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CIRCULATION PATHWAYS OF TREMATODES OF FRESHWATER GASTROPOD MOLLUSKS IN FOREST BIOCENOSES OF THE UKRAINIAN POLISSIA

E. P. Zhytova[1], L. D. Romanchuk, S. V. Guralska, O. Yu. Andreieva, M. V. Shvets

Zhytomyr National Agroecological University,
Staryi Blvd, 7, Zhytomyr, 10008 Ukraine
E-mail: elmi1969@meta.ua
[1]Corresponding author

Circulation Pathways of Trematodes of Freshwater Gastropod Mollusks in Forest Biocenoses of the Ukrainian Polissia. Zhytova, E. P., Romanchuk, L. D., Guralska, S. V., Andreieva, O. Yu., Shvets, M. V. — This is the first review of life cycles of trematodes with parthenitae and larvae in freshwater gastropods from forest biocoenoses of Ukrainian Polissia. Altogether 26 trematode species from 14 families were found circulating in 13 ways in molluscs from reservoirs connected with forest ecosystems of the region. Three-host life cycle is typical of 18 trematode species, two-host life cycle has found in 7 species, and four-host cycles has found in one species. *Alaria alata* Goeze, 1782, has three-host (Shults, 1972) and four-host cycles. *Opisthioglyphe ranae* (Froehlich, 1791) can change three-host life cycle to two-host cycle replacing the second intermediate host (Niewiadomska et al., 2006) with the definitive host. Species with primary two-host life cycle belong to Notocotylidae Lühe, 1909, Paramphistomidae Fischoeder, 1901 and Fasciolidae Railliet, 1758 families. Trematodes with three-host cycle have variable second intermediate hosts, including invertebrates and aquatic or amphibious vertebrates. Definitive hosts of trematodes are always vertebrates from different taxonomic groups. The greatest diversity of life cycles is typical for trematodes of birds. Trematodes in the forest biocoenoses of Ukrainian Polissia infect birds in six ways, mammals in three, amphibians in four, and reptiles in one way. The following species have epizootic significance: *Liorchis scotiae* (Willmott, 1950); *Parafasciolopsis fasciolaemorpha* Ejsmont, 1932; *Notocotylus seineti* Fuhrmann, 1919; *Catatropis verrucosa* (Frölich, 1789) Odhner, 1905; *Cotylurus cornutus* (Rudolphi, 1808); *Echinostoma revolutum* (Fröhlich, 1802) Dietz, 1909; *Echinoparyphium aconiatum* Dietz, 1909; *Echinoparyphium recurvatum* (Linstow, 1873); *Hypoderaeum conoideum* (Bloch, 1782) Dietz, 1909; *Paracoenogonimus ovatus* Kasturada, 1914; *Alaria alata* Goeze, 1782.
Key words: trematoda, molluscs, life cycles, circulation, definitive host, forest biocoenosis.

Introduction

Prevention of animal trematodosis and devising methods for detecting helminth transmission foci in hunting farms is an important problem (Akimova et al., 2017).

Trematodes are an important component of natural ecosystems (Poulin, 2014; Rastyazhenko et al., 2015). Like other parasitic organisms, they negatively affect organisms, populations, animal groups and food chains in general (Kuris et al., 2008). Trematodes are internal parasites with a complex life cycle which includes a number of stages with parthenogenetic and amphimictic (mostly hermaphroditic) generations, as well as alternating hosts, invertebrates and vertebrates (Blasco-Costa, Poulin, 2017; Zhytova, Kornyushin, 2017). The first intermediate host in that life cycle is almost always a molluscs (Serbina, 2014; Zhytova, Zhytov, 2016; Faltynkova, 2016; Gordy et al., 2016; Chontananarth, 2017), in which parthenogenetic generations of trematodes develop. The second intermediate host can be animals of different systematic groups, mainly invertebrates. Definitive hosts are representatives of different classes of vertebrates (Iskova et al., 1995; Cribb, 2016).

According to modern taxonomy, there are know more than 18,000 species of trematodes (Bray et al., 2008). More than 166 species of trematodes of animal are known in Ukrainian Polissia forest zone, and life cycles of 35 of them are not studied (Iskova et al., 1995). In particular, there are trematodes with life cycles that differ in evolutionary advancement. Formation and realization of parasitic trematode life cycles evolved with improving the mechanisms of infection transmission from one host to another. Reviewing studies on trematodes life cycles (Sharpilo, 1976, 1989; Iskova, 1985; Niewiadomska et al., 2006; Blasco-Costa, Locke, 2017) results in generalization on parasitic circulation, and similarities and differences in their life cycles.

Today, situation with wild animals, in particular, with game animals, in the region is rather complicated and ambiguous. This, in some way, is related to both the parasitic animal diseases and the anthropogenic influence on forest ecosystems. Studying trematodes and their circulation ways is necessary for successful management of hunting farms, in particular, for breeding wild animals in enclosures. Thus the purpose of present study was to summarize the information about life cycles of trematodes in forest biocoenoses of the region, to understand the parasitic circulation ways and transmission between hosts using trophic chains based on the "victim-predator" model. This will allow developing a system of measures aimed at reducing the negative influence of these parasites on populations of hunted animals and ecosystem in general.

Material and methods

The work was done during 2009–2012 and 2016 years. Trematode circulation ways are studied by analyzing species composition of trematodes in gastropods from reservoirs of forestries of Volyn, Rivne, and Zhytomyr Regions (fig. 1).

In total, 2756 trematode specimens from Lymnaeidae, Bulinidae, Planorbidae, Bithyniidae, and Viviparidae molluscs were collected. Identification of molluscs was carried out according to generally accepted methods (Stadnichenko, 1990, 2006; Anistratenko, Stadnichenko, 1994; Anistratenko, 2001). Morphology of various trematode life cycle stages (sporocysts, rediae, unformed cercariae, mature cercariae and metacercariae) was studied mainly on living specimens using vital dyes (Chernogorenko, 1983).

The living and fixed specimens of cercariae were measured using microscopes MBS-10, AxioImager M 1, MIKMED 1. Prevalence was determined by formula proposed by G. K. Petrushevsky, M. G. Petrushevskaya (1960). Scientific works describing the life cycles of trematodes, published in domestic and foreign journals from 1950 to 2008, were used in the paper. In the analysis of circulation pathways, the species of trematodes whose life cycles were *deciphered* were taken into account. For trematodes systematic determination, the system given in monographes "Keys to the Trematoda" was used (2002; 2005; 2008).

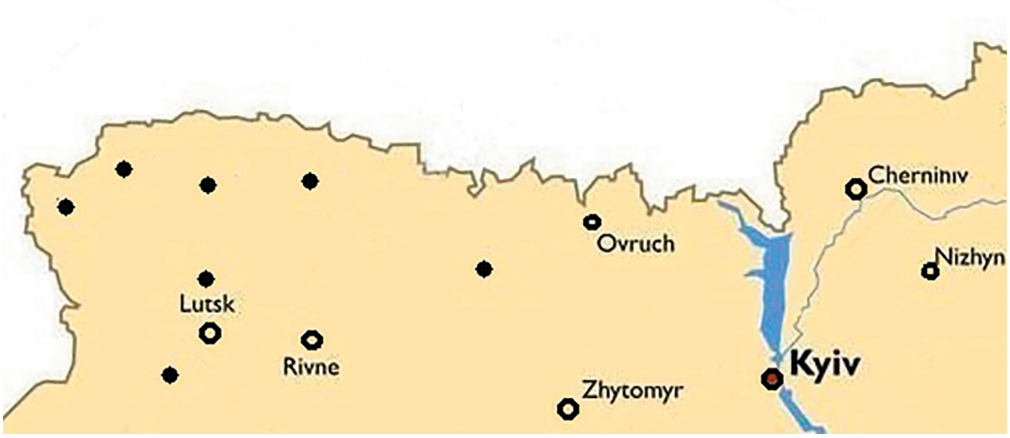

Fig. 1. Points — location of mollusc collection sites (ponds of Ukrainian Polissia).

Results and discussion

As a result of our studies, 26 species of trematodes from 14 families were found in aquatic ecosystems of Ukrainian Polissia forests (table 1). Circulation of the found trematodes occurs in 13 ways.

Most of the species (18) have three-host life cycle, seven have two-host one, and one has four-host life cycle. However, *Alaria alata* Goeze, 1782 can develop both in three-host and four-host life cycle, and *Opisthioglyphe ranae* (Froehlich, 1791) can develop in three-host and two-host life cycle via exclusion of the second intermediate host replaced by definitive host. The life cycles of animal parasites found in forest biocoenoses in the region are described below.

Table 1. Species composition of trematodes in molluscs from the water reservoirs of Ukrainian Polissia forest biocoenoses

Trematode species	Intermediate host	EI, %	Vertebrate definitive hosts (classes)
Family Diplodiscidae Cohn, 1904			
Diplodiscus subclavatus (Pallas, 1760) (Syn.: *Cercaria diplocotylea* Pagennstecher, 1857)	*Planorbis planorbis* (Linné, 1758)	4.58 ± 1.83	Amphibia Reptilia
	Segmentina nitida (Müller, 1774)	1.38 ± 0.32	
Family Paramphistomidae Fischoeder, 1901			
Liorchis scotiae (Willmott, 1950)	*P. planorbis*	2.03 ± 1.16	Mammalia
Family Leucochloridiomorphidae Allison, 1943			
Leucochloridiomorpha constantiae (Müller, 1935) Gover, 1938	*Contectiana contecta* (Millet, 1813)	28.57 ± 3.8	Aves
Family Fasciolidae Railliet, 1758			
Parafasciolopsis fasciolaemorpha Ejsmont, 1932	*Planorbarius corneus* (Linné, 1758)	2.1 ± 1.06	Mammalia
Family Echinostomatidae Looss, 1899			
Echinostoma revolutum (Fröhlich, 1802) Dietz, 1909	*Lymnaea stagnalis*(Linné, 1758)	2.13 ± 1.91	Aves Mammalia
	Lymnaea palustris palustris (O. F. Müller, 1774)	6.67 ± 6.44	
	Planorbarius corneus (Linné, 1758)	1.09 ± 0.54	
	P. planorbis	0.68 ± 0.68	
	Viviparus viviparous (Linnaeus, 1758)	2.0 ± 1.4	
Echinostoma stantchinskii Semenov, 1927 (Syn.: *Cercaria spinifera* Wesenb-Lund, 1934)	*P. corneus*	2.86 ± 2.82	Aves
	L. stagnalis	0.89 ± 0.63	
Echinostoma chloropodis (Zeder, 1800) Dietz, 1909	*Bithynia tentaculata*(Linne, 1758)	2.86 ± 2.82	Aves
Echinoparyphium aconiatum Dietz, 1909 (Syn.: *Cercariae chinata* Seibold, 1837)	*L. stagnalis*	0.44 ± 0.14	Aves
	Lymnaea corvus (Gmelin,1791)	1.08 ± 0.29	
	P. corneus	1.64 ± 0.94	
Echinoparyphium recurvatum (Linstow, 1873)	*L. stagnalis*	4.76 ± 4.65	Aves
	P. planorbis	2.33 ± 2.30	
	P. corneus	3.7 ± 2.09	
Patagifer bilobus (Rudolphi, 1819)	*P. planorbis*	0.68 ± 0.68	Aves
Hypoderaeum conoideum (Bloch, 1782) Dietz, 1909	*L. stagnalis*	0.44 ± 0.44	Aves
	Lymnaea ovata (Draparnaud, 1805)	5.88 ± 5.71	
	P. corneus	0.61 ± 0.6	

Family Notocotylidae Lühe, 1909			
Notocotylus seineti (Fuhrmann, 1919) (Syn.: *Cercaria ephemera* Nitzsch (= *Notocotylus ephemera* (Nitzsch, 1807) = *Notocotylus thienemanni* L. et U. Szidatcerc.)	*P. corneus*	1.23 ± 1.22	Aves Mammalia
Notocotylus sp.	*P. planorbis*	0.68 ± 0.68	Aves
Catatropis verrucosa (Frölich, 1789) Odhner, 1905	*Bithynia tentaculata* (Linné, 1758)	2.86 ± 2.82	Aves
Family Plagiorchiidae Lühe, 1901			
Plagiorchis mutationis (Panova, 1927)	*L. stagnalis*	3.67 ± 1.25	Aves
Plagiorchis sp.	*L. corvus*	0.08 ± 0.08	Aves
Haplometra cylindracea (Zeder, 1800)	*L. stagnalis*	7.14 ± 6.88	Amphibia
Family Omphalometridae Odening, 1960			
Rubenstrema exasperatum / Neoglyphe locellus complex (Syn.: *Cercaria pseudornata* Luhe, 1909 of Luhe (1909))	*P. corneus*	0.86 ± 0.61	Mammalia
Family Telorchiidae Looss, 1899			
Opisthioglyphe ranae (Fröhlich, 1791) (Syn.: *Cercaria armata* Siebold. 1837)	*L. stagnalis*	0.81 ± 0.57	Amphibia Reptilia
	L. corvus	0.23 ± 0.13	
Family Leptophallidae Dayal, 1938			
Lepthophallus nigrovenosus (Bellingham, 1844)	*L. stagnalis*	2.0 ± 1.98	Reptilia
Family Haematoloechidae Freitas et Lent, 1939			
Haematoloechus asper Looss, 1899	*P. corneus*	1.06 ± 0.75	Amphibia
Haematoloechus variegatus (Rudolphi, 1819)	*Planorbarius purpura* (O. F. Müller, 1774)	1.04 ± 0.68	Amphibia
	P. planorbis	2.33 ± 0.36	
Family Strigeidae Railliett, 1919			
Cotylurus cornutus (Rudolphi, 1808) (Syn.: *Cercaria strigea tardae* Mathias, 1925)	*L. stagnalis*	60.0 ± 3.36	Aves
	L. corvus	20.0 ± 12.7	
	L. ovata	2.44 ± 2.41	
	P. corneus	5.26 ± 3.62	
	Planorbarius banaticus (Lang, 1856)	3.33 ± 3.27	
Family Diplostomidae Poirier, 1886			
Tylodelphys clavata (Nordmann, 1832) (Syn.: *Cercaria letifera* (Fuhrt, 1916))	*L. stagnalis*	7.14 ± 0.72	Aves
Alaria alata Goeze, 1782	*P. planorbis*	1.37 ± 0.97	Mammalia
Family Cyathocotylidae Mühling, 1898			
Paracoenogonimus ovatus Kasturada, 1914 (Syn.: *Cercaria monostomi viviparae* L. Szid = *Linstowiella viviparae* (Linstow, 1877))	*C. contecta*	2.38 ± 2.35	Aves
	Viviparus viviparu (Linnaeus, 1758)	2.0 ± 1.4	

A. Two-host life cycles of trematode

This type of life cycle occurs only with two hosts, a mollusc and a vertebrate (fig. 2, *a*). It is typical of seven trematode species of families Notocotylidae, Fasciolidae, Paramphistomidae which develop in molluscs of families Lymnaeidae, Planorbidae, Bulinidae. After leaving mollusc, cercariae encyst, turning into adolescariae swallowed by definitive hosts with water and aquatic vegetation. Trematodes of the family Leucochloridiomorphidae, whose cercariae do not leave molluscs, develop similarly. All stages of development occur in molluscs of family Viviparidae. In forest biocoenoses of studied region, five circulation ways of two-host trematode species were revealed.

1. Molluscs–external environment (adolescariae)–amphibians. That circulation way is typical of *D. subclavatus*. The intermediate hosts are molluscs of family Planorbidae. Marita of *D. subclavatus* can also develop in reptiles.

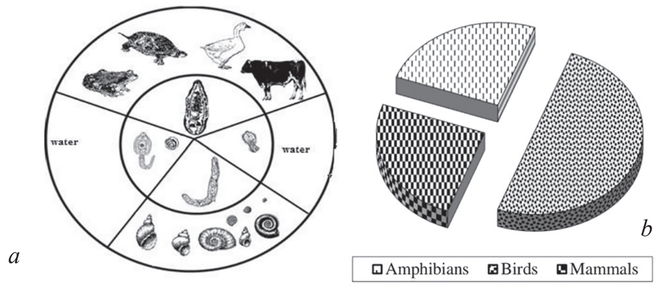

Fig. 2. Two-host life cycles of trematodes : *a* — alternation hosts; *b* — proportion of different classes of definitive hosts in life cycles.

2. Molluscs–external environment (adolescariae)–birds. That circulation way is typical of *N. seineti, Notocotylus* sp., *Catatropis verrucosa.* Intermediate hosts of Notocotylidae are molluscs from families Lymnaeidae, Bulinidae, Planorbidae and Bithyniidae. Definitive hosts, waterfowl are infected swallowing adolescariae with food.

3. Molluscs–external environment (adolescariae)–mammals. That circulation way is typical of *L. scotiae* and *P. fasciolaemorfa.* Their intermediate hosts are molluscs from families Planorbidae and Bulinidae.

Life cycles of the following trematode species do not have the adolescaria phase, definitive hosts are infected differently.

4. Molluscs–external environment (cercariae)–amphibians. That circulation way is typical of *O. ranae.* Cercariae can actively penetrate into different parts of tadpole body and encyst. Encysted in amphibians, metacercariae become infectious, leave cysts, and migrate through esophagus to stomach (Niewiadomska, et al., 2006) and intestines of host to mature.

5. Molluscs–(cercariae)–birds. Circulation of the species *L. constantiae* is different. Their cercariae do not leave the body of intermediate mollusc host to leave and encyst in animal tissues. Definitive hosts, mostly waterfowl, become infected by eating infected molluscs.

For most of studied trematode species with two-host life cycle (50 %), birds are the definitive hosts (fig. 2, *b*).

B. Three-host life cycles of trematodes

Three-host life cycles occur in 18 studied trematode species. In three-host cycle, as well as in two-host one, miracidii hatch in water from trematode eggs and infect molluscs. The second larvae, cercariae, also go out into water and infect hosts turning then into metacercariae. In turn, metacercarial hosts are a usual food for the definitive hosts, which are infected following the "victim-predator" model. In general, in the region, there are seven circulation ways of three-host trematode life cycles. And five of these circulation ways include invertebrates as the second intermediate hosts.

I. Three-host life cycles with invertebrates as the second intermediate hosts

There is a wide taxonomic diversity of the second intermediate hosts in that trematode life cycle. The hosts include hydrobionts and amphibionts (fig. 3).

Trematodes that develop in hydrobionts as their second intermediate hosts (leeches, crustaceans, molluscs) are represented by nine species (fig. 3, A, *a*).

1. Molluscs–molluscs–amphibians. This circulation is typical of trematodes *H. cylindracea* and *O. ranae* (if three-host). The first and second intermediate hosts of these trematodes can be a single lung snail species of family Lymnaeidae. The trematode *O. ranae*

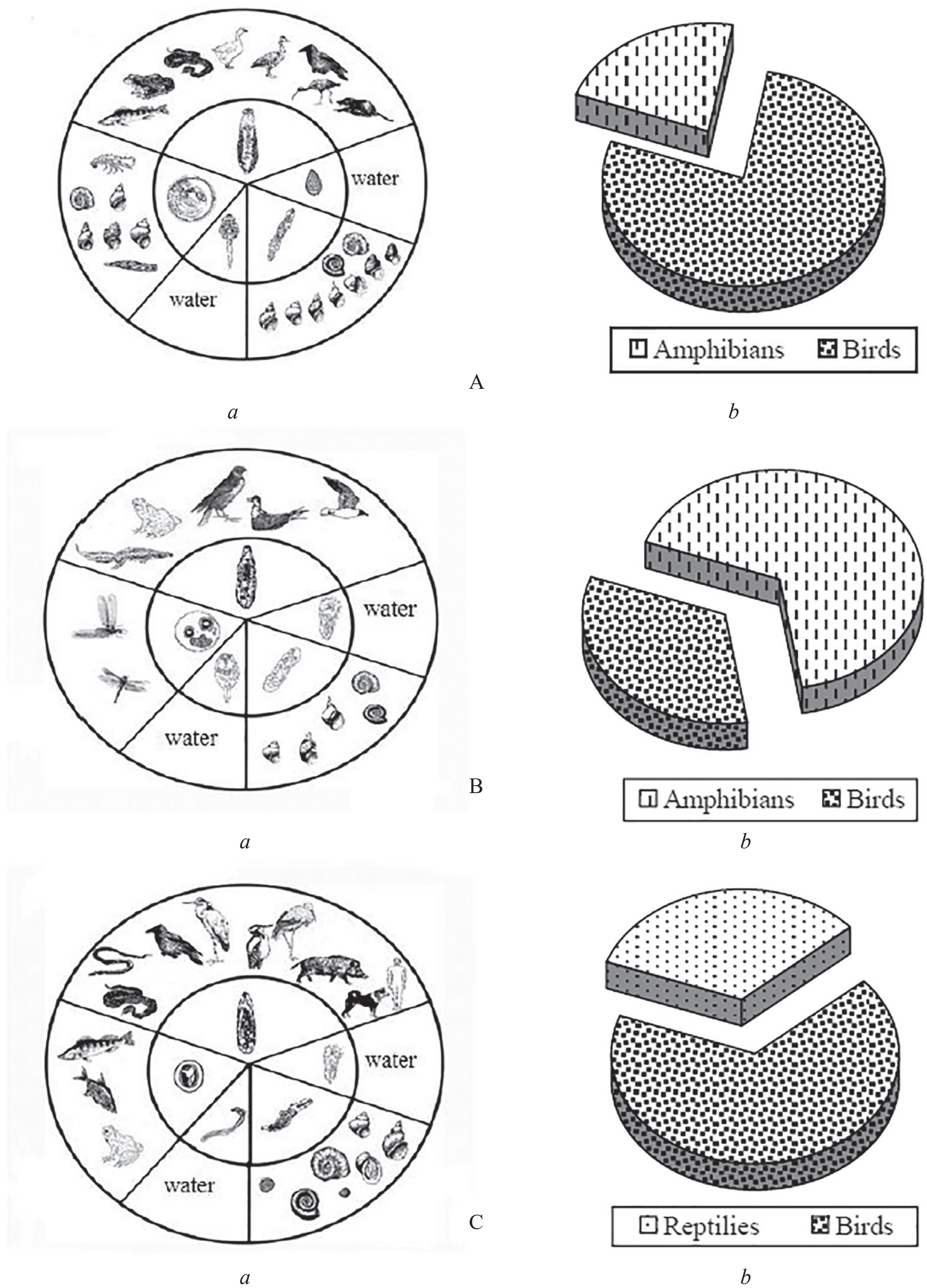

Fig. 3. Three-host life cycle of trematodes: A — second intermediate hosts are aquatic invertebrates; B — second intermediate hosts are amphibiontic invertebrates; C — second intermediate hosts are vertebrates; *a* — alternation hosts; *b* — biological structure of helminth fauna.

is capable of post-cyclic parasitism (ability of mature parasites eaten in their host by a predator to continue development), when reptiles eat infected amphibians.

2. Molluscs–molluscs–birds. This is the most common parasite circulation in the region. This life cycle is typical of trematodes, whose definitive hosts are mollusc-eating birds. This is circulation way of seven species from two families, Echinostomatidae (*E. revolutum, E. recurvatum, E. aconiatum, H. conoideum, E. stantschinskii, P. bilobus*) and Strigeidae (*C. cornutus*). Their intermediate hosts are molluscs of families Lymnaeidae, Planorbidae, Bulinidae, Bithyniidae, and Viviparidae. Most of these species are capable of amphixenia. The trematode *E. revolutum* can parasitize mammals too.

3. Molluscs–leeches–birds. This circulation way is typical of *C. cornutus.* Most of second intermediate hosts are leeches.

The obtained data indicate that the vast majority (77. 78 %) of trematodes which develop in aquatic animals as second intermediate hosts parasitize in birds (fig. 3, A, *b*).

Trematodes that develop in amphibionts (insects) as their second intermediate hosts are represented by three species (fig. 3, B, *a*).

1. Molluscs–insects–amphibians. This circulation is typical of *H. asper* and *H. variegatus.* Metacercariae of these species were found in imagines and larvae of dragonflies. Their first intermediate hosts are molluscs of families Bulinidae and Planorbidae.

2. Molluscs–insects–birds. This circulation is typical of *P. mutations* and *Plagiorchis* sp. Their first intermediate hosts are molluscs of the family Lymnaeidae.

Most (67 %) of recorded trematode species which develop in amphibiontic second intermediate hosts parasitize amphibians (fig. 3, B, *b*).

II. Three-host life cycle of trematodes with vertebrates as their second intermediate hosts

In cycles of trematodes, wich belonging to this type, among the second intermediate hosts in forests of region are fish, amphibians and definitive hosts include reptiles, birds (fig. 3, C, *a*). That life cycle is found in three studied trematode species.

1. Molluscs–fish–birds. That circulation is typical of two trematode species, *P. ovatus* and *T. clavata* in forest biocoenoses. Fish-eating birds play the main role in circulation of these trematode species. Their metacercariae encyst in organisms of various freshwater fish species. For *T. clavata,* the second intermediate hosts can also be amphibians.

2. Molluscs–amphibians–reptiles. This circulation is typical of *L. nigrovenosus.* Its parthenitae and cercariae develop in *L. stagnalis,* and metacercariae in amphibians (tadpoles). Snakes are its definitive hosts.

For majority (67 %) of recorded trematode species with that life cycle, definitive hosts are birds (fig. 3, C, *b*).

C. Four-host life cycle of trematodes

This circulation is typical of *A. alata*. Its first intermediate hosts are ramshorn snails (Planorbidae) (fig. 4).

Its metacercariae can develop in tadpoles and mature frogs. Various species of mammals, in particular, *Rattus norvegicus*, *Apodemus agrarius*, *Apodemus sylvaticus*, *Apodemus flavicollis*, *Martes zibellina*, *Mustela nivalis*, *Mustela putorius*, and *Martes martes* can become paratenic hosts. Its definitive hosts are wild predatory mammals and domestic dogs. The main role in maintaining the circulation of trematode *A. alata* in the region belongs to animals of order Rodentia.

Two thirds (66.67 %) of all studied trematode larvae belong to species with the Three-host life cycle, 25.93 % are two hosts, and 3.70 % have the four host life cycle. All definitive hosts are known for 26 studied trematode species found in molluscs from reservoirs in forests of Ukrainian Polissia (fig. 5).

Our results and analysis of literature (Iskova, et al., 1995; Kudlai, 2011) show that circulation of trematodes varies in different regions of Ukraine (forest ecosystems of Ukrainian Polissya and Northern Priazovye). Thus, trematode circulation in all classes of

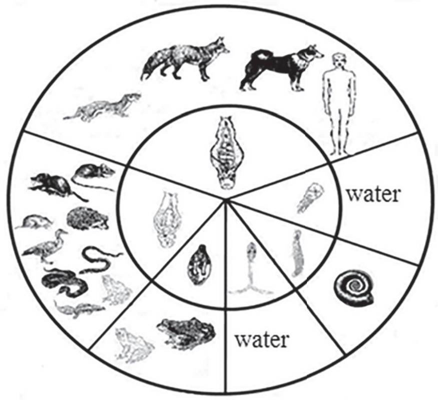

Fig. 4. Four-host life cycles of trematodes.

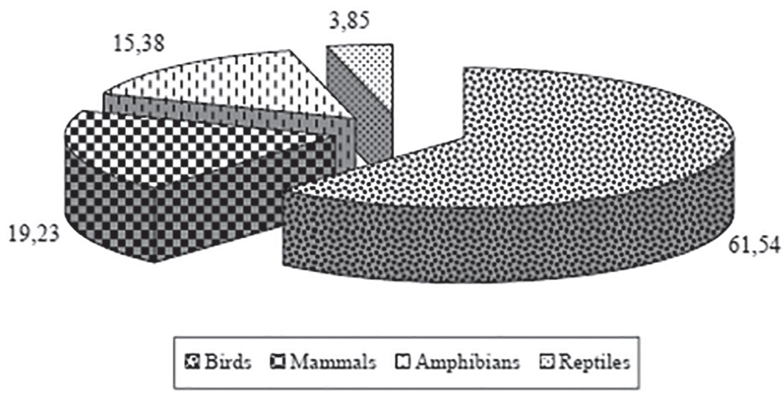

Fig. 5. The ratio of studied trematode species according to the classes of definitive hosts.

animals in the study area is more varied compared to that of trematodes from Northern Priazovye, with the only exception of fish trematodes. Moreover, trematodes with tetraxenic life cycle were not detected on studied territory. This difference, in our opinion, is due to the species composition of definitive hosts and their trematodes that develop in molluscs of forest biocoenoses of Ukrainian Polissia.

Conclusion

In forest biocenoses of Ukrainian Polissia, reptiles are infected with trematodes in one way, mammals in two ways, amphibians in four, and birds in six ways.

Birds as definitive hosts and pulmonary snails as intermediate hosts have the greatest importance in trematode circulation in forest biocoenoses of Ukrainian Polissia. Thus, avian trematodes and their hosts are characterized by the greatest variety of all studied taxa in forest biocenoses of the region. Also, compared to other vertebrate animals associated with aquatic biocoenoses, namely birds have close and constant trophic relationships with molluscs.

Eleven of found trematode species of 7 families have epizootological significance: Fasciolidae (*P. fasciolaemorpha*), Paramphistomidae (*L. scotiae*), Notocotylidae (*N. seineti, C. verrucosa*), Strigeidae (*C. cornutus*), Echinostomatidae (*E. revolutum, E. recurvatum, E. aconiatum, H. conoideum*), Diplostomidae (*A. alata*), and Cyathocotylidae (*P. ovatus*). These species are pathogens of dangerous diseases in wild birds, mammals and humans.

The trematode *A. alata* is very dangerous and causes perilous disease in humans and animals (alariasis) which occurs on the territory of Ukrainian Polissia (Shymalov, 2004; Zhytova, 2014).

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