speed of mass transportation; (3) exposure to new pathogens through ecosystem disruption; (4) intensification and monoculture in farming; (5) sophistication of food processing, and (6) evolutionary pressures through overpopulation.

4.2 Control

Control of the zoonotic trematode-caused diseases in people and animals must depend on the severity of pathology caused, transmission patterns, and available options for medical treatment of infection. For most of these infections, effective control needs to take a holistic approach following One-Health principles [113].

While recognizing that existing approaches to the control of zoonotic diseases will continue to benefit from their current vertical or horizontal structure, there is growing evidence for the benefits of a joint human and animal health approach [114]. The One Health concept integrates human and animal health resources and should be promoted, because many zoonoses can be better surveyed, diagnosed and controlled by considering human and animal health together [114]. In our view, the One-Health approach must take a holistic approach where all aspects of the parasite life cycle are considered and this is especially the case for zoonotic trematodes. Some of the zoonotic trematodes are closely linked to food production, and this is especially important in least developed countries.

Disease control programmes are typically integrated as there is a need to link surveillance, monitoring, and reporting all activities with actions taken by the health system and this is particularly the case for control of zoonotic diseases [114]. Such approaches may be biomedical (drug or vaccine), vector or intermediate host control (insects or snail), environmental, legislative (inspection and condemnation of infected products at slaughterhouses) or educational [114].

Some of these zoonotic trematode-caused diseases are serious problems of both public health and veterinary importance. Although infections by some of these trematodes in the final hosts can be effectively reduced through medical treatment, reinfection appears very quickly [36, 110, 115, 116]. Thus, it is necessary to take a holistic approach to control. Treatment of infections by trematodes involves the understanding of the multiple host species, environmental control, and behavior modifications and includes several scenarios. Interventions should include (1) attempts to reduce the contamination of water bodies with trematode eggs; (2) attempts to reduce the chance of eggs or miracidia infecting the first intermediate host and (3) attempts to reduce the likelihood that cercariae or metacercariae infect a final host [113].

1. The most effective means of reducing egg contamination would be medical treatment of the final hosts (humans and possibly reservoir hosts). This could be supplemented with sanitary improvements to reduce contamination of waterbodies with human feces or urine or prevention of reservoir hosts to have access to the water bodies e.g., dogs, cats, and wild birds for some of the fish-borne zoonotic trematodes [113]. Avoiding the use of untreated manure from domestic animals for fertilization of aquaculture ponds is an important way to reduce egg contamination of ponds and also prevention of rain run-off into the ponds is important [36].

2. Snail control using either habitat modification, chemical control, or biological control is important for reducing the chance of eggs or miracidia infecting the first intermediate host. Biological control should be attempted only using native species and might be a viable option in aquaculture ponds [117, 118]. Obviously, what is feasible depends on the type of habitat.

3. Snail control will also reduce cercariae production in transmission sites thus reducing infection in the final host. For schistosomiasis, transmission to people could be reduced through reducing water contact in transmission sites, e.g. through supply of safe water. For fish-borne zoonotic trematodes (FZT), behavioral changes reducing transmission include, e.g., not eating raw fish, cooking fish remains before feeding it to animals (pigs, dogs, and cats) and preventing especially cats and dogs access to the ponds [36].

Combining mass drug administration, provision of clean water and maintenance of good sanitation and hygiene, community health education towards modification of risky behaviors, surveillance, and veterinary public health interventions have been shown to be effective in combatting foodborne trematodiasis [119]. Finally, there is a need to reduce dependency on chemical compounds for control of the first intermediate hosts due to their costs and low sustainability, while management procedures could be more sustainable and long lasting.

5. Conclusions

Zoonotic trematodes cause a number of diseases some of which have major public health or animal health consequences or have huge financial implications. A key element in the parasites' life cycle are the first intermediate host which depending on the parasitic species particular species of gastropod mollusks. Control of these snails could be an important element in an integrated approach to control these diseases following the "One-Health" approach.

Author details

Henry Madsen[1*] and Jay R. Stauffer, Jr.[2,3]

1 Parasitology and Aquatic Diseases, Faculty of Health and Medical Sciences, Department of Veterinary Disease Biology, University of Copenhagen, Copenhagen, Denmark

2 Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA, USA

3 South African Institute for Aquatic Biodiversity, Makhanda, RSA

*Address all correspondence to: hmad@sund.ku.dk

References

[1] Torgerson PR, Macpherson CNL. The socioeconomic burden of parasitic zoonoses: Global trends. Veterinary Parasitology. 2011;**182**:79-95. DOI: 10.1016/j.vetpar.2011.07.017

[2] Miranda EM. Zoonotic Trematodiasis. In: Quiroz-Castañeda RE, editor. Farm Animals Diseases, Recent Omic Trends and New Strategies of Treatment. London: IntechOpen. DOI: 10.5772/intechopen.72632

[3] Betson M, Alonteb AJI, Ancog RC, Aquino AMO, Belizario VY Jr, Bordado AMD, et al. Zoonotic transmission of intestinal helminths in Southeast Asia: Implications for control and elimination. Advances in Parasitology. 2020;**108**:49-131. DOI: 10.1016/bs.apar.2020.01.036

[4] Doumenge J, Mott KE, Cheung C, Villenave D, Chapuis O, Perrin MF, et al. WHO Atlas of the Global Distribution of Schistosomiasis. Presses Universitaires de Bordeaux Bordeaux; 1987. p. 400

[5] Bergquist R, Gray DJ. Schistosomiasis elimination: Beginning of the end or a continued march on a trodden path. Tropical Medicine and Infectious Disease. 2019;**4**:76. DOI: 10.3390/tropicalmed4020076

[6] Vos T, Flaxman AD, Naghavi M, Lozano R, Michaud C, Ezzati M, et al. Years lived with disability (YLDs) for 1160 sequelae of 289 diseases and injuries 1990-2010: A systematic analysis for the global burden of disease study 2010. Lancet. 2012;**380**(9859):2163-2196. DOI: 10.1016/S0140-6736(12)61729-2

[7] Hotez P, Alvarado M, Basáñez M, Bolliger I, Bourne R, Boussinesq M, et al. (DALYs and HALE Collaborators). The global burden of disease study 2010: Interpretation and implications for the neglected tropical diseases. PLoS Neglected Tropical Diseases. 2014;**8**:e2865. DOI: 10.1371/journal.pntd.0002865

[8] Littlewood DTJ, Webster BL. Origins and evolutionary radiation of *Schistosoma*. In: Jamieson BGM, editor. *Schistosoma*: Biology, Pathology, and Control. Boca Raton: Taylor & Francis Group, CRC Press; 2016. pp. 1-8. ISBN 9781498744263 (e-book)

[9] Standley CJ, Mugisha L, Dobson AP, Stothard JR. Zoonotic schistosomiasis in non-human primates: Past, present and future activities at the human–wildlife interface in Africa. Journal of Helminthology. 2012;**86**:131-140. DOI: 10.1017/S0022149X12000028

[10] Gower CM, Vince L, Webster JP. Should we be treating animal schistosomiasis in Africa? The need for a one health economic evaluation of schistosomiasis control in people and their livestock. Transactions of the Royal Society of Tropical Medicine and Hygiene. 2017;**111**:244-247. DOI: 10.1093/trstmh/trx047

[11] Attwood SW, Fatih FA, Upatham ES. DNA-sequence variation among *Schistosoma mekongi* populations and related taxa; phylogeography and the current distribution of Asian schistosomiasis. PLoS Neglected Tropical Diseases. 2008;**2**(3):e200. DOI: 10.1371/journal.pntd.0000200

[12] Morgan JA, DeJong RJ, Lwambo NJ, Mungai BN, Mkoji GM, Loker ES. First report of a natural hybrid between *Schistosoma mansoni*

and *S. rodhaini*. The Journal of Parasitology. 2003;**89**:416-418. DOI: 10.1645/0022-3395(2003)089[0416:FROANH]2.0.CO;2

[13] Stauffer JR, Madsen H, Rollinson D. Introgression in Lake Malaŵi: Increasing the threat of human urogenital schistosomiasis? EcoHealth. 2014;**11**:251-254. DOI: 10.1007/s10393-013-0882-y

[14] Moné H, Holtfreter MC, Allienne J-F, Mintsa-Nguéma R, Ibikounlé M, Boissier J, et al. Introgressive hybridizations of *Schistosoma haematobium* by *Schistosoma bovis* at the origin of the first case report of schistosomiasis in Corsica (France, Europe). Parasitology Research. 2015;**114**:4127-4133. DOI: 10.1007/s00436-015-4643-4

[15] Madsen H. *Schistosoma* intermediate host snails. In: Jamieson BGM, editor. *Schistosoma*: Biology, Pathology and Control. Boca Raton: Taylor & Francis Group, CRC Press; 2016. pp. 38-55

[16] Wilke T. 21. Pomatiopsidae Stimpson, 1865. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 126-130

[17] Attwood SW. Mekong schistosomiasis: Where did it come from and where is it going? In: Campbell IC, editor. The Mekong: Biophysical Environment of an International River Basin. New York: Elsevier; 2009. pp. 273-295

[18] Attwood SW. Studies on the parasitology, phylogeography and the evolution of host-parasite interactions for the snail intermediate hosts of medically important trematode genera in south East Asia. Advances in Parasitology. 2010;**73**:405-440. DOI: 10.1016/S0065-308X(10)73013-X

[19] Davis GM. Snail hosts of Asian *Schistosoma* infecting man: Evolution and coevolution. The Mekong Schistosome. Malacological Review 1980;(Suppl. 2): 195-238

[20] Kali A. Schistosome infections: An Indian perspective. Journal of Clinical and Diagnostic Research. 2015;**9**(2):DE01-DE04. DOI: 10.7860/JCDR/2015/10512.5521

[21] Agrawal MC. Schistosomes and schistosomiasis in South Asia. Chapter 3. In: The Snail. New Delhi, India: Springer; 2012. pp. 51-84. DOI: 10.1007/978-81-322-0539-5_3

[22] Barbosa FS, Barbosa I, Morais RA. Laboratory infection of the snail *Planorbarius metidjensis* (Forbes) from French Morocco with a Brazilian strain of *Schistosoma mansoni*. Annals of Tropical Medicine and Parasitology. 1959;**53**:314-315

[23] Yacoubi B, Zekhnini A, Moukrim A, Rondelaud D. *Bulinus truncatus*, *Planorbarius metidjensis* and endemic bilharziosis in the southwestern Morocco. Bulletin de la Société de Pathologie Exotique. 2007;**100**:174-175

[24] Madsen H, Stauffer JR Jr. Density of *Trematocranus placodon* (Pisces: Cichlidae): A predictor of density of the schistosome Iintermediate host, *Bulinus nyassanus* (Gastropoda: Planorbidae), in Lake Malaŵi. EcoHealth. 2011;**8**:177-189. DOI: 10.1007/s10393-011-0737-3

[25] Brant SV, Loker ES. Discovery-based studies of schistosome diversity stimulate new hypotheses about parasite biology. Trends in Parasitology. 2013;**29**:449-460. DOI: 10.1016/j.pt.2013.06.004

[26] Brant SV, Bochte CA, Loker ES. New intermediate host records for the avian schistosomes *Dendritobilharzia*

pulverulenta, *Gigantobilharzia huronensis*, and Trichobilharzia querquedulae from North America. The Journal of Parasitology. 2011;**97**:946-949. DOI: 10.1645/GE-2743.1

[27] Flores V, Brant SV, Loker ES. Avian Schistosomes from the south American endemic gastropod genus *Chilina* (Pulmonata: Chilinidae), with a brief review of south American schistosome species. The Journal of Parasitology. 2015;**101**:565-576. DOI: 10.1645/14-639

[28] Horák P, Mikeš L, Lichtenbergová L, Skála V, Soldánová M, Brant SV. Avian schistosomes and outbreaks of cercarial dermatitis. Clinical Microbiology Reviews. 2015;**28**:165-190. DOI: 10.1128/CMR.00043-14

[29] Brandt AMR. The non-marine aquatic mollusca of Thailand. Archiv fuer Molluskenkunde. 1974;**105**:1-247

[30] Procop GW. North American paragonimiasis (caused by *Paragonimus kellicotti*) in the context of global paragonimiasis. Clinical Microbiology Reviews. 2009;**22**:415-446. DOI: 10.1128/CMR.00005-08

[31] Blair D. Paragonimiasis. In: Toledo R, Fried B, editors. Digenetic Trematodes. Advances in Experimental Medicine and Biology. Vol. 1154. Cham: Springer Nature Switzerland AG; 2019. pp. 105-138. DOI: 10.1007/978-3-030-18616-6_5

[32] Rabone M, Wiethase J, Clark PF, Rollinson D, Cumberlidge N, Emery AM. Endemicity of *Paragonimus* and paragonimiasis in sub-Saharan Africa: A systematic review and mapping reveals stability of transmission in endemic foci for a multi-host parasite system. PLoS Neglected Tropical Diseases. 2021;**15**(2):e0009120. DOI: 10.1371/journal.pntd.0009120

[33] Gunn A, Pitt SJ. Parasitology: An Integrated Approach. Blackwell, Chicester: John Wiley & Sons, Ltd; 2012. 442 pp

[34] Waikagul J, Thaenkham U. Approaches to Research on the Systematics of Fish-borne Trematodes. London: Elsevier, Academic Press; 2014. p. 108

[35] Hung NM, Madsen H, Fried B. Global status of fish-borne zoonotic trematodiasis in humans (invited review). Acta Parasitologica. 2013;**58**:231-258. DOI: 10.2478/s11686-013-0155-5

[36] Clausen JH, Madsen H, Van PT, Dalsgaard A, Murrell KD. Integrated parasite management: Path to sustainable control of fishborne trematodes in aquaculture. Trends in Parasitology. 2015;**31**:8-15. DOI: 10.1016/j.pt.2014.10.005

[37] De NV, Murrell KD, Cong LD, Cam PD, Chau LV, Toan ND, et al. The food-borne trematode zoonoses of Vietnam. Southeast Asian Journal of Tropical Medicine. 2003;**34**:12-34

[38] Nguyen HM, Van HH, Ho LT, Tatonova YV, Madsen H. Are *Melanoides tuberculata* and *Tarebia granifera* (Gastropoda, Thiaridae), suitable first intermediate hosts of *Clonorchis sinensis* in Vietnam? PLoS Neglected Tropical Diseases. 2021;**15**(1):e0009093. DOI: 10.1371/journal.pntd.0009093

[39] Chai J-Y, Shin E-H, Lee S-H, Rim H-J. Foodborne intestinal flukes in Southeast Asia. The Korean Journal of Parasitology. 2009;**47**(Supplement):S69-S102. DOI: 10.3347/kjp.2009.47.S.S69

[40] Phan VT, Ersbøll AK, Bui TQ, Nguyen HT, Murrell D, Dalsgaard A. Fish-borne zoonotic trematodes in cultured and wild-caught freshwater fish from the red River Delta, Vietnam. Vector-borne

and Zoonotic Diseases. 2010;**10**(9):861-866. DOI: 10.1089=vbz.2009.0134

[41] Tkach VV, Kudlai O, Kostadinova A. Molecular phylogeny and systematics of the Echinostomatoidea Looss, 1899 (Platyhelminthes: Digenea). International Journal for Parasitology. 2016;**46**:171-185. DOI: 10.1016/j.ijpara.2015.11.001

[42] Chai JY. Echinostomes in humans. In: Fried B, Toledo R, editors. The Biology of Echinostomes. Springer; 2009. pp. 147-183. DOI: 10.1007/978-0-387-09577-6_7

[43] Mas-Coma S, Bargues MD, Valero MA. Fascioliasis and other plant-borne trematode zoonoses. International Journal for Parasitology. 2005;**35**:1255-1278. DOI: 10.1016/j.ijpara.2005.07.010

[44] Mas-Coma S, Valero MA, Bargues MD. Fascioliasis in humans and animals. Reference Module in Biomedical Sciences. 2021. pp. 1-19. DOI: 10.1016/B978-0-12-818731-9.00058-6

[45] Squire SA, Yang R, Robertson I, Ayi I, Squire DS, Ryan U. Gastrointestinal helminths in farmers and their ruminant livestock from the coastal Savannah zone of Ghana. Parasitology Research. 2018;**117**:3183-3194. DOI: 10.1007/s00436-018-6017-1

[46] Lotfy WM, Brant SV, Ashmawy KI, Devkota R, Mkoji GM, Loker ES. A molecular approach for identification of paramphistomes from Africa and Asia. Veterinary Parasitology. 2010;**174**:234-240. DOI: 10.1016/j.vetpar.2010.08.027

[47] Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, et al. Revised classification, Nomenclator and Typification of gastropod and Monoplacophoran families. Malacologia. 2017;**61**:1-526. DOI: 10.4002/040.061.0201

[48] Thiele J. Handbuch der systematischen Weichtierkunde. Jena, Germany: II. Verlag von GustavFischer; 1931

[49] Kano Y, Fukumori H. 3. Neritidae Rafinesque, 1815. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the world. A distribution atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 31-36

[50] Kano Y. 2. Neritiliidae Schepman, 1908. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 27-30

[51] Van Bocxlaer B, Strong EE. 5. Viviparidae Gray, 1847. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 43-50

[52] Cowie RH, Hayes KA. 4. Ampullariidae Gray, 1824. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 37-42

[53] Nguma JFM, McCullough FS, Masha E. Elimination of *Biomphalaria pfeifferi*, *Bulinus tropicus* and *Lymnaea natalensis* by the ampullarid snail, *Marisa cornuarietis,* in a man-made dam in northern Tanzania. Acta Tropica. 1982;**39**:85-90

[54] Haridi AAM, El Safi SH, Jobin WR. Survival, growth and reproduction of the imported ampullarid snail *Marisa cornuarietis* in Central Sudan. The Journal of Tropical Medicine and Hygiene. 1985;**88**:135-144

[55] Haridi AAM, Jobin WR. Estimated risks and benefits from introducing *Marisa cornuarietis* into the Sudan. The Journal of Tropical Medicine and Hygiene. 1985;**88**:145-151

[56] Glaubrecht M, Neiber MT. 6. Hemisinidae Fischer & Crosse, 1891. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 51-55

[57] Neiber MT, Glaubrecht M. 7. Melanopsidae H. Adams & A. Adams, 1854. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 56-61

[58] Neiber MT, Glaubrecht M. 8. Pachychilidae Fischer & Crosse, 1892. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 62-67

[59] Neiber MT, Glaubrecht M. 9. Paludomidae Stoliczka, 1868. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 68-73

[60] Strong EE, Lydeard C. 10. Pleuroceridae P. Fischer, 1885. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 74-80

[61] Campbell DC. 11. Semisulcospiridae Morrison, 1952. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 81-85

[62] Glaubrecht M, Neiber MT. 12. Thiaridae Gill, 1871 (1823). In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 86-89

[63] Reid DG, Dyal P, Lozouet P, Glaubrecht M, Williams ST. Mudwhelks and mangroves: The evolutionary history of an ecological association (Gastropoda: Potamididae). Molecular Phylogenetics and Evolution. 2008;**47**:680-699. DOI: 10.1016/j.ympev.2008.01.003

[64] Köhler F, Dames C. Phylogeny and systematics of the Pachychilidae of mainland south-east asia-novel insights from morphology and mitochondrial DNA (Mollusca, Caenogastropoda, Cerithioidea). Zoological Journal of the Linnean Society. 2009;**157**:679-699. DOI: 10.1111/j.1096-3642.2009.00541.x

[65] Dudgeon D, Cheung PSC. Selection of gastropod prey by a tropical fresh-water crab. Journal of Zoology. 1990;**220**:147-155. DOI: 10.1111/j.1469-7998.1990.tb04299.x

[66] Yeung ACY, Dudgeon D. Production and population dynamics of the prosobranch snail *Sulcospira hainanensis* (Pachychilidae), a major secondary consumer in Hong Kong streams. Hydrobiologia. 2014;**724**:21-39. DOI: 10.1007/s10750-013-1703-6

[67] Köhler F, Seddon M, Bogan AE, Tu DV, Sri-Aroon P, Allen D. The status and distribution of freshwater molluscs of the indo-Burma region. In: Allen DJ, Smith KG, Darwall WRT, editors. The Status and Distribution of Freshwater Biodiversity in Indo-Burma. Cambridge, UK, Gland, Switzerland: IUCN; 2012. pp. 66-88

[68] Pointier J-P, David P, Jarne P. The biological control of the snail hosts of schistosomes: The role of competitor snails and biological invasions. In: Toledo R, Fried B, editors. Biomphalaria: Snails and Larval Trematodes. New York: Springer Science + Business Media; 2011. pp. 215-238. DOI: 10.1007/978-1-4419-7028-2_9

[69] Dudgeon D. The lifecycle, population dynamics and productivity of *Melanoides tuberculata* (Müller, 1774) (Gastropoda: Prosobranchia: Thiaridae) in Hong Kong. Journal of Zoology. 1986;**208**:37-53. DOI: 10.1111/j.1469-7998.1986.tb04707.x

[70] Dung BT, Madsen H, The DT. Distribution of freshwater snails in family-based VAC ponds and associated waterbodies with special reference to intermediate hosts of fish-borne zoonotic trematodes in Nam Dinh Province, Vietnam. Acta Tropica. 2010;**116**: 15-23. DOI: 10.1016/j.actatropica. 2010.04.016

[71] Clausen JH, Madsen H, Murrell KD, Van PT, Nguyen TTH, Dung TD, et al. Prevention and control of fish-borne zoonotic trematodes in fish nurseries, Vietnam. Emerging Infectious Diseases. 2012;**18**:1438-1445. DOI: 10.3201/ eid1809.111076

[72] Clark SA. 13. Amnicolidae Tryon, 1862. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 90-93

[73] Fukuda H. 14. Assimineidae H. & A. Adams, 1856. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 94-100

[74] Ponder W. Bithyniidae Gray, 1857. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 101-103

[75] Stephanie A, Clark SA. Cochliopidae Tryon, 1866. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 104-108

[76] Wilke T. 17. Helicostoidae Pruvot-Fol, 1937. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 109-110

[77] Wilke T, Delicado D. 18. Hydrobiidae Stimpson, 1865. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 111-117

[78] Clark SA. 19. Lithoglyphidae Tryon, 1866. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 118-121

[79] Clark SA. 22. Stenothyridae Tryon, 1866. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 131-133

[80] Davis GM. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. Monograph/Academy of Natural Sciences of Philadelphia. 1979;**20**:1-120

[81] Attwood SW, Ambu S, Meng XH, Upatham ES, Xu FS, Southgate VR. The phylogenetics of triculine snails (Rissooidea: Pomatiopsidae) from south-East Asia and southern China: Historical biogeography and the transmission of human schistosomiasis. Journal of Molluscan Studies. 2003;**69**:263-271. DOI: 10.1093/mollus/69.3.263

[82] Liu L, Huo GN, He HB, Zhou B, Attwood SW. A phylogeny

for the Pomatiopsidae (Gastropoda: Rissooidea): A resource for taxonomic, parasitological and biodiversity studies. BMC Evolutionary Biology. 2014;**14**:29. DOI: 10.1186/1471-2148-14-29

[83] Thanh DN, Hai HN. Freshwater Mollusca: Gastropoda and Bivalvia. In: Fauna of Vietnam. Hanoi: Vietnam Science and Technology Publisher (in Vietnamese); 2010

[84] Blair D, Davis GM, Wu B. Evolutionary relationships between trematodes and snails emphasizing schistosomes and paragonimids. Parasitology. 2001;**123**:S229-S243. DOI: 10.1017/S003118200100837X

[85] Doanh PN, Le NT, The DT. Distribution of *Paragonimus heterotremus* and its intermediate hosts in the northwest region of Vietnam. Journal of Biology. 2002;**3**:14-22 (in Vietnamese with English abstract)

[86] Doanh PN. Development of the *Paragonimus heterotremus* eggs and its larvae stages in the first intermediate host. Journal of Biology. 2004;**6**:6-10 (in Vietnamese with English abstract)

[87] Clewing C, Albrecht C. 24. Valvatidae Gray, 1840. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 139-142

[88] Burch JB. North American freshwater snails: Identification keys, generic synonymy, supplemental notes, glossary, references, index. Walkerana. 1982;**1**:1-365

[89] Strong EE, Gargominy O, Ponder WF, Bouchet P. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. Hydrobiologia. 2008;**595**: 149-166. DOI: 10.1007/s10750-007-9012-6

[90] Correa AC, Escobar JS, Durand P, Renaud F, David P, Jarne P, et al. Bridging gaps in the molecular phylogeny of the Lymnaeidae (Gastropoda: Pulmonata), vectors of fascioliasis. BMC Evolutionary Biology. 2010;**10**:381. DOI: 10.1186/1471-2148-10-381

[91] Correa AC, Escobar JS, Noya O, Velásquez LE, González-Ramírez C, Hurtrez-Boussès S, et al. Morphological and molecular characterization of Neotropic Lymnaeidae (Gastropoda: Lymnaeoidea), vectors of fasciolosis. Infection, Genetics and Evolution. 2011;**11**:1978-1988. DOI: 10.1016/j.meegid.2011.09.003

[92] Mas-Coma S, Bargues MD. Human liver flukes: A review. Research and Reviews in Parasitology. 1997;**57**:145-218

[93] Hubendick B. Recent Lymnaeidae, their variation, morphology, taxonomy, nomenclature and distribution. Kungliga Svenska Vetenskapsakademiens Handlingar. 1951;**3**:1-223

[94] Vinarski MV, Clewing C, Albrecht C. 29. Lymnaeidae Rafinesque, 1815. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 158-162

[95] Wethington AR, Lydeard C. 33. Physidae Fitzinger, 1833. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 175-180

[96] Wethington AR, Lydeard C. A molecular phylogeny of Physidae (Gastropoda: Basommatophora) based on mitoghondrial DNA sequences. Journal of Molluscan Studies. 2007;**73**:241-257. DOI: 10.1093/mollus/eym021

[97] Pip E, Franck JPC. Molecular phylogenetics of Central Canadian Physidae (Pulmonata: Basommatophora). Canadian Journal of Zoology. 2008;**86**:10-16. DOI: 10.1139/Z07-112

[98] Albrecht C, Clewing C. 32. Burnupiidae Albrecht, 2017. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 172-174

[99] Albrecht C, Stelbrink B, Clewing C. 31. Bulinidae P. Fischer & Crosse, 1880. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 167-171

[100] Albrecht C, Kuhn K, Streit B. A molecular phylogeny of Planorboidea (Gastropoda, Pulmonata): Insights from enhanced taxon sampling. Zoologica Scripta. 2006;**36**:27-39. DOI: /10.1111/j.1463-6409.2006.00258.x

[101] Jørgensen A, Kristensen TK, Stothard JR. An investigation of the "Ancylo- planorbidae" (Gastropoda, Pulmonata, Hygrophila): Preliminary evidence from DNA sequence data. Molecular Phylogenetics and Evolution. 2004;**32**:778-787. DOI: 10.1016/j.ympev.2004.02.011

[102] Mandahl-Barth G. Intermediate hosts of *Schistosoma*. African *Biomphalaria* and *Bulinus*. 2. *Bulinus*. Bulletin of the World Health Organization. 1957;**17**:1-65

[103] Mandahl-Barth G. The species of the genus *Bulinus,* intermediate hosts of *Schistosoma*. Bulletin of the World Health Organization. 1965;**33**:33-44

[104] Brown D. Freshwater Snails of Africa and their Medical Importance. 2nd ed. London: Taylor & Francis; 1994

[105] Albrecht C, Stelbrink B. Clewing C. 34. Planorbidae Rafinesque, 1815. In: Lydeard C, Cummings KS, editors. Freshwater Mollusks of the World. A Distribution Atlas. Baltimore: Johns Hopkins University Press; 2019. pp. 181-186

[106] Mandahl-Barth G. Intermediate Hosts of *Schistosoma*. African *Biomphalaria* and *Bulinus*. World Health Organization Monograph Series No. 37. Geneva: World Health Organization; 1958. 132 pp

[107] Madsen H, Frandsen F. The spread of freshwater snails including those of medical and veterinary importance. Acta Tropica. 1989;**46**:139-146. DOI: 10.1016/0001-706X(89)90030-2

[108] Kelly-Hope L, Thomson MC. Climate and infectious diseases. In: Thomson MC et al., editors. Seasonal Forecasts, Climatic Change and Human Health. Dordrecht: Springer Science + Business Media BV; 2008

[109] Lotfy WM. Climate change and epidemiology of human parasitosis in Egypt: A review. Journal of Advanced Research. 2014;**5**:607-613. DOI: 10.1016/j.jare.2013.06.009

[110] Kariuki HC, Madsen H, Sturrock RF, Ouma JH, Butterworth AEB, Dunne D, et al. Focal molluscicidng using niclosamide (Bayluscide) in stream habitats and its effect on transmission of schistosomiasis mansoni following community-based chemotherapy at Kibwezi in Makueni District, Kenya. Parasites & Vectors. 2013;**6**:107. DOI: 10.1186/1756-3305-6-107

[111] Kalinda C, Chimbari M, Mukaratirwa S. Implications of changing temperatures on the growth, fecundity and survival of intermediate host snails of schistosomiasis: A systematic review. International Journal of Environmental

Research and Public Health. 2017;**14**:80. DOI: 10.3390/ijerph14010080

[112] Gibbs EP. Emerging zoonotic epidemics in the interconnected global community. The Veterinary Record. 2005;**157**:673-679

[113] Stauffer JR, Madsen H. A one health approach to reducing schistosomiasis transmission in Lake Malawi. Preventive Medicine and Community Health. 2018;**1**:1-4. DOI: 10.15761/PMCH.1000115

[114] Research Priorities for Zoonoses and Marginalized Infections. Technical Report of the TDR Disease Reference Group on Zoonoses and Marginalized Infectious Diseases of Poverty. WHO Technical Report Series 971

[115] Wilkins HA. Reinfection after treatment of schistosome infections. Parasitology Today. 1989;**5**:83-88. DOI: 10.1016/0169-4758(89)90008-2

[116] Lier T, Do DT, Johansen MV, Nguyen TH, Dalsgaard A, Asfeldt AM. High reinfection rate after preventive chemotherapy for fish borne zoonotic trematodes in Vietnam. PLoS Neglected Tropical Diseases. 2014;**8**:e2958. DOI: 10.1371/journal.pntd.0002958

[117] Hung NM, Nguyen VD, Stauffer JR Jr, Madsen H. Use of black carp (*Mylopharyngodon piceus*) in biological control of intermediate host snails of fish-borne zoonotic trematodes in nursery ponds in Vietnam. Parasites & Vectors. 2013;**6**:142. DOI: 10.1186/1756-3305-6-142

[118] Makoni P, Chimbari MJ, Madsen H. Interactions between fish and snails in a Zimbabwe pond, with particular reference to *Sargochromis codringtonii* (Pisces: Cichlidae). African Journal of Aquatic Science. 2005;**30**(1):45-48. DOI: 10.2989/16085910509503833

[119] Tenorio JCB, Molina EC. Monsters in our food: Foodborne trematodiasis in the Philippines and beyond. Veterinary Integrative Sciences. 2021;**19**(3):467-485. DOI: 10.12982/VIS.2021.038