

PARASITOLOGY  
OF HYDROBIONTS

Freshwater Trematodes *Sanguinicola* (Digenea: Aporocotylidae)  
in Europe: Distribution, Host Range, and Characteristics  
of Fish and Snail Infestation (Review)

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**Abstract**—Data on trematode life cycles, fish host distribution, transmission, and fish and snail infection are reported in this review. European freshwater trematodes of the genus *Sanguinicola* (Aporocotylidae) remain an insufficiently studied group of trematodes. Five species of Aporocotylidae (*Sanguinicola armata*, *S. inermis*, *S. intermedia*, *S. volgensis*, and *S. rutili*) in freshwater fish of Europe are described. In addition, they have been found in the water bodies of Central Asia and West Siberia (Ob-Irtysh River basin). The life cycle allowing us to assign the cercariae and adults to a certain species is known only for *S. armata*, *S. inermis*, and *S. rutili*. Trematodes of the genus *Sanguinicola* are found in 26 fish species assigned to 7 families and 4 orders and 24 gastropod species assigned to 7 families. With few exceptions, the sanguinicolid infection of fish and snails is rather low in the natural water bodies.

**Keywords:** trematodes, *Sanguinicola*, freshwater fish, snails

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INTRODUCTION

Trematodes, also called “blood flukes” (Digenea: Schistosomatoidea), parasitizing the blood vessels of vertebrates, are allocated into three families; each family corresponds to a certain group of definitive hosts. Schistosomes (Schistosomatidae) infect birds and mammals; they are considered the most studied group of trematodes (Brant et al., 2006). Spirorchids (Spirorchidae) are parasites of marine and freshwater turtles. Trematodes of the family Aporocotylidae Odhner, 1900 parasitize marine and freshwater fish. Blood flukes in fish usually develop with the participation of one intermediate host, which can be a species from gastropods, bivalves, and polychaetes (Peoples, 2013). They parasitize the cartilaginous and bony marine, estuarine, and freshwater fish throughout the world, mainly localized in the blood, body cavity, and (infrequently) other organs (Alama-Bermejo et al., 2011). At present, aporocotylids comprise 165 species assigned to 39 genera (Oréllis-Ribeiro et al., 2014; Warren and Bullard, 2019). New genera and species of this family are being found at a relatively high rate compared to that for other families of fish trematodes; diversity in it is apparently underestimated (Cribb and Bray, 2011). Nevertheless, this family remains a very

poorly studied trematode. Blood flukes in freshwater fish are insufficiently studied when compared with the marine fish trematode. Thus, only 6 of 39 genera of aporocotylids are blood parasites of the freshwater fish. Species of the genus *Acipensericola* Bullard, Snyder, Jensen et Overstreet, 2008 parasitize the freshwater sturgeon species in North America (Warren et al., 2017). Representatives of the genera *Plehnella* Szidat, 1951; *Cladocaeum* Oréllis-Ribeiro & Bullard, 2016; *Kritsky* Oréllis-Ribeiro & Bullard, 2016; and *Nomasanguinicola* Truong & Bullard, 2013 infect catfish species (Siluriformes) in South America, West Asia, and Southeast Asia (Truong and Bullard, 2013; Oréllis-Ribeiro, Bullard, 2015). The largest genus *Sanguinicola* Plehn, 1907 includes species known as freshwater, marine, and estuarine fish. Freshwater *sanguinicola* species are recorded in fish on every continent except Australia. Five species of Aporocotylidae—*Sanguinicola armata* Plehn, 1905; *S. inermis* Plehn, 1905; *S. intermedia* Ejsmont, 1926; *S. volgensis* (Rasin, 1929) McIntosh, 1934; and *S. rutili* Simon-Martin, Rojo-Vazquez & Simon-Vicente, 1987—are described in the freshwater fish of Europe. In addition, some of these trematodes were found in fish and snails in the water bodies of Central Asia and West Siberia (the Ob-Irtysh River basin). No molecular genetic test was performed for any of these species.

**Abbreviations:** intensity of infection (II); prevalence (P).



Fig. 1. Map of the locations of *Sanguinicola* found in the freshwater fish (●) and snails (■) in Europe and some countries in Asia.

This paper presents data on the spreading, host distribution, and fish infection with freshwater aporocotylids; their diversity; and snail infection with cercariae.

The deficiency in information on trematodes of the genus *Sanguinicola* can be explained by the fact that sanguinicolae are small transparent worms 1–2 mm in length localized in the fish heart, gill vessels, and kidneys. It is difficult to remove these organs accurately. When the blood vessels break, trematodes exit from them and escape; therefore, it is rather difficult to find them, especially upon low intensities of invasion. Rather commonly, researchers cannot find the trematodes themselves, but indicate eggs that are detectable through the gill filament vessels of fish. It is quite possible that sanguinicolae are rarely found because blood vessels and the heart are rarely observed within routine parasitology testing in fish. It cannot be excluded that most sanguinicolae are occasionally detected. Any of those indicated above can be proven by the fact that sanguinicolae found in snails and underyearling in some water bodies were not observed in adult fish. Thus, the underyearling of roach, ide, and pikeperch were infected with sanguinicolae (Kulemina, 1969), while sanguinicolae were not detected in adult fish (Shul'man and Kulemina, 1969). The report of Stenko (1979) provides data on the large infection of snails *Lymnaea auricularia* L., 1758 with sanguinicolae in various water bodies on the Crimean Peninsula, while these trematodes were not found in the fish there (Miroshnichenko, 2008). Further examples may be provided.

#### Distribution

The literature source data on the fish and snail infection show that European *Sanguinicolae* are widely distributed across Europe and Central Asia (Kazakhstan, Uzbekistan, and Kyrgyzstan). In addition, they are found in the southern part of West Siberia (Ob River basin) and in Caucasus (Fig. 1). The northern boundary of their distribution narrowly fails to reach the Article Circle (Mezen and Pechora Rivers) (Ekimova, 1962, 1976; Dorovskikh, 1997). *S. inermis* has been reported in wild carp from the Zeya River in the Amur River basin (Strelkov, 1971). The recently described *Sanguinicola rutili* has the most limited distribution, with evidence gathered so far only from Spain (Simon-Martin et al., 1987). Three species of sanguinicolae (*S. armata*, *S. inermis*, and *S. volgensis*) are found in fish in England; in addition, *S. inermis* is an introduced species (Kirk and Lewis, 1994).

A comparison of the records of trematodes found in fish and snails (Fig. 1) shows a considerable discrepancy in the distribution of both host parasites. Thus, the snails of five species infected with sanguinicolae cercariae were found in different water bodies across the whole territory of Kazakhstan (Butenko, 1967; Smirnova and Irbasheva, 1967; Belyakova, 1975, 1981; Belyakova and Mazina, 1990). Adult *S. inermis* trematodes within the territory of Kazakhstan were found only in the carp on a fish farm near Alma-Ata (Agapova, 1966) and in the wild carp and the ide in the Bukhtarma Reservoir (Bragina, 1972). In Crimea, snails infected with cercariae were found in five different water bodies of high infection, up to 71.4%

(Stenko, 1979). However, sanguinicolae were not found in fish in the Crimean Peninsula (Miroshnichenko, 2008). Sanguinicolae in fish and snails occur in water bodies and watercourses of different types: firths (Dogel and Petrushevsky, 1933; Mekhraliev and Mikailov, 1982), lakes, and lowland and upland rivers (Belyakova, 1975; Olenev, 1979; Ermolenko et al., 1998).

#### *Life Cycles*

Life cycles of European *Sanguinicola* species studied to a level allowing us to assign their cercariae and adults to a certain species are well-described for a limited number of species. Cercariae and sporocysts of *S. armata* found in the snail *Lymnaea stagnalis* (L., 1758) are described (Sendersky et al., 2002; Sendersky and Dobrovolsky, 2004). The authors found infected *L. stagnalis* snails in a pond inhabited by only one fish, the crucian *Carassius carassius* (L., 1758). The trematodes found in the crucian were determined as *S. armata*. The life cycles and morphology of the *Sanguinicola inermis* cercariae and maritae in the *Cyprinus carpio* (L.) and *Lymnaea peregra* (O.F. Müller, 1774) species experimentally infected have been studied (Kirk and Lewis, 1993). Moreover, the life cycle of *Sanguinicola rutili* has been studied (Simon-Martin et al., 1987). A description of cercariae, sporocysts, and maritae isolated from the snail *Ancylus fluviatilis* (O.F. Müller, 1774) and the fish *Achondrostoma arcasii* Steindachner, 1866 is reported in the paper.

#### *Distribution and Host Range*

It has been traditionally considered that European *Sanguinicolae* generally parasitize the Cyprinidae. An analysis of the literature source data has shown (Table 1) that this is only partly true. *S. volgensis* has a wide range of hosts (12 species); this species is more frequently recorded in pike. In addition, *S. volgensis* is found in Percidae (ruff, perch, and pikeperch) and eight species of Cyprinidae. *S. inermis* has a wide range of hosts (13 species); with a few exceptions, they are generally assigned to Cyprinidae (the wild carp is most frequent). *S. armata*, parasitizing ten fish species, generally the Tench, may be called a species typical for the Cyprinidae. A similar so-called “Cyprinida” species is the *S. intermedia*, more frequently occurring in crucians and found only in four fish species. The endemic *S. rutili* species is found only in the Spanish roach *Achondrostoma arcasii* (Steindachner, 1866) in Spain. Table 1 presents a list of fish species infested with trematodes indicated as *Sanguinicola* sp. Among the hosts, the catfish *Silurus glanis* L., 1758 (trematode fragments are found); the stone loach *Barbatula barbatula* L., 1758; and the Peled *Coregonus peled* Gmelin, 1789 are recorded. An analysis of the European *Sanguinicola* records can prove that they parasitize fish of seven families: Cyprinidae (18 species),

Esocidae (pike), Balitoridae (bearded stone loach), Cobitidae (loach), Percidae (perch, ruff, and pikeperch), Siluridae (catfish), and Coregonidae (peled); overall, they comprise 26 fish species.

The record of *Sanguinicola* sp. found in the peled from the Pechora River has been reported (Ekimova, 1976). However, the peled is not found in the Pechora River, according to the data of ichthyologists (Reshetnikov, 2003). If the fish species was incorrectly identified, it could be the broad whitefish *Coregonus nasus* Pallas, 1776, which inhabit the Pechora River. *Sanguinicola* sp. found in the common whitefish caught in the Pechora River can probably be considered occasional, since these trematodes are not found in the other European and North Asian Salmonidae. However, Salmonidae (taimen and lenok) are recorded as the hosts of sanguinicolae in the Amur River basin (Strelkov, 1971; Ermolenko et al., 1998). Five species of *Sanguinicola* parasitizing the Salmonidae are known in North America (Warren et al., 2017).

The stone loach *Barbatula barbatula* L., 1758 is probably a nonrandom host choice by *Sanguinicola* sp., since it is a single record in Europe (Shevchenko, 1956). Sanguinicolae are found in the Siberian stone loach *B. toni* Dybowski, 1869 within the Primorie maritime region (*Sanguinicola* sp.) (Ermolenko, 2004) and Japan (*S. hasegawai* Shimazu, 2013) (Shimazu, 2013) and the Tibetan stone loach *Triplophysa stoliczkaei* Steindachner, 1866 within Uzbekistan (*S. inermis*) (Bykhovskaya and Kulakova, 1987). In addition, a singular record of *Sanguinicola* sp. in catfish in the Volga River delta (Kurochkin, 1968) does not seem random, since aporocotylids in the Siluridae are found in Africa, West Asia, and Southeast Asia (Truong and Bullard, 2013).

The experimental datasets on the life cycles can provide more information on the specificity of *Sanguinicolae*. The in vitro cultivation of *S. inermis* has proven that the specific host of this species is carp (wild carp). Trematodes infected tench only in the case of a high level of infection with cercariae. The crucian carp appeared unsusceptible to the invasion of the cercaria *S. inermis* (Kirk, Lewis, 1992).

#### *Characteristics of Fish Infection*

It is rather difficult to determine the importance of the quantitative variables for infection, since they are dependent on the sample size, which can frequently be small. Data analysis shows that the prevalence (P) of fish by sanguinicolae is generally low (Table 1). Examples of rare occasions when prevalence exceeds 30% are associated with the small sample sizes or the fish P assessment by trematode eggs found in the gills. In addition, the high P was usually recorded in the limnephilus fish (crusian, tench, and wild carp) in lakes and reservoirs. The intensity of infection (II) is also low, generally no more than several units; >10 worms per

**Table 1.** Distribution and fish infection with freshwater trematodes of the genus *Sanguinicola*

Fish host	N	P, %	II (MA)	Water basin/region	Literature reference source -
<b><i>Sanguinicola volgensis</i></b>					
Pike	50	13	1–2	Rybinsk Reservoir (Volga River)	Izyumova, 1960
	12	7.6	1	The same	Babushkin and Tikhomirova, 1964
	57	1.75	1	Upper Volga River	Sokolov, 2000
	–	6.6	–	Vyatka River (Volga River basin)–	Grevtseva, 1976
	–	–	1–2	Neva Bay (Baltic Sea)	Dogel and Petrushevsky, 1933
	–	–	–	Danube River, Tisza River, and Lake Balaton (Hungary)	Molnar, 1969
	–	–	–	Water bodies in England	Kirk and Lewis, 1994
	–	–	1	Lake Yakty-Kul in Bashkiria	Diachenko et.al. 2006
	58	1.7	2	Sukhona River	Kudryavtseva, 1959
Roach	595	0.5	0.02	Lake Kubena	Radchenko, 2002
	–	–	–	Upper Volga River	Sokolov, 2000
	–	–	–	Ivankovo Reservoir (Volga River)	Strizhak, 1972
	–	–	–	Water bodies in England	Kirk and Lewis, 1994
Bleak	–	–	1–2	Danube River, Tisza River, and Lake Balaton (Hungary)	Molnar, 1969
Ide	110	0.91	1	Lake Dabie, Poland	Sobecka et al., 2004
	15	1.3	8–12	Kama River (Volga River basin)	Kashkovsky, 1971
	7	14.8	5	Rybinsk Reservoir (Volga River)	Izyumova and Shigin, 1958
Dace	–	–	–	Water bodies in England	Kirk and Lewis, 1994
Chub	–	–	–	The same	The same
Wild carp	33	6.1	2–6	Volga River delta	Ivanov, 2002
Silver bream	34	3.2	0.03	Lake Kubena	Radchenko, 2002
Sabrefish	17	11.8	1–4	Rybinsk Reservoir (Volga River)	Izyumova and Shigin, 1958
	27	3.7	1	Gorky Reservoir (Volga River)	The same
	–	20	1–3	Volga River, city of Saratov	Rašín, 1929
Ruff	19	5.2	1	Rybinsk Reservoir (Volga River)	Zhokhov, 2000
	66	1.5	0.01	Lake Belaye (Volga River basin)	Radchenko, 1999
Pikeperch	521	–	Units	Lake Kubena	The same
Perch	–	–	–	Water bodies in England	Kirk, Lewis, 1994
–	–	–	–	Don River	Krasilnikova, 1966
<b><i>S. armata</i></b>					
Tench	223	14.8	1–	Belaya River (Volga River basin)	Kazadaev, 1957
	–	–	11(3.4)	Lakes in Lithuania	Rautskis, 1988
	1/1	–	2	Kakhovka Reservoir (Dnieper River)	Malevitskaya and Lopukhina, 1955
	–	–	–	Lake Druzno (Poland)	Kozicka, 1959
	15	93.3	Eggs	Lake Zhuvintas (Lithuania)	Krotas, 1968
	–	–	–	Water bodies in Lithuania	Khussein, 1983
	–	–	–	Moscow River	Vasilkov et al., 1965
	11	29.2	4	The same	Kamensky and Ponomareva, 1964
	–	–	–	Water bodies in Germany	Plehn, 1905
	–	–	1–3	Danube River, Tisza River, and Lake Balaton (Hungary)	Molnar, 1969
	–	–	–	Water bodies in England	Kirk, Lewis, 1994
Roach	–	–	1–3	Danube River, Tisza River, and Lake Balaton (Hungary)	Molnar, 1969
	–	3.13	2	Lake Glubokoye, Moscow	Nikitina, 1991
	–	–	–	Mezen River	Dorovskikh, 1997
Chub	–	–	1–3	Danube River, Tisza River, and Lake Balaton (Hungary)	Molnar, 1969
Ide	–	–	1–3	The same	The same

Table 1. (Contd.)

Fish host	N	P, %	II (MA)	Water basin/region	Literature reference source -
Wild carp	317	0.63	1	Lake Ak Gel (Dagestan)	Astakhova et al., 1972
	—	—	—	Water bodies in Dagestan	Aligadzhiev, 1969
Nase	—	—	—	Dyje River (Czechia)	Moravec, 2001
Barbel	108	35	Eggs	Danube River (Hungary)	Moravec et al., 1997
Crucian carp				Ob River	Skipchenko et al., 1971; Sous, 1975
Loach	10	20	1	Danube River	Kulakovskaya and Koval, 1973
	—	—	—	Dyje River (Czechia)	Moravec, 2001
Pike	—	—	—	Water bodies in England	Kirk, Lewis, 1994
<i>S. intermedia</i>					
Golden carp	29	33	1–3	Volgograd Reservoir (Volga River)	Bogdanova, 1962
Crucian carp	10	—	—	Pechora River	Ekimova, 1962
	—	—	—	Vychegda River (Severnaya Dvina River basin)	Dorovskikh, 1986
	—	—	—	Lakes in Lithuania	Rautskis, 1988
	41	2.4	2	Seversky Donets River (Don River basin)	Shevchenko, 1956
	15	20	Eggs	Lake Zhuvintas (Lithuania)	Krotas, 1968
	14	7.1	5	Moscow River (Volga River basin)	Kamensky and Ponomareva, 1964
	—	—	—	The same	Vasilkov et al., 1965
	—	—	—	Water bodies in Lithuania and Belorussia	Khussein, 1983
Wild carp	—	—	—	The same	The same
Loach	—	—	—	Dyje River (Czechia)	Moravec, 2001
<i>S. inermis</i>					
Wild carp	—	5.9	7	Volgograd Reservoir (Volga River)	Bogdanova, 1961
	50	6	3–5	Volga River delta	Kurochkin, 1968
	—	1.6	—	Zeravshan River (Aral Sea basin, Uzbekistan)	Osmanov, 1971
	15	35.7	1–8	Lake Dautkul (Aral Sea basin, Uzbekistan)	Yusupov, 1980
	9	100	2	Kakhovka Reservoir (Ukraine)	Iskov and Koval, 1965
	—	—	—	Lake Shilyan (Georgia)	Kurashvili et al., 1980
	—	—	—	Water bodies in Germany	Plehn, 1905
	157	4.3	1–3	Kashkadarya River (Aral Sea basin, Uzbekistan)	Karaev and Koval, 1978
	9	44.4	1–3	Lake Macha (Czechia)	Moravec, 1978
	124	15	1–4	The same	Moravec, 1983
	—	—	—	Fish Farm (Kazakhstan)	Agapova, 1966
	4	26.7	Eggs	Batak Reservoir (Bulgaria)	Margaritov, 1964
	—	50.7	—	Kremenchug Reservoir (Ukraine)	Titov, 1989
	—	10	—	Kakhovka Reservoir (Ukraine)	The same
	2/2	—	4–24	The same	Malevitskaya and Lopukhina, 1955
	—	—	—	Water bodies in England	Kirk and Lewis, 1994
	—	—	1–17	Tisza River (Hungary)	Molnar, 1969
	—	—	—	Bukhtarma Reservoir (Cherny Irtysh River)	Bragina, 1972
	—	—	—	Dyje, Tisza, Elbe, and Oder Rivers (Czechia)	Moravec, 2001
Crucian carp	—	—	—	Water bodies in England	Kirk and Lewis, 1994
	—	—	1–17	Tisza River (Hungary)	Molnar, 1969
	—	—	—	Water bodies in Dagestan	Alogadzhiev, 1969,
	—	20	1–2	Lake Goryunovo (West Siberia)	Razmaskin et al., 1984
	22	4.5	2	Volga River delta	Ivanov, 2002
	214	4.7	1–3	The same	Kalmykov et al., 2013
	—	—	—	Ob River	Razmaskin and Shirshov, 1981

Table 1. (Contd.)

Fish host	N	P, %	II (MA)	Water basin/region	Literature reference source -
Ide	—	6.6	1–2	Lake Chikhovo (West Siberia)	Razmaskin et al., 1984
	—	—	—	Bukhtarma Reservoir (Cherny Irtysch River)	Bragina, 1972
	—	—	—	Vyatka River (Volga River basin)	Grevtseva, 1976
Tench	12	8.3	2	Lake Syamozero (Karelia)	Shul'man, 1961
Bream	—	—	—	Water bodies in England	Kirk and Lewis, 1994
	15	6.6	1	Lake Galstas (Lithuania)	Rautskis, 1977
Rudd	—	—	—	Lakes in Lithuania	Rautskis, 1988
	15	33.3	Eggs	Lake Zhuvintas (Lithuania)	Krotas, 1968
	—	—	—	Dyje, Tisza, Elbe, and Oder Rivers (Czechia)	Moravec, 2001
Silver bream	—	—	—	Lakes in Lithuania	Rautskis, 1988
	—	—	—	The same	The same
Asp	—	—	—	Vyatka River (Volga River basin)	Grevtseva, 1976
Bleak	15	—	—	Lake Nobel (Ukraine)	Ivasik and Kulakovskaya, 1958
Loach	—	—	—	Dyje, Tisza, Elbe, and Oder Rivers (Czechia)	Moravec, 2001
Pike	12	6.6	1	Gorky Reservoir (Volga River)	Izyumova et al., 1982
Roach	15	6.6	1	Lake Vrevo (St. Petersburg)	Gurkina, 1983
<i>Sanguinicola rutili</i>					
Spanish roach	—	—	—	Spain (Cilloruelo River)	Simon-Martin et al., 1987
<i>Sanguinicola sp.</i>					
Asp	—	—	—	Volga River delta	Kurochkin, 1968
Rudd	—	—	—	The same	The same
Wels catfish	—	—	—	» »	» »
Rudd	—	—	—	» »	Zabolotskaya, 1967
Peled	21	—	—	Pechora River	Ekimova, 1962
Bream	60	1.7	—	Lake Kortowka (Poland)	Dzika et al., 2008
Barbel	—	—	—	Jihlava River (Chechia)	Moravec, 2001
Tench	—	7.7	—	Alol Lakes (Pskov city)	Kha-Ki, 1964
Bleak	2/2	—	1	Kanev Reservoir (Ukraine)	Seregina, 1978
	1/1	—	1	Kakhovka Reservoir (Ukraine)	Malevitskaya and Lopukhina, 1955
Stone loach	17	11.8	1–1	Seversky Donets River (Ukraine)	Shevchenko, 1956
Wild carp	111	0.9	1	Bulgaria	Kakacheva-Avramova, 1965
Roach	40	17.5	1–10	Lake Verkhneye Vrevo (St. Petersburg)	Lopukhina and Strelkov, 1972a
Ide	16	6.3	1	The same	The same
Tench	10	10	1	» »	» »
Perch	27	3.7	Eggs	» »	» »
Bleak (juveniles)	—	4	1	» »	Lopukhina and Strelkov, 1972b; Yunchis, 1972
Ide (juveniles)	—	6.3–26.6	1–2	» »	The same
Roach	—	6.3–20	1–2	» »	» »
Ide (juveniles)	—	—	—	Lake Seliger (Volga River)	Kulemina, 1969
	—	—	—	The same	The same
Pikeperch (juveniles)	—	—	—	» »	» »
Zope	12	16.7	1	Rybinsk Reservoir (Volga River)	Authors' data
Silver bream	54	1.9	1	The same	The same
Ide	36	16.7	1–2	» »	» »
—	—	—	—	Don River	Krasilnikova, 1966

Notes: (N) number of analyzed fish, (II) intensity of infection, (MA) mean abundance, and (–) unavailable data.

fish is quite rare (Table 1). Very high II (>100 units per fish) is measured only in carps, probably of large sizes (Strelkov, 1971; Kirk and Lewis, 1994). It is considered that sanguinicolae are more frequently found in fish of the southern regions. With respect to *S. volgensis*, this statement is not proven by the data in Table 1. It is partly true for wild carp infection with *S. inermis*; however, the wild carp itself is a thermophilic fish more frequently found in southern regions.

There is almost no open data on fish infection associated with age. The analysis of large datasets on the wild carp infection with *S. inermis* reveals no age dependency ratio (Kirk and Lewis, 1994). A high level of infection was observed in both juveniles and old fish (10+). These authors have revealed that two species of sanguinicolae (*S. volgensis* and *S. inermis*) may simultaneously parasitize the fish. With respect to the other datasets (Scheuring, 1922), *S. inermis* is found in larger quantities in juvenile carp, rather than in old fish. Sanguinicolae infect fish at the early life stages. Young *Sanguinicola* sp. found in the branchial artery of roach larvae at the age of 59 days, in ide larvae at the age of 34–35 days (Lopukhina and Strelkov, 1972b; Yunchis, 1972). Other data shows that sanguinicolae infect roach larvae 8–11 mm in body length at the age of 10 days, ide larvae of 18–22 mm body length at the age of 25 days, and pikeperch larvae 7–12.5 mm in body length at the age of 15–20 days (Kulemina, 1969). The carp larvae at the pond fish farms are usually infected with *S. inermis* at the age of 29–30 days (Chechina, 1959).

#### Snail Hosts

Pulmonate gastropods and prosobranchs of the families Lymnaeidae, Planorbidae, Valvatidae, Neritidae, Lithoglyphidae, Bithyniidae, and Melanopsidae, totally comprising 24 species (the number of species may be lower due to adjusting the variations in the systematics of snails), are registered as the first intermediate hosts of European sanguinicolae (Table 2). Among the listed families, the sanguinicola sporocysts and cercariae were more frequently found in lymneids (*Lymnaea stagnalis*; *L. pereger*; *L. palustris*; *L. corvus* Gmelin, 1791; *Radix ovata*; *R. auricularia*; and *R. auricularia m. lagotis*) and melanopsids (*Melanopsis premorsa* L., 1758; *Fagotia acicularis* Férussac, 1823; *F. esperi* Férussac, 1823; *Microcolpia ucrainica* Starobogatov, Alexenko & Levina, 1992; *M. canaliculata* Bourguignat, 1884; and *M. potamoctebia* Bourguignat, 1870). The sanguinicolid hosts recorded were represented by three species among valvatidae (*Valvata piscinalis* O.F. Müller, 1774; *V. macrostoma* Mörch, 1864; and *V. pulchella* Studer, 1789) and two species among bithyniidae (*Bithynia tentaculata* L., 1758 and *B. leachii* Sheppard, 1823). Among lithoglyphidae, neritidae, and planorbidae, they were represented by one species each (*Lithoglyphus naticoides* C. Pfeiffer, 1828; *Theodoxus fluviatilis* L., 1758; and *Ancylus fluviatilis*, respectively).

Some cercariae found in the snails were identified as *S. inermis*, *S. armata*, and *S. intermedia*, while the others were given temporary or symbolic names by the authors (Table 2).

Morphology of cercariae is too poorly studied. Therefore, most of the cercariae found in hosts are unidentified as species. Thus, M.N. Chernogorenko (1976) identified five cercaria species isolated from seven snail species, which are different in morphology and body sizes.

Articles providing drawings of cercaria and data on their sizes (Ejmont, 1926; Khan, 1961; Butenko, 1967; Olenev, 1979; Simon-Martin et al., 1987; Belyakova and Mazina, 1990; Kirk and Lewis, 1993; Sendersky and Dobrovolsky, 2004; Faltynkova et al., 2007) deal with snails assigned to a small number of species of all studied species. They include only *Lymnaea stagnalis*, *L. peregra*, *Radix ovata*, *R. auricularia*, *Valvata macrostoma*, *V. piscinalis*, *Melanopsis premorsa*, *Ancylus fluviatilis*, and *Bithynia leachi*. The morphology of sanguinicolid cercariae released from the other species of snails is not studied. Therefore, the true diversity of the cercariae *Sanguinicola* parasitizing the snails remains unknown.

According to a quantitative assessment, the snail infestation with sanguinicolae at cercarial stages is low in total (Table 2). The infection of small species of the families Valvatidae, Neritidae, Lithoglyphidae, Bithyniidae, and Melanopsidae is no more than 10%, despite the large sizes of the analyzed samples. The large species of lymneids are infected even more weakly. Stenko (1979) reports about the very heavy infection (71.4%) of *Lymnaea auriculari* in the water bodies of the Crimean Peninsula; however, there is no information on quantity of the analyzed snails in the article.

It is very difficult to define the specificities of sporocysts and cercariae in relation to snails based on faunistic data. Thus, cercariae under the name *Sanguinicola inermis* were found in several species of lymneids and *Bithynia tentaculata*, while cercaria *S. armata* were found in *Lymnaea stagnalis* and *Bithynia leachi* (Table 2). The limited data on their life cycles can indicate that *Sanguinicola inermis* may be developed only in *Lymnaea peregra* and *L. auricularia*, while *L. stagnalis* is unsusceptible to the invasion of *Sanguinicola inermis* (Kirk and Lewis, 1992). Taking into consideration the specificity of *S. inermis* in relation to wild carp and the data in Table 2, it becomes clear why snails *Lymnaea peregra* and *L. auricularia* infected by *Sanguinicola* (and probably *S. inermis*) are found only in the southern regions, where wild carp inhabit the natural freshwater environments.

According to a quantitative assessment, the snail infection with sanguinicolae at cercarial stages is low in total (Table 2). Infection of small species of the families Valvatidae, Neritidae, Lithoglyphidae, Bithyniidae, and Melanopsidae is no more than 10%, despite

**Table 2.** Distribution and infection of snails with cercariae of freshwater trematodes of the genus *Sanguinicola*

Species name from the prime source	Species/Name of cercaria	P, %	Water basin/Region	Literature source
<i>Lymnaea stagnalis</i>	<i>Sanguinicola</i> sp.	—	Volga River delta	Kurochkin, 1968
	<i>S. inermis</i>	—	Lithuania	Kiselene, 1984
	The same	0.5	Lake Sultan Keldy and Lake Isei (Kazakhstan)	Belyakova, 1981
	» »	2	Poland	Żbikowska, 2007
	» »	—	Germany	Lühe, 1909
	» »	—	Western Kazakhstan	Belyakova, 1975
	» »	—	Poland	Wisniewski, 1958
	» »	—	Germany	Scheuring, 1922
	» »	—	The same	Odening, 1965
	» »	—	Czechia	Gelnar, 1980
	» »	—	Poland, Germany, Ukraine, and Denmark	Cichy et al., 2011
	<i>S. armata</i>	—	St. Petersburg	Sendersky et al., 2002
	<i>Cercaria cristata</i>	0.71	Lake Zhaltyrkol (Western Kazakhstan)	Smirnova and Irbasheva, 1967
	<i>S. sp.</i>	—	Ukraine	Stadnichenko, 1976
	The same	0.09–0.23	Dnieper River (Ukraine)	Chernogorenko, 1983
<i>L. auricularia</i>	<i>S. inermis</i>	—	Southern Southeastern, Eastern and Western Kazakhstan	Belyakova, 1975
	The same	2.8	Lake Issyk Kul (Kyrgyzstan)	Tokobaev and Chibichenko, 1978
	<i>S. sp.</i>	71.4	Crimean Peninsula	Stenko, 1979
	<i>S. sp. I</i>	0.04	Lake Dautkul, Amu Darya River delta (Uzbekistan)	Arystanov, 1968
	<i>S. sp. II</i>	0.08	Kunya Darya River and Amu-Darya River delta (Uzbekistan)	The same
<i>Radix auricularia</i>	<i>S. inermis</i>	3.0–11.6	Dnieper River (Ukraine)	Chernogorenko, 1989
	The same	6.8	Lake Bilikol, Chu River (Kazakhstan)	Butenko, 1967
	» »	—	Poland, Germany, Ukraine, and Denmark	Cichy et al., 2011
	<i>Cercaria cristata</i>	2.56	Lake Zhaltyrkol (Western Kazakhstan)	Smirnova and Irbasheva, 1967
<i>R. auricularia m. lagotis</i>	<i>Sanguinicola</i> sp.	—	Devechi-Liman Firth (Caspian Sea, Azerbaiian)	Mekhraliev and Mikailov, 1982
<i>Lymnaea pereger</i>	<i>S. inermis</i>	—	Western and Central Kazakhstan	Belyakova, 1975
<i>L. palustris</i>	The same	—	Central Kazakhstan	The same
<i>L. pereger</i>	» »	—	Northern Kazakhstan	» »
	» »	0.4	Lake Sultan Keldy and Lake Isei (Kazakhstan)	Belyakova, 1981
	<i>S. sp.</i>	—	Southeastern Kazakhstan	Belyakova, 1975
	The same	—	Turgay River (Kazakhstan)	Belyakova and Mazina, 1990
	<i>Cercaria cristata</i>	—	Germany	Bursian-Hartung, 1965
	<i>C. kentensis</i>	—	England	Khan, 1961
	<i>C. cristata</i>	4	Lake Zhaltyrkol (Western Kazakhstan)	Smirnova and Irbasheva, 1967
<i>Galba palustris</i>	<i>Sanguinicola</i> sp.	0.11–1.0	Dnieper River (Ukraine)	Chernogorenko, 1989
	The same	—	Volga River delta	Kurochkin, 1968
<i>Stagnicola palustris</i>	<i>S. inermis</i>	—	Poland, Germany, Ukraine, and Denmark	Cichy et al., 2011



Table 2. (Contd.)

Species name from the prime source	Species/Name of cercaria	P, %	Water basin/Region	Literature source
<i>Lymnaea corvus</i>	<i>S. sp.</i>	—	Ukraine	Stadnichenko, 1976
<i>Radix ovata</i>	<i>S. inermis</i>	1.1	Lake Bilikol, Chu River (Kazakhstan)	Butenko, 1967
	<i>S. sp.</i>	0.1	Lake Bilikol (Kazakhstan)	The same
	» »	—	Gorky Reservoir (Volga River)	Kupriyanova-Shakhmatova, 1964
<i>R. ovata</i>	» »	—	Volga River delta	Kurochkin, 1968
<i>Valvata piscinalis</i>	» »	—	Northern and Western Kazakhstan	Belyakova, 1975
	» »	—	Lithuania	Spirin et al., 1986
	» »	1.8–10.1	Dnieper River and its reservoirs (Ukraine)	Chernogorenko, 1989
	» »	0.46	Rybinsk Reservoir (Volga River)	Ginetsinskaya, 1959
	<i>Cercaria cristata</i>	3.67	Lake Zhaltyrkol (Western Kazakhstan)	Smirnova and Irbasheva, 1967
	The same		Oredezh River	Sukhanova, 1958
<i>V. macrostoma</i>	<i>Sanguinicola sp.</i>	3.2	Finland	Faltynkova et al., 2007
<i>V. pulchella</i>	The same	1.07	Rybinsk Reservoir (Volga River)	Ginetsinskaya, 1959
<i>Bithynia tentaculata</i>	» »	0.71–5.20	Dnieper River (Ukraine)	Chernogorenko, 1989
	» »	—	Lithuania	Spirin et al., 1986
	<i>S. inermis</i>	—	The same	Kiselene, 1984
<i>B. leachi</i>	<i>S. intermedia</i>	0.20–0.37	Dnieper River (Ukraine)	Chernogorenko, 1989
	<i>Cercaria cristata</i>	—	Seversky Donets River (Ukraine)	Vergun, 1957
	<i>Sanguinicola armata</i>	—	Poland	Ejsmont, 1926
<i>Lithoglyphus naticoides</i>	<i>S. sp.</i>	3.9–6.0	Dnieper River (Ukraine)	Chernogorenko, 1989
	The same	5.8	The same	Chernogorenko, 1965
	» »	2.81	Lithuania	Stanevičiūtė et al., 2008
	» »	—	Dniester River (Ukraine)	Stadnichenko, 1976
	» »	1.10	Rybinsk Reservoir (Volga River)	Perova et al., 2018
<i>Theodoxus fluviatilis</i>	» »	1.25	Dnieper River (Ukraine)	Chernogorenko, 1965
	» »	0.76–10.0	The same	Chernogorenko, 1989
<i>Fagotia acicularis</i>	» »	2.2–3.8	» »	The same
	» »	0.83	Danube River delta (Ukraine)	Chernogorenko, 1969
<i>F. esperi</i>	» »	2.5–7.0	Dnieper River (Ukraine)	The same
<i>F. berlani</i>	<i>Cercaria cristata</i>	3.4–3.8	Ukraine	Gradovsky, 1999
<i>F. dneprensis</i>	The same	4.7–5.6	The same	The same
<i>F. danubialis</i>	» »	4.5–5.2	» »	» »
<i>Microcolpia ucrainica</i>	» »	7.3–9.1	» »	» »
<i>M. canaliculata</i>	» »	6.3–6.9	» »	» »
<i>M. potamoctebia</i>	» »	2.6	» »	» »
<i>Ancyclus fluviatilis</i>	<i>Sanguinicola rutili</i>	—	Spain	Simon-Martin et al., 1987
<i>Melanopsis premorsa</i>	<i>Cercaria sanguinicola sp.</i>	0.2–1.0	Georgia	Olenev, 1979

Notes: Averages and min and max value sets of P (prevalence) are given for several samples.

the large sizes of the samples. The large species of lymneids are infested even more weakly. Stenko (1979) reports about the very heavy infestation (71.4%) of *Lymnaea auriculari* in the water bodies of the Crimean Peninsula; however, there is no information on the quantity of the analyzed snails in the article.

Molecular genetic data on the larval stages of sanguinicolae from snails are sparse. Research has begun on genotyping sanguinicolae that invade various species of freshwater snails (Khrisanfova et al., 2013, 2019).

## CONCLUSIONS

European freshwater trematodes of the genus *Sanguinicola* remain an insufficiently studied group of trematodes. Research into these trematodes seems not to be going anywhere. It is considered definite that only five species of sanguinicolae parasitize European fish. Research over the last 20 years has proven the existence of well-known species parasitizing some species of fish and snails in different water bodies. This review is taken as an attempt to compile as much data as possible on the distribution and biology of these trematodes. The toughest challenge associated with studying the freshwater sanguinicolae is a lack of knowledge of true diversity of this group. Assessing open data sources has shown that the number of species of sanguinicola cercariae found in the snails is larger than the number of species described as adult trematodes. In addition, the morphological description of almost all known cercariae cannot be considered sufficient. Taking into account that the parthenogenetic generation of trematodes is very specific in relation to the host, with few exceptions, it may be assumed that a great number of species of sanguinicolae parasitize the snails of 24 species that are recorded as hosts of sanguinicolae known at the moment. Fish of 26 species assigned to seven families and four orders were identified as hosts of European sanguinicolae. The richness of more than five known species of blood flukes may be expected with such an abundant diversity of hosts. All information available in literature sources on the distribution of sanguinicolae throughout the host range, based on faunistic data, shows that each of them, except for *Sanguinicola rutili*, parasitizes several or many fish species. However, the example described above for *S. inermis* in vitro cultivation can prove that this species is very specific and parasitizes fish of one–two species. This is probably true in relation to the other known but undescribed species of sanguinicolae.

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## COMPLIANCE WITH ETHICAL STANDARDS

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*Statement of welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The article does not concern any researches using animals as objects.

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