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Unclear host taxonomy hinders parasite studies: An up-to-date checklist of the protozoan and metazoan parasites of *Phoxinus* minnows (Teleostei: Leuciscidae)

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Abstract

Phoxinus minnows are small freshwater fish found throughout Eurasia. The taxonomy of this genus is still under investigation, and new species are regularly described. They are frequently introduced outside their native range due to their use as live bait for angling, and such fish introductions can have diverse impacts on the recipient areas. Before the rise in interest regarding the diversity of this genus in the past 15 years, studies carried out on their biology and ecology reported their findings for the Eurasian minnow *Phoxinus phoxinus* Linnaeus, 1758, which was then considered ubiquitous. A parasites checklist for *Phoxinus* minnows has yet to be published, and the recent progress on the taxonomy of this genus has enabled us to propose a reassignment of parasite records to their proper host. The most thoroughly studied potential species were the North European species *Phoxinus* sp. 7 sensu Palandačić et al. 2017, *Phoxinus isetensis*, and *P. phoxinus*. We were able to highlight a gap in knowledge for numerous species that have received little-to-no attention in terms of parasitology. Systematic molecular identification of *Phoxinus* minnows should be conducted when studying their parasites, as a reliable identification of the host is vital in parasitology research. Future research will certainly reveal a species-specific composition of the parasitofauna occurring in *Phoxinus*, especially among widespread parasites such as *Gyrodactylus* and *Diplostomum*. Such specificities could even become tools for assessing the introduction routes of *Phoxinus* species.

KEYWORDS

knowledge gap, parasites, *Phoxinus* complex, species introduction, species reassignment

1 | INTRODUCTION

Small freshwater minnows of the genus *Phoxinus* Rafinesque, 1820 (Teleostei: Leuciscidae) are cryophilic and rheophilic species spanning a wide range of habitats throughout Eurasia (Freyhof & Kottelat, 2007; Keith et al., 2020). The total number of *Phoxinus*

species is yet to be determined, as this genus' taxonomy is still being explored following advances in molecular tools (e.g., Bogutskaya et al., 2020, 2023; Denys et al., 2020; Palandačić et al., 2015, 2017; Turan et al., 2023). Several difficulties are encountered in the species delineation in this genus: (1) This genus is an example of cryptic diversity highlighted by molecular data (Bayçelebi et al., 2024; Bogutskaya

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et al., 2023; Corral-Lou et al., 2019; Denys et al., 2020; Kottelat, 2007; Palandačić et al., 2017; Vucić et al., 2018; Turan et al., 2023); (2) there is phenotypic diversity within the genetic lineages (Bianco & De Bonis, 2015; Bogutskaya et al., 2020; Collin & Fumagalli, 2015; Ramler et al., 2017); (3) in Europe, the distribution of lineages and species tends not to follow zoogeographical patterns and to cross drainage basin boundaries (Corral-Lou et al., 2019; Denys et al., 2020; De Santis et al., 2021; Garcia-Raventós et al., 2020; Palandačić et al., 2015, 2017, 2020, 2022), (4) different genetic lineages were shown to produce hybrids under natural conditions (Corral-Lou et al., 2019; Palandačić et al., 2015, 2017); and (5) the resulting management of minnows—if there is any—was further blurred by numerous anthropogenic introduction events. Introductions have been documented for several species and are reported to result from the use of *Phoxinus* minnows as live bait for trout angling (Corral-Lou et al., 2019; De Santis et al., 2021; Miró & Ventura, 2015; Palandačić et al., 2020, 2022), even if the study of the mosaic-like distribution created through translocations is still at its very beginning.

As interest in *Phoxinus* taxonomy has only arisen in the past 15 years (Bayçelebi et al., 2024; Bogutskaya et al., 2020, 2023; Corral-Lou et al., 2019; Denys et al., 2020; De Santis et al., 2021; Garcia-Raventós et al., 2020; Kottelat, 2007; Kuszniarz et al., 2023; Palandačić et al., 2017, 2020, 2022; Turan et al., 2023), studies focusing on the biology and ecology of these fish mostly mention *Phoxinus phoxinus* Linnaeus, 1758. This species was thought to be ubiquitous, but it is known today to be native only to the Seine, Meuse, Thames, and Rhine drainage basins. As an example, parasite records were attributed to *P. phoxinus* from as far as Russia and Mongolia (Boutorina & Reznik, 2015; Dorovskikh & Stepanov, 2008; Ergens & Dulmaa, 1967; Lumme et al., 2017). As a result of these confusions, numerous parasite–host records for this genus outside of the four previously mentioned drainages basins, or in Ireland where it has been introduced, are most likely incorrectly attributed to a different species than the one actually studied.

The introduction of non-native fish species, such as those documented for *Phoxinus* minnows, impacts both native species and ecosystems, with effects ranging from interaction alterations (increased predation pressure, increased prey availability, competition for trophic resource) and habitat modifications to genetic impacts (via hybridization and introgression) (Cucherousset & Olden, 2011; Ellender & Weyl, 2014; Ribeiro & Leunda, 2012; Tadese & Wubie, 2021; Witkowski & Grabowska, 2012). An additional consequence is the possibility of co-introducing associated parasites and pathogens along with the introduced host species (Ellender & Weyl, 2014; Goedknecht et al., 2016; Ribeiro & Leunda, 2012; Tadese & Wubie, 2021; Taraschewski, 2006). Such co-introduction phenomena arise frequently and may have a severe impact on native host species, as a lack of co-evolution between non-native parasites and native hosts may lead to a lack of efficient immune response to the non-native pathogen (Gozlan, 2008; Lambert, 1997; Peeler et al., 2011; Prenter et al., 2004; Taraschewski, 2006). Such impacts can be difficult to assess when host species introductions go unnoticed, as can be the case with cryptic species such as *Phoxinus* minnows.

Another limitation is the lack of a baseline with which to compare recent findings. To date, a comprehensive checklist of the protozoan and metazoan parasites occurring in the genus *Phoxinus* has yet to be published. The most comprehensive lists are confined to specific countries (UK, Ireland, and Poland) or parasite taxa, and an up-to-date checklist of *Phoxinus* parasite fauna is lacking (Holland & Kennedy, 1997; Kennedy, 1974; Prost, 1974). The most complete and accessible list recorded a total of 32 parasite species in *P. phoxinus* in Great Britain and Ireland (Kennedy, 1974).

The aim of the present literature survey was to summarize the available data on the parasite fauna of minnows in an updated and comprehensive checklist that can serve as a baseline for future comparisons and analyses, to reassign parasite records incorrectly attributed to *P. phoxinus*, and to suggest research perspectives for the near future and how to approach them, taking into account the origin and genetic identity of *Phoxinus* hosts.

2 | MATERIALS AND METHODS

2.1 | *Phoxinus* species reassignment

To address the issue of *Phoxinus* taxonomy, host species were reassigned following the distribution range presented in Table 1 based on the most recent studies.

2.2 | Compilation of parasitological bibliographical records

The checklist was compiled from existing reports retrieved from the available literature. Considered articles were published in international journals indexed by Web of Science and Scopus. Only articles published in English were included. The search date range was not limited by a starting date and ran to March 13, 2022, the date on which the search was carried out. The keywords used were “*Phoxinus phoxinus*” AND Parasit*, with the “*” in search terms representing the wildcard symbol used to broaden the search for words starting with the same letters. The same search terms were used to retrieve any article that would have been focusing on other *Phoxinus* species (Table 1). Duplicates and inaccessible articles were excluded. Titles and abstracts of 121 articles were reviewed, and only articles and previous checklists focusing on parasites reported from *Phoxinus* were compiled. This selection resulted in the inclusion of 62 publications. The bibliography of selected articles was then carefully checked and relevant, and accessible references were added (25 additional documents out of 143 inspected publications) for a total of 87 retrieved publications (Figure 1). Additionally, five supplementary publications were analysed following the advice of two anonymous reviewers (Almeida et al., 2024; Esposito et al., 2024; Dorovskikh & Stepanov, 2013; Vainutis, 2020; Vainutis et al., 2021). Data were compiled to allow the checklist to provide a detailed overview of parasites reported to date, their localities, as well as, when available, the number of analysed

TABLE 1 List of *Phoxinus* species and lineages according to Palandačić et al. (2017) and their distribution areas summarized in Catalog of Fishes by Fricke et al. (2024).

<i>Phoxinus</i> species	Distribution area	Source
<i>Phoxinus abanticus</i> Turan, Bayçelebi, Özüluğ, Gaygusuz & Aksu, 2023	Asia Minor: Lake Abant basin, Filyos River drainage basin (Turkey)	(Çiçek et al., 2023; Turan et al., 2023)
<i>Phoxinus bigerri</i> Kottelat, 2007	Southwestern Europe: Adour, Leyre, and Ebro basins (France and Spain); introduced in the Aude and Garonne river drainages basins (France), as well as in Galicia and Duero river basins (Spain)	(Corral-Lou et al., 2019; Denys et al., 2020; Kottelat, 2007)
<i>Phoxinus brachyurus</i> Berg, 1912	North Asia: Ili basin (Kazakhstan)	(Mitrofanov et al., 1987; Zhang & Zhao, 2016)
<i>Phoxinus chrysoprasius</i> (Pallas, 1814)	Southeast Europe: Salhir River drainage (Crimea)	(Bogutskaya et al., 2023; Dyldin et al., 2023)
<i>Phoxinus colchicus</i> Berg, 1910	Caucasian Black Sea basin (Georgia, Russia, and Turkey)	(Çiçek et al., 2023; Dyldin et al., 2023; Turan et al., 2023)
<i>Phoxinus csikii</i> Hankó, 1922	Europe: Danube River system: from the Balkans to Germany and the upper Rhine basin west to Swiss lakes; introduced in the lower and middle Rhine (Germany, Netherlands, France, and northern Italy)	(Alexander & Seehausen, 2021; Denys et al., 2020; De Santis et al., 2021; Palandačić et al., 2017, 2020, 2022)
<i>Phoxinus dragarum</i> Denys, Dettaï, Persat, Daszkiewicz, Hauteceur & Keith, 2020	Western Europe: Garonne River basin, France; introduced in Corsica (France), the Ebro and Guadalquivir drainage basin (Spain)	(Denys et al., 2020)
<i>Phoxinus fayollarum</i> Denys, Dettaï, Persat, Daszkiewicz, Hauteceur & Keith, 2020	Western Europe: Loire River basin and Sèvre Niortaise catchment (France); introduced in Garonne and Rhône river basins (France)	(Denys et al., 2020)
<i>Phoxinus grumi</i> Berg, 1907	East Asia: Turfan Lake, Xinjiang Province (China)	(Zhang & Zhao, 2016)
<i>Phoxinus isetensis</i> Georgi, 1775	North Asia: Arctic Ocean basin, from Murman coast to East Siberian Sea basin (Kolyma drainage); rivers of northern and western Sea of Okhotsk drainage (Ola and Uda rivers), rivers of Peter the Great Bay drainage, probably Amur River basin and northwestern Sakhalin Island (Russia)	(Dyldin et al., 2023)
<i>Phoxinus issykkulensis</i> Berg, 1912	Central Asia: Lake Issyk-Kul (Kyrgyzstan)	(Berg, 1949)
<i>Phoxinus karsticus</i> Bianco & De Bonis, 2015	Southeastern Europe: Skadar Lake drainage (Bosnia-Herzegovina)	(Bianco & De Bonis, 2015; Palandačić et al., 2017)
<i>Phoxinus krkae</i> Bogutskaya, Jelić, Vucić, Jelić, Diripasko, Stefanov & Klobučar, 2019	Southeastern Europe: upper Krka River drainage, Knin Valley (Croatia)	(Bogutskaya et al., 2020)
<i>Phoxinus lumaireul</i> (Schinz, 1840)	Southeastern Europe: North Adriatic Sea basin and middle Danube drainage (Italy, Slovenia, Croatia and Bosnia, and Herzegovina)	(Čaleta et al., 2019; Kottelat, 2007; Lorenzoni et al., 2019; Palandačić et al., 2017)
<i>Phoxinus marsilii</i> Heckel, 1836	Europe: middle and lower Danube drainage (Austria, Hungary, and Croatia)	(Čaleta et al., 2019; Palandačić et al., 2017)
<i>Phoxinus phoxinus</i> Linnaeus, 1758	Western Europe: Rhine, Meuse, and Seine river drainages, coastal catchments of Normandy and English Channel and Thames River drainage (France, Germany, and England). Introduced in Italy, Corsica, and Ireland.	(Denys et al., 2020; Palandačić et al., 2017, 2020, 2022)
<i>Phoxinus poljakowii</i> Kessler, 1879	Central Asia: Lake Balkhash (Kazakhstan)	(Mitrofanov et al., 1987)
<i>Phoxinus radeki</i> Bayçelebi, Aksu & Turan 2024	Asia Minor: Ergene River, Aegean Sea Basin (Turkey)	(Bayçelebi et al., 2024)
<i>Phoxinus septimaniae</i> Kottelat, 2007	Western Europe: Rhône River basin and the French coastal Mediterranean catchments (France); introduced in the Roya and Rhine river drainages (France, Germany, and Catalonia, Spain) and alpine lakes (Italy, Switzerland)	(Alexander & Seehausen, 2021; Corral-Lou et al., 2019; Denys et al., 2020; De Santis et al., 2021; Palandačić et al., 2017, 2022)
<i>Phoxinus strandjae</i> Drensky, 1926	Southeastern Europe: Black Sea watersheds, Bulgaria and Istanbul and Kirklareli Provinces (Turkey)	(Çiçek et al., 2023; Palandačić et al., 2017)

(Continues)

TABLE 1 (Continued)

<i>Phoxinus</i> species	Distribution area	Source
<i>Phoxinus strymonicus</i> Kottelat, 2007	Southeastern Europe: Struma River basin (Macedonia, Greece, and probably Bulgaria)	(Barbieri et al., 2015; Freyhof & Kottelat, 2007; Palandačić et al., 2017)
<i>Phoxinus tchangj</i> Chen, 1988	East Asia: Weifen River (northern China)	(Chen, 1988)
<i>Phoxinus tumensis</i> Luo, 1996	East Asia: northern China	(Dyldin & Orlov, 2016; Zhang & Zhao, 2016)
<i>Phoxinus ujmonensis</i> Kaschenko, 1899	Central and east Asia: Mongolia, China, Kazakhstan and Russia	(Dyldin et al., 2023; Kottelat, 2006; Romanov et al., 2017)
<i>Phoxinus</i> cf. <i>morella</i> (Leske, 1774)	Central Europe: Elbe River drainage (Czech Republic and Germany)	(Palandačić et al., 2017, 2020, 2022)
<i>Phoxinus</i> sp. 1	South Europe: Neretva and middle Danube drainage (Bosnia Herzegovina)	(Palandačić et al., 2017)
<i>Phoxinus</i> sp. 2	South Europe: Plavsko Lake (Montenegro)	(Palandačić et al., 2017)
<i>Phoxinus</i> sp. 3	South Europe: Drina River, middle Danube drainage (Bosnia Herzegovina)	(Palandačić et al., 2017)
<i>Phoxinus</i> sp. 5	South Europe: Ohrid Lake basin (Macedonia)	(Palandačić et al., 2017)
<i>Phoxinus</i> sp. 7	North Europe: North England, Baltic Sea basin, Caspian Sea basin	(Palandačić et al., 2017; Freyhof, personal communication)

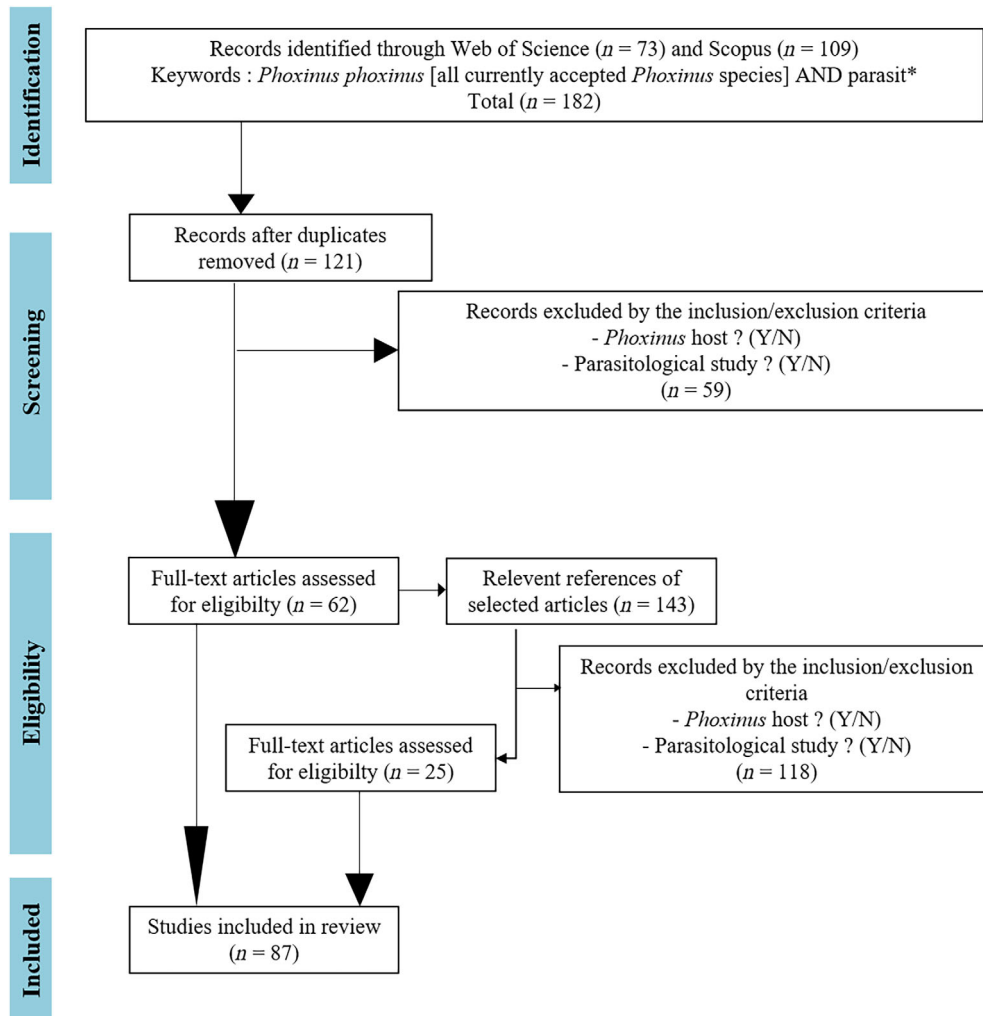


FIGURE 1 Workflow diagram used for the bibliographical search as defined in the PRISMA methodology, according to Moher et al. (2015).

individual hosts and the prevalence, abundance, and intensity of infection. The recorded parasites are arranged by phylum and, when appropriate, by class, family, and genus. Species within a genus are ordered alphabetically. Each species record is accompanied, when available in the source document, by the corresponding developmental stage, infected organs, habitat type, locality, and country. The recorded countries are listed alphabetically.

3 | RESULTS

The results of the present checklist should be interpreted in the light of the following limitation: the host species indicated in the checklist is the one reported in the source publication (Table 2). However, the taxonomy of the genus *Phoxinus* is still not thoroughly understood, and authors have reported parasites from minnows identified as *P. phoxinus* that are most likely other *Phoxinus* species. Among all *Phoxinus* species used to search bibliographical databases, only *P. phoxinus* allowed retrieval of a substantial number of publications, and only one publication dealing with the parasite fauna of *Phoxinus septimaniae* was retrieved, which had already been obtained with the previous search. Considering all records from *Phoxinus* spp., a total of 117 parasite species/taxa encompassing 8 phyla, 14 classes, and 39 families were recorded from 17 countries in Eurasia. The Protozoa parasites consist of the Ciliophora classes Oligohymenophorea (14 species) and Phyllopharyngea (1 species), and the Euglenozoa Kinetoplasta (2 species). The Metazoa parasites encompass the Acanthocephala Eoacanthocephala (1 species) and Palaeacanthocephala (2 species), the Arthropoda Copepoda (2 species) and Ichthyostira (1 species), the Cnidaria Myxozoa (18 species), the Mollusca Bivalvia (3 species), the Nematoda Chromadorea (12 species) and Enoplea (3 species), and the Platyhelminthes Cestoda (7 species), Monogenea (34 species), and Trematoda (17 species) (Figure 2). Among macroparasites, Monogenea, Trematoda, and Nematoda are the most species-rich taxa. *Philometra ovata* (Zeder, 1803) and *Raphidascaris acus* (Bloch, 1779) are the most widely distributed Nematoda, with their presence being reported in five countries each. The Monogenea *Gyrodactylus* is the most diversified genus to be reported from *Phoxinus* minnows in Eurasia, with 25 species. Several *Gyrodactylus* are reported from a relatively wide geographical range: *Gyrodactylus macronychus* Malmberg, 1957 (seven countries), *Gyrodactylus aphyae* Malmberg, 1957 (six countries), *Gyrodactylus laevis* Malmberg, 1957, *Gyrodactylus pannonicus* Molnár, 1968 and *Gyrodactylus phoxini* Malmberg, 1957 (five countries each), and *Gyrodactylus limneus* Malmberg, 1957 and *Gyrodactylus magnificus* Malmberg, 1957 (four countries each). The most abundant parasite compiled in the checklist are the metacercariae of *Diplostomum phoxini*, with the highest reported intensity of infection being 2265 individuals in the brain of a *Phoxinus* minnow from Lake Obersee in Switzerland (Müller, 1995). This species is also among the most prevalent, with the percentage of infected individuals often reaching 100%, and among the most widely distributed, with its presence reported from seven countries from northern, western, and southern Europe.

To resolve the issue of host taxonomy, *Phoxinus* species were reassigned based on their distribution areas. This allowed the assignment of parasite records to *Phoxinus* sp. 7 sensu Palandačić et al., 2017 in the Baltic and North Sea basins (excluding the North Sea southern coast), *Phoxinus isetensis* Georgi, 1775 in the Arctic Ocean basin, *Phoxinus marsilii* Heckel, 1836 in the middle Danube drainage basin, *P. phoxinus* in the Rhine and North Sea basins, *P. septimaniae* in Mediterranean coastal streams, *Phoxinus csikii* in the Rhine drainage, *Phoxinus* cf. *morella* in the Elbe and Danube drainages, *Phoxinus lumaireul* in the North Adriatic Sea basin, *Phoxinus tumensis* Luo, 1996 in eastern Asia, and *Phoxinus ujmonensis* in Mongolia (Figure 3a,b). The results of this reassignment should, however, be analysed taking into account the presence of hybridization zones in, for example, Spain, Italy, France, Germany, and Austria as a limitation (Corral-Lou et al., 2019; Denys et al., 2020; De Santis et al., 2021; Knebelberger et al., 2015; Palandačić et al., 2020). Based on the reassignment, the highest parasite diversity would be recorded for *Phoxinus* sp. 7 (36 parasite species), for *P. isetensis* (30 parasite species), and for *P. phoxinus* (31 parasite species) (Supplementary Data S1). Northern Europe shows the highest concentration (almost half) of parasite records for *Phoxinus* minnows, with numerous host-parasite associations reported from the UK, Finland, and Norway (Figure 4a). With approximately a third of total records, eastern Europe was also well studied. Southern and western Europe were comparatively understudied, as was Eastern Asia. Concerning *Phoxinus* hosts species, *Phoxinus* sp. 7 sensu Palandačić et al. (2017) would have attracted the most attention from parasitological research and had the highest number of records (Figure 4b), followed by *P. isetensis*, *P. phoxinus*, and *P. septimaniae*. *P. cf. morella*, *P. lumaireul*, and *P. marsilii* would have attracted less attention among studied species. Numerous species (e.g., *Phoxinus fayollarum* Denys, Dettai, Persat, Daszkiewicz, Hautecoeur & Keith, 2020, *Phoxinus grumi* Berg, 1907, and *Phoxinus poljakowii* Kessler, 1879) appeared to have never been the subject of parasitological studies and thus do not appear in Figure 4b.

4 | DISCUSSION

At the Eurasian scale, 82 species of Metazoan macroparasites (i.e., excluding Myxosporidia), including 76 helminths, were reported from *Phoxinus* minnows, most of which were attributed originally to *P. phoxinus*. Considering studies focusing on wild parasite communities in restricted areas, which are more likely to have examined a single host species, species richness ranges from 45 helminths reported from Frongoch Lake in the UK and a mountain water system in southern Norway (Ashworth & Bannerman, 1927; Bibby, 1972; Kristoffersen & Teigland, 1997) to 14 helminth species in the River Pechora, Russia (Dorovskikh & Stepanov, 2008, 2009), and 14 parasite species, including helminths and Copepoda in the rivers Chulman and Ungra, Russia (Boutorina & Reznik, 2015). The low parasite diversity in the UK could be a result of its insular situation, whereas in the Norwegian water system, *Phoxinus* minnows were described as recently introduced.

TABLE 2 Checklist of Protozoa and Metazoa parasites of *Phoxinus* minnows.

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
Phylum Ciliophora													
Class Oligohymenophorea													
Family Epistylididae													
<i>Apiosoma campanulatum</i> (Timofeev in Shulman, 1962) Lom, 1966	<i>Phoxinus phoxinus</i>	<i>Phoxinus</i> sp. or <i>Rhynchocypris percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Apiosoma phoxini</i> Lom, 1966	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Apiosoma piscicolum</i> Blanchard, 1885	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Apiosoma</i> sp. Blanchard, 1885	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
<i>Epistylis phoxini</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
Family Ichthyophthiriidae													
<i>Ichthyophthirius multifiliis</i> Fouquet, 1876	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>P. phoxinus</i>	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
Family Trichodinidae													
<i>Paratrachodina incisa</i> , possible misspelling of <i>Paratrachodina incisa</i> (Lom, 1959) Lom, 1963	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>P. incisa</i> (Lom, 1959) Lom, 1963	<i>P. phoxinus</i>	-	-	Gills	Natural	-	-	-	-	-	-	-	(Lom & Haldar, 1977)
<i>Paratrachodina phoxini</i> Lom, 1963	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
<i>Trichodina acuta</i> Lom, 1961	<i>P. phoxinus</i>	<i>Phoxinus marsilli</i>	-	Renal tubules	Natural	Morávka water-supply reservoir	Czech Republic	3	-	-	-	-	(Rehulka et al., 2020)
<i>Trichodina intermedia</i> Lom, 1960	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Skin or fins	Natural	Castle Semple Water	UK	4	-	-	-	-	(Gaze & Wootten, 1998)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Gills, skin	Natural	Castle Semple Water, Lake Bala, Allt Loin, River Almond	UK	4, 5, 6, 7	-	-	-	-	(Gaze & Wootten, 1998)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Trichodina mira</i> Kaschkovsky, 1974	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Trichodina reticulata</i> Hirschmann and Partsch, 1955	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	(Kane, 1966) in (Kennedy, 1974)
<i>Trichodina</i> sp. (possible misspelling for <i>Trichodina</i> sp.)	<i>P. phoxinus</i>	<i>Phoxinus isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	-	(Dorovskikh & Stepanov, 2009)
<i>Trichodina</i> sp. Ehrenberg, 1830	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	-	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Halmer	Russia	62	63	-	-	-	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966; Chubb, 1970) in (Kennedy, 1974)
	<i>Phoxinus septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.9–1.3	(Cruz et al., 2022)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	2.7–5.4	(Almeida et al., 2024)
Family Urceolaridae													
<i>Tripartiella copiosa</i> (Lom, 1959) Raabe, 1963	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
Class Phyllopharyngea													
Family Trichophryidae													
<i>Capriana</i> sp. Strand, 1928	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
Phylum Euglenozoa													
Class Kinetoplasta													
Family Trypanosomatidae													
<i>Trypanosoma cobitis</i> Mitrophanow, 1883	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	Blood	Natural	River Lee	UK	11	87	20	-	-	(Letch, 1979)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	Blood	Natural	River Lee	UK	11	88	18	-	-	(Letch & Ball, 1979)
<i>Trypanosoma</i> sp. Gruby, 1843	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Lake Windermere	UK	12	-	-	-	-	(Hawking, 1957) in (Kennedy, 1974)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
Phylum Acanthocephala													
Class Eoacanthocephala													
Family Neoechinorhynchidae													
<i>Neoechinorhynchus rutili</i> (Müller, 1780) Hamann in Stiles & Hassall, 1905	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Intestine	Natural	Brook Kuusjoja, Brook Uuronpuro	Finland	13	-	-	-	-	(Kekäläinen et al., 2011)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.07	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–53.3	-	0.07–0.8	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	Stomach, intestine	Natural	Frongoch Lake	UK	14	650	16.5	-	-	(Bibby, 1972)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.2–0.7	(Cruz et al., 2022)
Class Palaeacanthocephala													
Family Echinorhynchidae													
<i>Echinorhynchus fruttiae</i> Schrank, 1788	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	-	Ireland	-	-	-	-	-	(Kane, 1966) in (Holland & Kennedy, 1997)
Family Pomphorhynchidae													
<i>Pomphorhynchus laevis</i> (Zoega in Müller, 1776) Porta, 1908	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Boyne catchment	Ireland	15	-	-	-	-	(Kane, 1966) in (Holland & Kennedy, 1997)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Corrib catchment	Ireland	16	-	-	-	-	(Conneely & McCarthy, 1984) in (Holland & Kennedy, 1997)
	<i>P. phoxinus</i>	<i>P. marsilii</i>	-	Alimentary tract	Natural	Small Vihorlat Lake	Slovakia	17	129	88.9	6.6 (1–29)	-	(Dudiňák & Špakulová, 2003)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Culm	UK	18	-	-	-	-	(Kennedy, 1999)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
Phylum Arthropoda													
Class Copepoda													
Family Ergasilidae													
<i>Ergasilus briani</i> Markevich, 1933	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Ergasilus sieboldi</i> von Nordmann, 1832	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.2–0.9	(Cruz et al., 2022)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.2–4.2	(Almeida et al., 2024)
Class Ichthyostraca													
Family Argulidae													
<i>Argulus foliaceus</i> (Linnaeus, 1758)	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.5	(Cruz et al., 2022)
Phylum Cnidaria													
Class Myxozoa													
Family Chloromyxidae													
<i>Chloromyxum carassii</i> Achmerov, 1960	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Chloromyxum phoxini</i> Quadri, 1962	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Pansporoblast, spores	Gall bladder	Natural	Lake Windermere	UK	12	15	6.7	-	-	(Quadri, 1962)
Family Myxididae													
<i>Myxidium macrocapsulare</i> Auerbach, 1910	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7	-	0.07	(Dorovskikh & Stepanov, 2009)
<i>Myxidium rhodei</i> Léger, 1905	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.07–1.33	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–20	-	0.07–1.27	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Plasmodia	Kidney	Natural	River Tyne	UK	19	1825	0.1	-	-	(Longshaw et al., 2005)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Myxobolus bramae</i> Reuss 1906	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.2	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	20	-	0.27	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Plasmodia	Gills (intralamellar)	Natural	River Derwent, River Tees	UK	20, 21	1825	0.2	-	-	(Longshaw et al., 2005)
<i>Myxobolus buckei</i> Longshaw and Feist, 2003 (uncertain)	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	Natural	-	UK	-	1798	-	-	-	(Longshaw et al., 2003)
<i>Myxobolus cybinae</i> Mitenev, 1971	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7	-	0.13	(Dorovskikh & Stepanov, 2009)
<i>Myxobolus dogieli</i> Bykhovskaya-Pavlovskaya & Bykhovski, 1940	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Myxobolus ellipsoides</i> Thélohan, 1892	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Myxobolus lomi</i> Donets and Kulakovskaya in Shulman, 1962	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.13–1.73	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	20–26.7	-	0.47–0.67	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Halmer	Russia	62	63	11.1	-	0.1	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Myxobolus mongolicus</i> Pronin, 1973	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Myxobolus muelleri</i> Bütschli, 1882	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Myxobolus muscili</i> Keysseitz, 1908	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.13–0.33	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–26.7	-	0.13–0.33	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Sea-U, River Kara	Russia	62–63	63	6.7–20	-	0.1–0.8	(Dorovskikh & Stepanov, 2013)

TABLE 2 (Continued)

Parasite species	Host according to original record		Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7 or <i>R. percnurus</i>												
	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7 or <i>R. percnurus</i>	<i>P. phoxinus</i> sp. 7 or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	<i>P. phoxinus</i> sp. 7	Plasmodia	Skeletal musculature	Natural	River Aire, River Calder, River Dearne, River Derwent, River Don, River Nidd, River Ouse, River Swale, River Tees, River Tyne, River Ure, River Wear, River Wharfe	UK	19, 20, 21, 22	1825	35	-	-	(Longshaw et al., 2005)
<i>Myxobolus</i> sp.	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	<i>P. phoxinus</i> sp. 7	-	-	Natural	Loch Leven	UK	23	-	-	-	-	(Campbell, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Fran Goch	UK	14	-	-	-	-	Personal communication in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. phoxinus</i> sp. 7	<i>P. phoxinus</i> or <i>P. phoxinus</i> sp. 7	-	Kidney	Natural	-	UK	-	1825	-	-	-	(Longshaw et al., 2005)
<i>Zschokkella nova</i> Klokacheva, 1914	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7 or <i>R. percnurus</i>	<i>P. phoxinus</i> sp. 7 or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
Extrasporogonic type 1	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	<i>P. phoxinus</i> sp. 7	-	Kidney tubule and urinary bladder epithelial cells (intracellular)	Natural	River Derwent, River Swale/Tees	UK	22	1825	0.1	-	-	(Longshaw et al., 2005)
Plasmodial type 1	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	<i>P. phoxinus</i> sp. 7	-	Kidney tubule and urinary bladder lumen	Natural	River Aire, River Derwent, River Nidd, River Swale, River Ure, River Wharfe	UK	22	1825	0.5	-	-	(Longshaw et al., 2005)
Family Saccosporidae														
<i>Buddenbrockia</i> sp. Schröder, 1910	<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> csikii	-	Kidney	Experimental	-	Austria	Not applicable	-	-	-	-	(Grabner & El-Matbouli, 2010)
Phylum Mollusca														
Class Bivalvia														
Family Unionidae														
<i>Anodonta anatina</i> (Linnaeus, 1758)	<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	Glochidia	Gills	Experimental	-	Finland	Not applicable	-	-	-	-	(Kekäläinen, Pirhonen, & Taskinen, 2014)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. csikii</i> or <i>Phoxinus</i> cf. <i>morella</i>	Glochidia	Gills	Experimental	-	Germany	Not applicable	-	-	-	-	(Beggel & Geist, 2015)
<i>Unio crassus</i> Philipsson, 1788	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. csikii</i> or <i>P. cf. morella</i>	Glochidia	Gills	Experimental	-	Germany	Not applicable	-	-	-	-	(Denic et al., 2015)
	<i>P. phoxinus</i>	<i>P. cf. morella</i> or <i>P. marsilii</i>	Glochidia	Gills	Experimental	-	Czech Republic	Not applicable	-	-	-	-	(Douda et al., 2012)
	<i>P. phoxinus</i>	<i>P. cf. morella</i> or <i>P. marsilii</i>	Glochidia	Gills	Experimental	-	Czech Republic	Not applicable	-	-	-	-	(Douda, 2015)
	<i>P. phoxinus</i>	<i>P. csikii</i> and <i>P. phoxinus</i>	Glochidia	Gills	Natural	River Aire, River Brénon, River Esch, River Halbmuehlbach, River Longeau, River Mazeley, River Ormain, River Sormonne	France	24, 25, 26, 27	121	15.0–100.0	1–7.8	0.31–7.8	(Lamand et al., 2016)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. csikii</i> or <i>P. cf. morella</i>	Glochidia	Gills	Experimental	-	Germany	Not applicable	-	-	-	-	(Taubert, Gum, & Geist, 2012)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. csikii</i> or <i>P. cf. morella</i>	Glochidia	Gills	Experimental	-	Germany	Not applicable	-	-	-	-	(Taubert, Martinez, et al., 2012)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. csikii</i> or <i>P. cf. morella</i>	Glochidia	Gills	Experimental	-	Germany	Not applicable	-	-	-	-	(Taubert et al., 2014)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Glochidia	Gills	Experimental	-	Sweden	Not applicable	-	-	-	-	(Schneider et al., 2017)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Glochidia	Gills	Natural	River Tommarpsån	Sweden	28	140	-	-	8.6	(Schneider et al., 2019)
Unionidae sp.	<i>Phoxinus dragarum</i>	<i>P. dragarum</i>	Glochidia	Gills	Natural	River Tavignano	France	64	120	-	-	-	(Esposito et al., 2024)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.6–1.1	(Cruz et al., 2022)
Phylum Nematoda													
Class Chromadorea													
Family Camallanidae													
<i>Camallanus lacustris</i> (Zoega in Müller, 1776) Railliet & Henry, 1915	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.3	(Cruz et al., 2022)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.3–0.5	(Almeida et al., 2024)
Family Acuariidae													
<i>Streptocara crassicauda</i> (Creplin, 1829) Skrijabin, 1916	<i>P. phoxinus</i>	-	Larvae	Stomach wall, intestine wall, liver	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
Family Anisakidae													
<i>Contracaecum rudolphii</i> Hartwich, 1964	<i>P. phoxinus</i>	<i>P. cf. morella</i> or <i>P. marsilii</i>	Third-stage larvae	Intestine	Experimental	-	Czech Republic	Not applicable	-	-	-	-	(Moravec, 2009)
Family Philometridae													
<i>Philometra ovata</i> (Philometra abdominalis) (Zeder, 1803) Skrijabin, 1923	<i>P. phoxinus</i>	<i>P. cf. morella</i>	Gravid female	-	Natural	River Rokytká	Czech Republic	29	-	-	-	-	(Moravec, 1977)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	-	-	Body cavity	Natural	Brook Kuusojä, Brook Uuronpuro	Finland	13	-	-	-	-	(Kekäläinen et al., 2011)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	Adult female	Adult female	Body cavity	Natural	Brook Kuusojä	Finland	13	734	5.6–13.6	-	-	(Lai et al., 2012)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	Larvae	Larvae	Swim bladder	Natural	Brook Kuusojä	Finland	13	1027	20–70	2.0 ± 1.5	-	(Lai et al., 2015)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	Adult female	Adult female	Body cavity	Natural	Brook Kuusojä	Finland	13	1027	<14	2.0 ± 1.5	-	(Lai et al., 2015)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	Adult	Adult	Body cavity	Natural	Brook Kuusojä, Brook Uuronpuro	Finland	13	-	-	-	-	(Lai et al., 2016a)
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	-	-	Body cavity	Natural	Brook Kuusojä, Brook Uuronpuro	Finland	13	87	<15	-	-	(Lai et al., 2016b)
<i>P. phoxinus</i>	<i>P. marsilii</i>	Adult	Adult	Abdominal cavity	Natural	-	Hungary	-	-	-	-	-	(Molnár, 1967) in (Moravec, 1994)
<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	-	Natural	River Pechora	Russia	8	105	20–40	-	0.07	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. phoxinus</i> sp. 7	-	-	Body cavity	Natural	-	UK	-	-	-	-	-	(Barber & Huntingford, 1996)
Family Quimperiidae													
<i>Paraquimperia tenerima</i> (von Linstow, 1878) Baylis, 1934	<i>P. phoxinus</i>	<i>P. phoxinus</i>	L3 Larvae	Swim bladder	Natural	River Otter, River Clyst	UK	18	53	15.6–38.1	-	-	(Shears & Kennedy, 2005)
<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>P. phoxinus</i> sp. 7	-	L3 Larvae	Swim bladder	Experimental	-	UK	Not applicable	-	-	-	-	(Shears & Kennedy, 2005)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
Family Raphidascaritidae													
<i>Hysterothylacium aduncum</i> (Rudolphi, 1802) Deardorff & Overstreet, 1981	<i>P. phoxinus</i>	-	Adult	Oesophagus, stomach, intestine	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
<i>Raphidascaris acus</i> (Raphidascaris cristata) (Bloch, 1779) Railliet & Henry, 1915	<i>P. phoxinus</i>	<i>Phoxinus lumaireul</i>	Larvae	Liver, pancreas	Natural	Province of Padua	Italy	30	48	37.5	20 ± 3 (2–46)	-	(Dezfuli et al., 2000)
	<i>P. phoxinus</i>	<i>P. lumaireul</i>	Encysted larvae	Liver, pancreas	Natural	River Brenta	Italy	30	25	-	6.8 ± 4.7 (1–15)	-	(Dezfuli et al., 2009)
	<i>P. phoxinus</i>	<i>P. lumaireul</i>	Encysted larvae	Liver	Natural	River Brenta	Italy	30	25	44	5.27 ± 2.28 (1–8)	-	(Dezfuli et al., 2015)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.2–2.07	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	20–86.7	-	0.47–4.33	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Sea-U, River Halmer, River Kara	Russia	62, 63	63	5.6–25	-	0.1–2.2	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. phoxinus</i>	<i>P. marsilli</i>	Larvae	Stomach, intestine	Natural	-	Slovakia	-	-	-	-	-	(Žitňan, 1973)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966; Chubb, 1970) in (Kennedy, 1974)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.6–1.1	(Cruz et al., 2022)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.1	(Almeida et al., 2024)
<i>Raphidascaris</i> sp. Railliet & Henry, 1915	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
Family Rhabdochoniidae													
<i>Rhabdochona denudata</i> (Dujardin, 1845) Railliet, 1916	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Lake Windermere	UK	12	-	-	-	-	(Rawson, 1952) in (Kennedy, 1974)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Rhabdochona phoxini</i> Moravec, 1968	<i>P. phoxinus</i>	<i>P. marsilli</i>	Adult	Intestine	Natural	-	Czech Republic, Ukraine, Hungary	-	-	-	-	-	Several references in (Moravec, 1994)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	Intestine	Natural	Kola Peninsula	Russia	31	-	-	-	-	(Kazakov, 1973) in (Moravec, 1994)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.07	(Dorovskikh & Stepanov, 2008)
Family Cystidicolidae													
<i>Cystidicoloides</i> sp. Skinner, 1931	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Lake Windermere	UK	12	-	-	-	-	(Rawson, 1952) in (Kennedy, 1974)
<i>Salmonema ephemeridarum</i> (Cystidicoloides ephemeridarum) (von Linstow, 1872) Moravec, Santos & Brasil-Sato, 2008	<i>P. phoxinus</i>	-	Larvae	Stomach, intestine	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
Class Enoplea													
Family Capillariidae													
<i>Pseudocapillaria tomentosa</i> (Dujardin, 1843) Lomakin & Trofimenko, 1982	<i>P. phoxinus</i>	-	Adult	Intestine	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
<i>Schulmanella petruschewskii</i> (Schulman, 1948) Ivashkin, 1964	<i>P. phoxinus</i>	-	Adult	Liver parenchyma	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
Family Dioctophymatidae													
<i>Eustrongylides excisus</i> Jägerskiöld, 1909	<i>P. phoxinus</i>	-	Larvae	Abdominal cavity	-	-	-	-	-	-	-	-	Several references in (Moravec, 1994)
Phylum Platyhelminthes													
Class Cestoda													
Family Diphylobothriidae													
<i>Ligula intestinalis</i> (Linnaeus, 1758) Gmelin, 1790	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Øvre Heimdalsvatn	Norway	2	3500	-	-	-	(Lien, 1981)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Plerocercoid	Abdominal cavity	Natural	Lake Negaardsjøen	Norway	2	876	5–70	-	-	(Museum, 2001)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Abdominal cavity	Natural	Edinburgh Region, Loch Lubnaig Stream	UK	32, 33	-	-	-	-	(Ashworth & Bannerman, 1927)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Coelom	Natural	Frongoch Lake	UK	14	650	1.7	(1–4)	-	(Bibby, 1972)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.9	(Cruz et al., 2022)
<i>Ligula</i> sp. Bloch, 1782	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	Natural	-	UK	-	-	-	-	-	(Olson et al., 2002)
Family Lytcestidae													
<i>Caryophyllaeides fennica</i> (Schneider, 1902) Nybelin, 1922	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Roding	UK	11	-	-	-	-	(Shillcock, 1972) in (Kennedy, 1974)
Family Proteocephalidae													
<i>Proteocephalus longicollis</i> (Zeder, 1800) Benedict, 1900	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe	Russia	61	63	15	-	0.3	(Dorovskikh & Stepanov, 2013)
<i>Proteocephalus tortulosus</i> (Batsch, 1786) Nufer, 1905	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Proteocephalus exiguus</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.6–0.8	(Cruz et al., 2022)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.2–0.8	(Almeida et al., 2024)
Family Triaenophoridae													
<i>Triaenophorus nodulosus</i> (Pallas, 1781) Rudolphi, 1793	<i>P. phoxinus</i>	<i>P. csikii</i>	Plerocercoid	Liver	Natural	Königssee	Germany	34	108	1.9–2.8	(4–10)	-	(Hoffmann et al., 1986)
Class Monogenea													
Family Ancyrocephalidae													
<i>Cleidiscus brachus</i> Mueller, 1938	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
Family Dactylogyridae													
<i>Dactylogyrus auriculatus</i> (<i>Dactylogyrus auricularis</i>) (von Nordmann, 1832) Diesing, 1850	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Gills	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
<i>Dactylogyrus borealis</i> Nybelin, 1937	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Köyhänoja Stream	Finland	35	10	50	-	0.6 ± 0.7 (?-2)	(Blazek et al., 2008)
	<i>P. phoxinus</i>	<i>Phoxinus ujmonensis</i>	-	Gills	Natural	River Tui, Lake Dod tsagan	Mongolia	36, 37	-	-	-	-	(Ergens & Dulmaa, 1967)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.07–0.13	(Dorovskikh & Stepanov, 2008)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–53.3	-	0.07–1.87	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe, River Sea-U, River Halmer	Russia	61, 62, 63	63	6.7–16.7	-	0.1–0.2	(Dorovskikh & Stepanov, 2013)
<i>Dactylogyrus phoxini</i> Malevitskaia, 1949	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Roding	UK	11	-	-	-	-	(Shillcock, 1972) in (Kennedy, 1974)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	1.6–1.8	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	5.1–7.2	(Almeida et al., 2024)
<i>Dactylogyrus</i> sp. Diesing, 1850	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966) in (Kennedy, 1974)
<i>Pellucidhaptor merus</i> (Dactylogyrus merus) (Zaika, 1961) Chien & Rogers, 1970	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Gills	Natural	Edinburgh Region, Loch Lubnag Stream	UK	32	-	-	-	-	(Ashworth & Bannerman, 1927)
	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Nasal cavities, gill cavity, gills, skin	Natural	River Tul	Mongolia	36	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	Köyhänoja Stream	Finland	35	10	10	-	0.1 ± 0.3 (?-1)	(Blazek et al., 2008)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.13	(Dorovskikh & Stepanov, 2009)
Family Diplozoidae													
<i>Diplozoon paradoxum</i> von Nordmann, 1832	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Gills	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
<i>Paradiplozoon homoion</i> (Bychowsky & Nagibina, 1959)	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Köyhänoja Stream	Finland	35	10	20	-	0.2 ± 0.4 (?-1)	(Blazek et al., 2008)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	0.7–0.8	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	0.6–1.3	(Almeida et al., 2024)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Paradiplozoon homioion gracile</i> (Diplozoon <i>gracile</i>) (Reichenbach-Klinke, 1961)	<i>P. phoxinus</i>	<i>P. septimaniae</i>	-	Gills	Natural	River Hérault	France	40	-	-	-	-	(Le Brun et al., 1988)
Family Gyrodactylidae													
<i>Gyrodactylus albolacustris</i> Lumme et al., 2017	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	Adult	Skin or fins	Natural	River Tuul	Mongolia	36	-	-	-	-	(Lumme et al., 2017)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	Skin or fins	Natural	River Sirelna	Russia	31, 42	-	-	-	-	(Lumme et al., 2017)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Adult	Skin or fins	Natural	River Vdilitsa, River Bol'shaya Uya	Russia	41	-	-	-	-	
<i>G. albolacustris</i> × <i>Gyrodactylus botnicus</i> hybrid	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	Skin or fins	Natural	Hangaspuro, River Oulankajoki	Finland	43	-	-	-	-	(Lumme et al., 2017)
<i>Gyrodactylus aphyae</i> Malmberg, 1957	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	-	Natural	Prague Region	Czech Republic	29	-	-	-	-	(Ergens, 1976)
	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	Fins	Natural	River Rokytka	Czech Republic	29	100	50–100	3.41–16.10 (1–57)	-	(Matejusová et al., 2000)
	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	-	Natural	River Dyje, River Morava, River Vlára	Czech Republic	44, 45, 46	-	-	-	-	(Matejusová et al., 2001)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Bothnian Bay	Finland	47	-	-	-	-	(Ziętara & Lumme, 2002)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Bothnian Bay	Finland	47	-	-	-	-	(Ziętara et al., 2008)
	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Gills, fins	Natural	River Tui, Lake Dod tsagan, Lake Tirkhin	Mongolia	36, 37, 38	-	-	-	-	(Ergens & Dulmaa, 1967)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Merenoja, River Oulankajoki	Finland	43	-	-	-	-	(Ziętara & Lumme, 2002)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Oulankajoki	Finland	43	-	-	-	-	(Ziętara et al., 2008)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Adult	Caudal fin	Natural	River Lykaser, River Drammen, River Glomma, River Trysil, River Sørli, River Alta, River Tana, River Hallingdal, River Begna, River Vinstra, River Sjoa, River Otta, River Tovdal	Norway	2, 48, 49, 50, 51	1278	3.0–100.0	-	-	(Pettersen et al., 2016)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Salnica	Russia	31	-	-	-	-	(Ziętara & Lumme, 2002)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.07–9.20	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Salnica, River Bolshie, River Vidlitsa	Russia	31	-	-	-	-	(Ziętara et al., 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–?	-	0.13–35.67	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe, River Sea-U, River Halmer	Russia	61, 62, 63	63	5–?	-	0.1–1.9	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Chubb, 1964; Powell, 1966) in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Rother	UK	52	-	-	-	-	(Harris, 1985)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	River Endrick	UK	4	9	-	-	-	(Grano-Maldonado et al., 2011)
<i>G. botnicus</i> Lumme et al., 2017	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Adult	Skin or fins	Natural	Gulf of Bothnia, River Kiiminkijoki	Finland	47	-	-	-	-	(Lumme et al., 2017)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	Skin or fins	Natural	River Oulankajoki	Finland	43	-	-	-	-	(Lumme et al., 2017)
<i>Gyrodactylus carassii</i> Malmberg, 1957	<i>P. phoxinus</i>	-	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
<i>Gyrodactylus danastriae</i> Lumme et al., 2017	<i>P. phoxinus</i>	<i>P. marsilii</i>	Adult	Skin or fins	Natural	River Strwiąż	Poland	53	-	-	-	-	(Lumme et al., 2017)
<i>Gyrodactylus elegans</i> von Nordmann, 1832	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Gills	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Lake District	UK	12	-	-	-	-	Personal communication in (Kennedy, 1974)
<i>Gyrodactylus jussii</i> Ziętara & Lumme, 2003	<i>P. phoxinus</i>	-	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
<i>Gyrodactylus konovalovi</i> Ergens, 1976	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Gyrodactylus laevis</i> Malmberg, 1957	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	Fins	Natural	River Rokytk	Czech Republic	29	100	0–41.1	0–11.0 (0–64)	-	(Matejusková et al., 2000)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Gills	Natural	Köyhänoja Stream	Finland	35	10	30	-	0.5 ± 0.9 (?–3)	(Blazek et al., 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	Gills	Natural	River Merenoja, River Oulankajoki	Finland	43	-	-	-	-	(Ziętara & Lumme, 2004)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.07–0.33	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–?	-	0.07–0.13	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe, River Halmer	Russia	61, 62	63	25–?	-	0.1–0.4	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Gills	Natural	River Tul	Mongolia	36	-	-	-	-	(Ergens & Dulmaa, 1967)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966) in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Rother	UK	52	-	-	-	-	(Harris, 1985)
<i>Gyrodactylus limneus</i> Malmberg, 1964	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	Fins	Natural	River Rokytká	Czech Republic	29	100	59.1–86.4	2.38–4.53 (1–28)	-	(Matějusková et al., 2000)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Fins	Natural	Köyhänoja Stream	Finland	35	10	90	-	12.5 ± 14.9 (?–50)	(Blazek et al., 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.13–1.40	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.13–1.73	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966) in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Rother	UK	52	-	-	-	-	(Harris, 1985)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	River Endrick	UK	4	9	-	-	-	(Grano-Maldonado et al., 2011)
<i>Gyrodactylus llewellyni</i> Ergens & Dulmaa, 1967	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Nasal cavities, fins	Natural	River Tul, Lake Dod tsagan	Mongolia	36, 37	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>Gyrodactylus macronychus</i> Malmberg, 1957	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	-	Natural	Prague Region	Czech Republic	29	-	-	-	-	(Ergens, 1976)
	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	Fins	Natural	River Rokytká	Czech Republic	29	100	68.2–96	5.07–12.11 (1–83)	-	(Matějusková et al., 2000)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	-	Natural	River Dyje, River Morava, River Vlára	Czech Republic	44, 45, 46	-	-	-	-	(Matejusová et al., 2001)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Bothnian Bay	Finland	47	-	-	-	-	(Ziętara & Lumme, 2003)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Skin	Natural	Köyhänoja Stream	Finland	35	10	100	-	8.6 ± 4.5 (?-17)	(Blazek et al., 2008)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Merenjoja Brook, River Oulankajoki	Finland	43	-	-	-	-	(Ziętara & Lumme, 2003)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. ujonensis</i>	-	Nasal cavities, fins	Natural	River Tui, River Selhe, Lake Dod tsagan, Lake Tirkhin	Mongolia	36, 37, 38	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Adult	Caudal fin	Natural	River Lykaser, River Glomma, River Trysil, River Sørli, River Tana, River Hallingdal, River Vinstra, River Sjøa	Norway	48, 49, 51	1278	3.3–25.0	-	-	(Pettersen et al., 2016)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.13–2.80	(Dorovskikh & Stepanov, 2008)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7?	-	0.07–7.13	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe	Russia	61	63	5	-	0.1	(Dorovskikh & Stepanov, 2013)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Powell, 1966) in (Kennedy, 1974)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Rother	UK	52	-	-	-	-	(Harris, 1985)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	River Endrick	UK	4	9	-	-	-	(Grano-Maldonado et al., 2011)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	6.4–8.9	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	0.2–3.4	(Almeida et al., 2024)
<i>Gyrodactylus magnificus</i> Malmberg, 1957	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	Fins	Natural	River Oulankajoki	Finland	43	-	-	-	-	(Ziętara & Lumme, 2004)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Fins	Natural	Köyhänoja Stream	Finland	35	10	10	-	0.1 ± 0.3 (?-1)	(Blazek et al., 2008)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Nasal cavities, gills, fins	Natural	River Tuli, River Kherlen, Lake Dod tsagan, Lake Tirkhin	Mongolia	36, 37, 38, 39	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Adult	Caudal fin	Natural	River Lykaser, River Glomma, River Trysil, River Sørli, River Hallingdal, River Vinstra, River Sjoa	Norway	48, 49, 51	1278	1.6–100.0	-	-	(Pettersen et al., 2016)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.2	(Dorovskikh & Stepanov, 2008)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	2.4	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Sea-U	Russia	63	63	6.7	-	0.1	(Dorovskikh & Stepanov, 2013)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Gyrodactylus malimbergensis</i> Prost, 1974	<i>P. phoxinus</i>	-	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
<i>Gyrodactylus medius</i> Katharner, 1895	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Fins, skin	Natural	Edinburgh Region, Loch Lubnaig Stream	UK	32, 33	-	-	-	-	(Ashworth & Bannerman, 1927)
<i>Gyrodactylus minimus</i> Malmberg, 1957	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	-	Lake Windermere, Edinburgh	UK	12, 32	-	-	-	-	(Baylis, 1928; Rawson, 1952) in (Kennedy, 1974)
<i>Gyrodactylus montanus</i> Bychowsky, 1957	<i>P. phoxinus</i>	<i>P. ujmomensis</i>	-	Gills	Natural	River Tuli, Lake Dod tsagan	Mongolia	36, 37	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>Gyrodactylus pannonicus</i> Molnár, 1968	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	Natural	River Rother	UK	52	-	-	-	-	(Harris, 1985)
	<i>P. phoxinus</i>	-	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
	<i>P. phoxinus</i>	<i>P. cf. morella</i>	-	Fins	Natural	River Rokytka	Czech Republic	29	100	4–86.4	1.00–4.89 (1–27)	-	(Matejusková et al., 2000)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	Bothnian Bay, River Kiminkijoki	Finland	47	-	-	-	-	(Ziętara & Lumme, 2002)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Fins	Natural	Köyhänoja Stream	Finland	35	10	60	-	4.5 ± 64 (?–17)	(Blazek et al., 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	Adult	-	Natural	River Pechora	Russia	8	105	-	-	0.13	(Dorovskikh & Stepanov, 2008)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.13–0.27	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Halmer	Russia	62	63	-	-	0.1	(Dorovskikh & Stepanov, 2013)
<i>P. phoxinus</i>	<i>P. marsilii</i>	<i>P. marsilii</i>	Adult	Skin or fins	Natural	River Topla, River Ondava	Slovakia	54	-	-	-	-	(Lumme et al., 2017)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	River Endrick	UK	4	9	-	-	-	(Grano-Maldonado et al., 2011)
<i>Gyrodactylus phoxini</i> Malmberg, 1957	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	Fins	Natural	Gulf of Bothnia	Finland	47	-	-	-	-	(Ziętara & Lumme, 2004)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	Fins	Natural	River Merenoja, River Oulankajoki	Finland	43	-	-	-	-	(Ziętara & Lumme, 2004)
<i>P. phoxinus</i>	<i>P. ujmomensis</i>	<i>P. ujmomensis</i>	-	Gills	Natural	River Tui, Lake Dod tsagan	Mongolia	36, 37	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Adult	Caudal fin	Natural	River Alta, River Hallingdal	Norway	2, 48, 50	1278	3.3–38.1	-	-	(Pettersen et al., 2016)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	Fins	Natural	River Pislom, River Titovka	Russia	55	-	-	-	-	(Ziętara & Lumme, 2004)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	2.8–3.3	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	-	Natural	Tordera Stream	Spain	10	204	-	-	0.1–4.0	(Almeida et al., 2024)
<i>Gyrodactylus prostrae</i> Ergens, 1963	<i>P. ujmomensis</i>	<i>P. ujmomensis</i>	-	Gills	Natural	River Tui	Mongolia	36	-	-	-	-	(Ergens & Dulmaa, 1967)
<i>Gyrodactylus salaris</i> Malmberg, 1957	-	-	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
<i>Gyrodactylus somnaensis</i> Ergens & Yuhkimenko, 1990	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Experimental	-	Norway	Not applicable	-	-	-	-	(Bakke et al., 2006)
<i>Gyrodactylus somnaensis</i> Ergens & Yuhkimenko, 1990	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	-	-	-	-	-	-	-	(Harris et al., 2004)
<i>Gyrodactylus tumbulli</i> Harris, 1986	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	River Main	Ireland	16	-	-	-	-	(Kane, 1966) in (Holland & Kennedy, 1997)
	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	Loch Leven	UK	23	-	-	-	-	(Campbell, 1974)
	-	-	-	Fins	Experimental	-	-	Not applicable	-	-	-	-	(King & Cable, 2007)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Gyrodactylus vimbi</i> Shulman, 1954	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Fins	Natural	Köyhänoja Stream	Finland	35	10	60	-	2.4 ± 2.9 (?-9)	(Blazek et al., 2008)
<i>Gyrodactylus</i> spp. von Nordmann, 1832	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Lough Neagh	Ireland	56	-	-	-	-	(Vickers, 1951) in (Holland & Kennedy, 1997)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Adult	Skin, fins	Natural	River Asco, River Casaluna, River Fium Alto, River Golo, River Tartagine, River Tavignano	France	64	84	53.6	29.9 ± 68.0	16.0 ± 51.7	(Esposito et al., 2024)
	<i>P. csikii</i>	<i>P. csikii</i>	Adult	Skin, fins	Natural	River Casaluna	France	64	7	57.1	2.3 ± 1.9	1.3 ± 1.8	(Esposito et al., 2024)
	<i>P. dragarum</i>	<i>P. dragarum</i>	Adult	Skin, fins	Natural	River Abatesco, River Consigliese, River Fium Orbo, River Tavignano, River Vecchio	France	64	120	54.2	8.1 ± 17.2	4.4 ± 13.3	(Esposito et al., 2024)
	<i>P. septimaniae</i>	<i>P. septimaniae</i>	Adult	Skin, fins	Natural	River Corsigliese, River Tavignano	France	64	12	33.3	3.5 ± 2.6	1.2 ± 2.2	(Esposito et al., 2024)
Class Trematoda (Subclass Digenea)													
Family Allocreadiidae													
<i>Allocreadium carparum</i> (Macrolecithus papilliger) Odening, 1959	<i>P. phoxinus</i>	<i>P. csikii</i>	Adult	Gut	Natural	Obersee	Switzerland	57	80	44	-	1.40 ± 0.25 (0-11)	(Müller & Ward, 1995)
	<i>P. phoxinus</i>	<i>P. csikii</i>	-	Gut	Natural	Obersee	Switzerland	57	327	37.5-59.5	-	1.04-2.68	(Müller, 1995)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	-	Loch Achray, Lake Windermere	UK	4, 12	-	-	-	-	Personal communication in (Kennedy, 1974) (Rees, 1968)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	Stomach, intestine	Natural	Fron Goch Lake	UK	14	-	0.9-100	-	-	(Bibby, 1972)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	Stomach, intestine	Natural	Frongoch Lake	UK	14	650	32	-	-	(Nicoll, 1924)
<i>Allocreadium isoporum</i> (Looss, 1894) Looss, 1902	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Intestine	Natural	-	UK	-	-	-	-	-	(Kristoffersen & Teigland, 1997)
	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	-	Natural	-	Norway	2	-	-	-	-	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.2	

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7	-	0.07	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Sea-U, River Halmer	Russia	62, 63	63	6.7–11.1	-	0.1–0.2	(Dorovskikh & Stepanov, 2013)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Chubb, 1964) in (Kennedy, 1974)
<i>Allocreadium transversale</i> (Rudolphi, 1802) Odhner, 1901	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe	Russia	61	63	5	-	0.1	(Dorovskikh & Stepanov, 2013)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.3–0.4	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.3–0.8	(Almeida et al., 2024)
<i>Allocreadium</i> sp.	<i>P. phoxinus</i>	<i>Phoxinus tomentum</i>	Adult	Intestine	Natural	River Nezhinka	Russia	65	2	-	-	-	(Vainutis 2020)
<i>Bunodera luciopercae</i> (Müller, 1776) Lühe, 1909	<i>P. phoxinus</i>	<i>P. tomentum</i>	-	-	Natural	River Nezhinka	Russia	65	-	-	-	-	(Vainutis et al., 2021)
Family Bucephalidae	<i>P. phoxinus</i>	<i>Phoxinus sp. or R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>Rhipidocotyle campanula</i> (Rhipidocotyle Illense) (Dujardin, 1845) Dollfus, 1968	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Roding	UK	11	-	-	-	-	(Shillcock, 1972) in (Kennedy, 1974)
Family Diplostomidae	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Halmer	Russia	62	63	22.2	-	0.9	(Dorovskikh & Stepanov, 2013)
<i>Diplostomum commutatum</i> (Diesing, 1850) Dubois, 1937	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.7	(Cruz et al., 2022)
<i>Distomum phoxini</i> possible misspelling of <i>Diplostomum phoxini</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Cysts	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
<i>D. phoxini</i> (<i>Diplostomulum peimatoides</i> , <i>Tetracotyle phoxini</i>) (Faust, 1919) Arvy & Buttner, 1954	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Brain	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Main	Ireland	16	-	-	-	-	(Vickers, 1951) in (Holland & Kennedy, 1997) (Rees, 1968)
<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Brain	Experimental	-	UK	Not applicable	-	-	-	-	(Kane, 1966) in (Holland & Kennedy, 1997) (Kekäläinen, Lai, et al., 2014)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Experimental	-	Finland	Not applicable	-	-	-	-	(Kane, 1966) in (Holland & Kennedy, 1997) (Kekäläinen, Lai, et al., 2014)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Kuusjoja	Finland	13	171.2 ± 182.7 (24–922)	100	171.2 ± 182.7 (24–922)	171.2 ± 182.7 (24–922)	(Kortet et al., 2015)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Utsjoki	Finland	58	60	100	4.1 (3–17)	-	(Lebedeva et al., 2021)
<i>P. phoxinus</i>	<i>P. csikii</i> or <i>P. phoxinus</i>	<i>P. csikii</i> or <i>P. phoxinus</i>	Metacercariae	Brain	Natural	River Ruhr	Germany	59	15	-	-	-	(Schwelm et al., 2021)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	-	Norway	2	-	-	-	-	(Kristoffersen & Teigland, 1997)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	14.27–93.4	(Dorovskikh & Stepanov, 2008)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	100	-	74.76–399.93	(Dorovskikh & Stepanov, 2009)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe, River Sea-U, River Halmer, River Kara	Russia	61, 62, 63	63	100	-	11.3–74.7	(Dorovskikh & Stepanov, 2013)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	100	2.0–68.0	2.0–68.0	(Boutorina & Reznik, 2015)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Uksa	Russia	41	60	93	8.3 (1–36)	-	(Lebedeva et al., 2021)
<i>P. phoxinus</i>	<i>P. isetensis</i>	<i>P. isetensis</i>	Metacercariae	Brain	Natural	River Varzuga	Russia	31	60	100	51 (8–97)	-	(Lebedeva et al., 2021)
<i>P. phoxinus</i>	<i>P. csikii</i> or <i>P. septimaniae</i> or <i>P. lumaireul</i>	<i>P. csikii</i> or <i>P. septimaniae</i> or <i>P. lumaireul</i>	-	-	Experimental	-	Switzerland	Not applicable	-	-	-	-	(Ballabeni & Ward, 1993)
<i>P. phoxinus</i>	<i>P. csikii</i>	<i>P. csikii</i>	-	-	Natural	Seelapsee, Obersee	Switzerland	57	-	100	-	-	(Ballabeni, 1994)
<i>P. phoxinus</i>	<i>P. csikii</i>	<i>P. csikii</i>	-	-	Experimental	-	Switzerland	Not applicable	-	-	-	-	(Ballabeni, 1994)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. csikii</i> or <i>P. septimaniae</i> or <i>P. lumaireui</i>	<i>P. csikii</i>	Metacercariae	Brain	Natural	Obersee	Switzerland	57	80	100	431.72 ± 35.36 (102–2000)	431.72 ± 35.36 (102–2000)	(Müller & Ward, 1995)
<i>P. phoxinus</i>	<i>P. csikii</i>	<i>P. csikii</i>	-	Brain	Natural	Obersee	Switzerland	57	327	100	231–448 (5–2265)	231–448 (5–2265)	(Müller, 1995)
<i>P. phoxinus</i>	<i>P. csikii</i>	<i>P. csikii</i>	-	-	Natural	Giesse Stream	Switzerland	60	-	-	-	-	(Hoby et al., 2022)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	-	Edinburgh, Loch Lubnaig, Perth, Frongoch Lake, Loch Leven, Loch Lomond, Royal Canal, River Main, River Roding	UK	11, 15, 16, 23, 32, 33	-	-	-	-	(Baylis, 1928; Vickers, 1951; Bell & Hopkins, 1956; Copland, 1957; Kane, 1966; Shillcock, 1972) in (Kennedy, 1974)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	Brain	Natural	Edinburgh Region, Loch Lubnaig Stream	UK	32, 33	-	-	-	-	(Ashworth & Bannerman, 1927)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Brain, spinal cord, eyes	Natural	Fron Goch Pool	UK	14	-	-	-	-	(Rees, 1955)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Endrick, River Clyde, Loch Eck	UK	4	-	-	-	-	(Berrie, 1960)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Brain	Natural	Windermere Lake, Grasmere Lake	UK	12	-	-	-	-	(Erasmus, 1962)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Brain	Natural	Fron Goch Lake	UK	14	-	-	-	-	(Bibby & Rees, 1971)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Brain	Natural	Frongoch Lake	UK	14	650	100	81 (62–106)	81 (62–106)	(Bibby, 1972)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	-	-	Natural	Loch Leven	UK	23	-	-	-	-	(Campbell, 1974)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Brain	Natural	Frongoch Pool	UK	14	17	-	-	-	(Ali, 1982)
<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	Experimental	-	UK	Not applicable	-	-	-	-	(Ali, 1984)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Endrick, Loch Maragan	UK	4	7	-	21–220	-	(Barber & Crompton, 1997b)
<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Endrick, Loch Maragan	UK	4	195	96.2–100	6.0–245.0 (1–477)	-	(Barber & Crompton, 1997a)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Endrick	UK	4	34	50	-	13.7 ± 2.6	(Dezfuli, Capuano, et al., 2007)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	Metacercariae	Brain	Natural	River Endrick	UK	4	34	50	13.7 ± 2.6 (1–38)	-	(Dezfuli, Giari, & Shimm, 2007)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.4	(Cruz et al., 2022)
<i>Diplostomum</i> sp. von Nordmann, 1832	<i>P. phoxinus</i>	<i>P. uijmonensis</i>	Metacercariae	Brain	Natural	River Tuul	Mongolia	36	60	93	12.7 (1–58)	-	(Lebedeva et al., 2021)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. or <i>R. percnurus</i>	-	-	Natural	River Chulman, River Ungra	Russia	1	117	-	-	-	(Boutorina & Reznik, 2015)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Brain	Natural	Edinburgh Region, Loch Lubnaig Stream	UK	32, 33	-	-	-	-	(Ashworth & Bannerman, 1927)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	-	-	-	UK	-	-	-	-	-	Several references in (Kennedy, 1974)
<i>P. phoxinus</i>	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Eye	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	1.0–4.9	(Almeida et al., 2024)
<i>Hysteromorpha triloba</i> (Rudolphi, 1819) Lutz, 1931	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.4–1.2	(Cruz et al., 2022)
<i>Posthodiplostomum cuticola</i> (Diplostomum cuticola) (von Nordmann, 1832) Dubois, 1936	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.7–0.8	(Almeida et al., 2024)
	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Subcutaneous cysts	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Avon	UK	14	-	-	-	-	(Hockley, 1935) in (Kennedy, 1974)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	Metacercariae	Skin, fins	Natural	River Asco, River Casaluna, River Tartagine	France	64	84	19	21.3 ± 60.3	4.0 ± 27.0	(Esposito et al., 2024)
	<i>P. csikii</i>	<i>P. csikii</i>	Metacercariae	Skin, fins	Natural	River Casaluna	France	64	7	14.3	0.1 ± 0.4	1	(Esposito et al., 2024)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>P. dragarum</i>	<i>P. dragarum</i>	<i>P. dragarum</i>	Metacercariae	Skin, fins	Natural	River Abatesco, River Fium'Orbo, River Tavignano, River Vecchio	France	64	120	9.2	4.3 ± 4.9	0.4 ± 1.9	(Esposito et al., 2024)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	2.8–3.9	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	1.0–7.3	(Almeida et al., 2024)
<i>Tyodelphys clavata</i> (von Nordmann, 1832) Diesing, 1850	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Eye	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.6	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.4–1.4	(Almeida et al., 2024)
Family Gorgoderidae													
<i>Phyllostomum folium</i> (Olfers, 1816) Braun, 1899	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	-	-	0.13	(Dorovskikh & Stepanov, 2008)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	River Pechora	Russia	8	105	6.7–26.7	-	0.13–0.4	(Dorovskikh & Stepanov, 2009)
	<i>P. phoxinus</i>	<i>P. isetensis</i>	-	-	Natural	Lake Krivoe	Russia	61	63	5	-	0.1	(Dorovskikh & Stepanov, 2013)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	Llyn Padarn	UK	9	-	-	-	-	(Chubb, 1964, 1970) in (Kennedy, 1974)
Family Opcoelidae													
<i>Plagioparus angusticollis</i> (Allocreadium angusticollis) (Hausmann, 1896) Dobrovolsky, 1939	<i>P. phoxinus</i>	<i>Phoxinus</i> sp. 7	-	Liver, stomach	Natural	Edinburgh Region, Loch Lubnaig Stream	UK	32, 33	-	-	-	-	(Ashworth & Bannerman, 1927)
<i>Sphaerostoma bramae</i> (Müller, 1776) Lühe, 1909	<i>P. phoxinus</i>	<i>P. phoxinus</i> or <i>Phoxinus</i> sp. 7	-	Intestine	Natural	-	UK	-	-	-	-	-	(Nicoll, 1924)
	<i>P. phoxinus</i>	<i>P. phoxinus</i>	-	-	-	River Roding	UK	11	-	-	-	-	(Shillcock, 1972) in (Kennedy, 1974)
Family Strigeidae													
<i>Apatemon</i> sp. Szidat, 1928	<i>P. phoxinus</i>	<i>P. isetensis</i>	Larvae	-	Natural	River Pechora	Russia	8	105	-	-	0.13–1.1	(Dorovskikh & Stepanov, 2008)

(Continues)

TABLE 2 (Continued)

Parasite species	Host according to original record	Reassigned host	Stage	Infection site	Natural/experimental infection	Locality	Country	Nb map	n	P (%)	MI	MA	Reference
<i>Ichthyocotylurus platycephalus</i> (Creplin, 1825) Odening, 1969	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.7–1.6	(Cruz et al., 2022)
<i>P. septimaniae</i>	<i>P. septimaniae</i>	<i>P. septimaniae</i>	-	-	Natural	Tordera Stream	Spain	10	204	-	-	0.1–0.6	(Almeida et al., 2024)

Note: Parasites are ordered by phylum, class, and family. Species within families are arranged alphabetically. Each record is listed when available, along with its developmental stage, infection site, the natural or experimental status of the infection, the locality, country, number of examined hosts (n), prevalence (P), mean intensity (MI), and mean abundance (MA) ranges. The reference is listed for each record. The parasite and host species listed are the currently accepted names of the species indicated in the reference documents, according to the World Register of Marine Species (WoRMS) database. When a synonym was used in the source reference, it is indicated between parentheses, after the currently accepted name. Dashes “-” indicate data unavailable from source publications. The numbers provided in the column “Nb Map” are the sites reported in Figure 3.

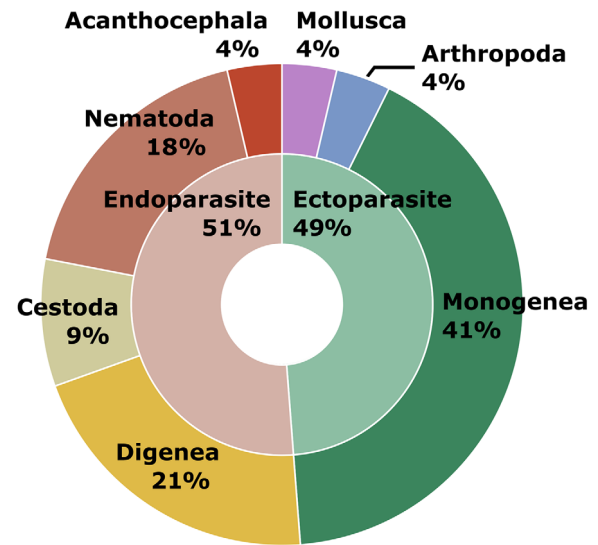


FIGURE 2 Taxonomic composition of Metazoa macroparasites reported from *Phoxinus minnow*.

The high apparent diversity of *P. phoxinus* parasites is the result of the simultaneous consideration of several host species. The host species reassignment allowed discrepancies to be highlighted in the parasitological research effort toward the various *Phoxinus* species. The most thoroughly studied species were *Phoxinus* sp. 7 sensu Palandačić et al., 2017, *P. isetensis*, and *P. phoxinus* (Supplementary Data S1) (e.g. Blazek et al., 2008; Holland & Kennedy, 1997; Kekäläinen et al., 2011; Kennedy, 1974; Lai et al., 2012, 2015, 2016a). For *P. septimaniae* and *P. ujmonensis*, a noteworthy part of parasite diversity is known despite the few studies focused on these hosts: 24 parasites recorded with only 4 studies for *P. septimaniae* and 12 parasites with 3 studies for *P. ujmonensis* (Cruz et al., 2022; Ergens & Dulmaa, 1967; Le Brun et al., 1988; Lebedeva et al., 2021; Lumme et al., 2017). For several species, for example, *P. marsilii*, *P. csikii*, *P. cf. morella*, and *P. lumaireul*, only a few parasites were recorded, and for other recently confirmed species, for example, *Phoxinus bigerri* (Bay of Biscay, Ugarna drainage), *Phoxinus colchicus* (Black Sea basin, Natanebi drainage), and *Phoxinus karsticus* (Adriatic Sea basin, Skadar Lake drainage), no parasitological records could be found in the present survey. The host species reassignment thus enabled us to evidence gaps in the current knowledge of parasite diversity of *Phoxinus* minnows throughout their distribution range: most parasitological studies were conducted in northern Europe where *P. phoxinus*, *P. isetensis*, and *Phoxinus* sp. 7 occur, whereas southern Europe is comparatively understudied. This gap in the knowledge of *Phoxinus* minnow parasites in southern Europe is all the more regrettable, as this is where the specific diversity of this genus is the highest and thus a high parasite diversity might be expected. Further parasitological survey effort should be directed at poorly known species, alongside the work of taxonomists currently reassessing *Phoxinus* host taxonomy. In addition, fish parasites are also undergoing molecular revisions, allowing improved understanding of

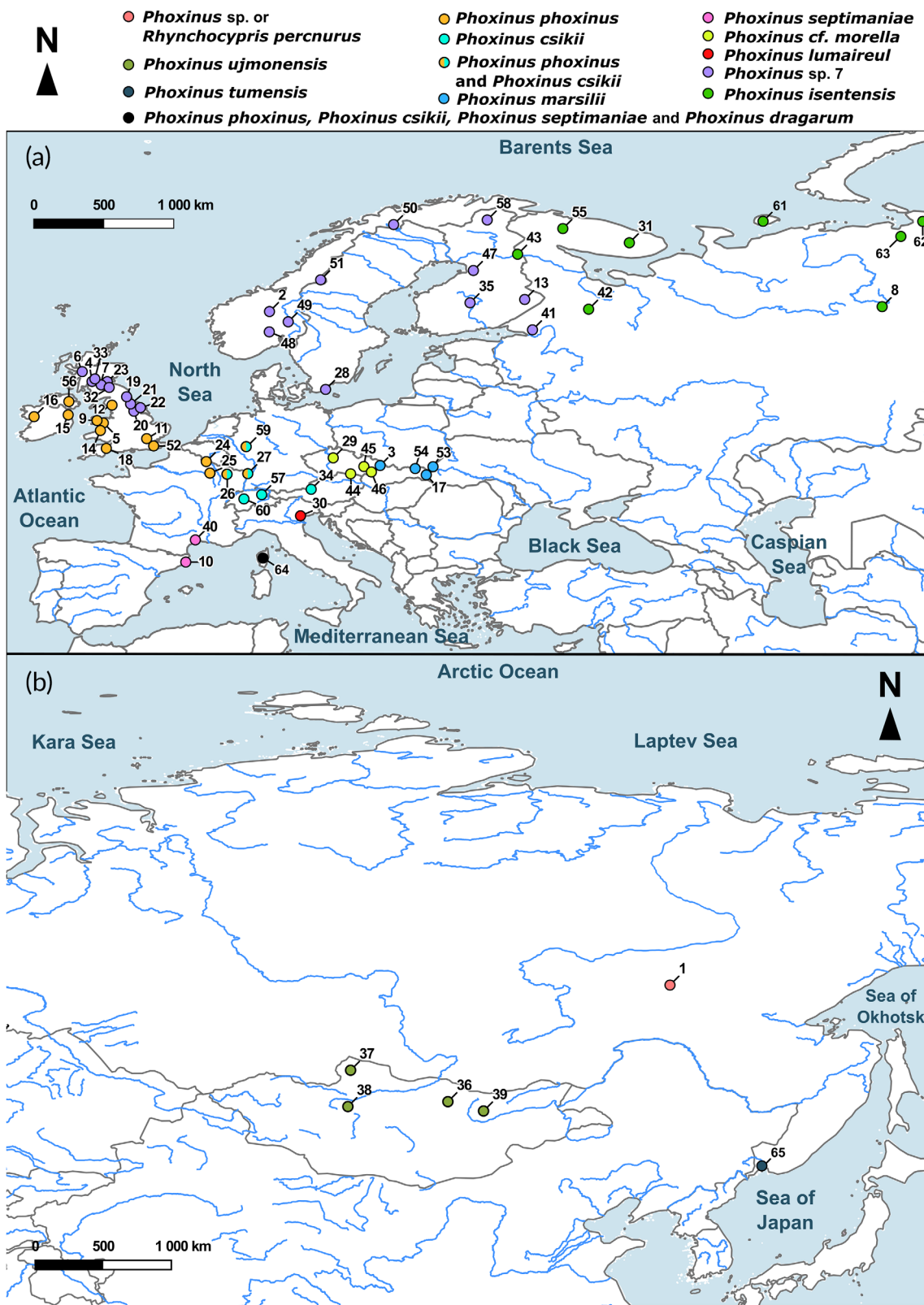


FIGURE 3 Geographical distribution of parasitological records for *Phoxinus* minnows in (a) Europe and (b) Asia, integrating host species reassignment. Numbers correspond to the numbers reported in the parasite checklist table (Table 2, column Nb Map).

cryptic diversity, parasite evolutionary history, life cycles, and biogeographical distribution (Scholz & Kuchta, 2022). Because of the presence of cryptic species in both *Phoxinus* minnows and their

parasites, the approach for studying these organisms should include molecular determination of species for both the hosts and parasites.

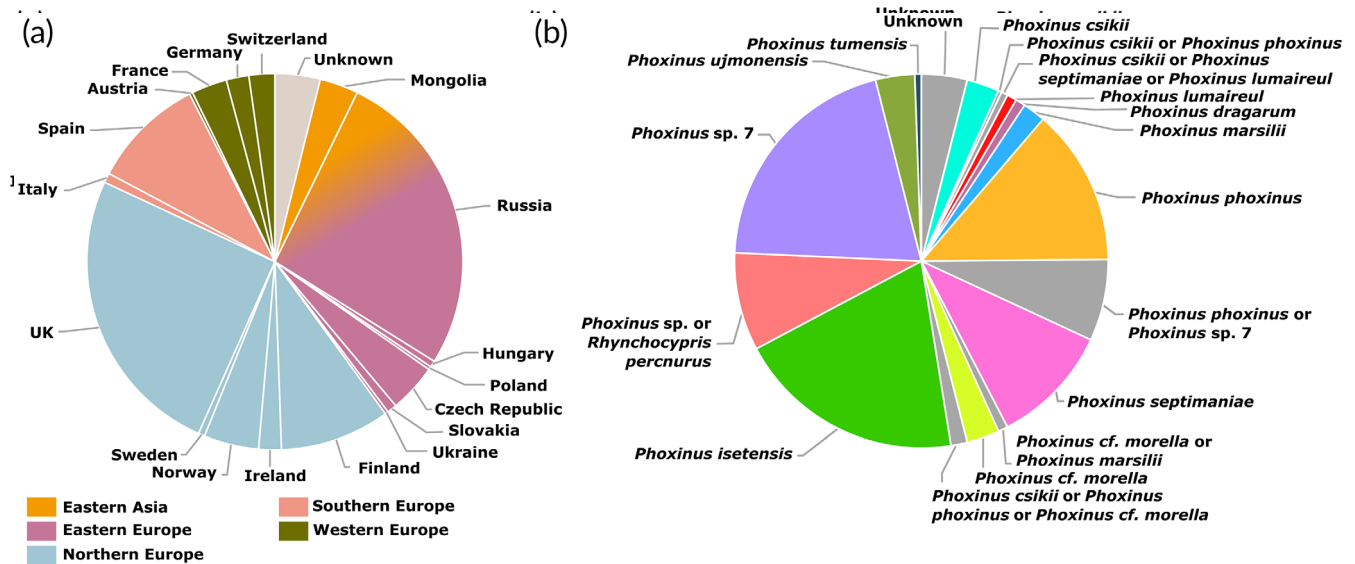


FIGURE 4 Distribution of parasitological records based on the (a) geographical range and (b) *Phoxinus* host identity.

4.1 | *Gyrodactylus* in *Phoxinus* minnows: Overestimated or underestimated diversity?

Members of the genus *Gyrodactylus* (Platyhelminthes: Monogenea) are extremely diverse, viviparous ectoparasites recovered from the fins, gills, and skin of a wide range of fish (Bakke et al., 2007). *P. phoxinus* was reported to host the greatest diversity of *Gyrodactylus* described in any fish species in the Palearctic (Bakke et al., 2007; Harris et al., 2004; Lumme et al., 2017). In the present bibliographical study, reports concerning 25 *Gyrodactylus* species were compiled. However, the reassignment of host species showed that this tremendous diversity is the result of taking into account several species of *Phoxinus* at once.

Some species of *Gyrodactylus* were only reported from few sampling sites and a few reassigned *Phoxinus* species, for example, *Gyrodactylus albolacustris* Lumme et al., 2017 from Russia (reassigned to *Phoxinus* sp. 7 and *P. isetensis*) and Mongolia (*P. ujmonensis*), *Gyrodactylus botnicus* Lumme et al., 2017 from Finland (*Phoxinus* sp. 7 and *P. isetensis*), *Gyrodactylus danastriae* Lumme et al., 2017 from Poland (*P. marsilii*) (Lumme et al., 2017), *Gyrodactylus konovalovi* Ergens, 1976 from Russia (either *Phoxinus* sp. or *Rhynchocypris percunurus*) (Boutorina & Reznik, 2015) or *Gyrodactylus llewellyni* Ergens & Dulmaa, 1967 from Mongolia (*P. ujmonensis*) (Ergens & Dulmaa, 1967). Molecular delineation for both *Gyrodactylus* and their *Phoxinus* host would help to determine these parasites' host ranges.

Several species have been reported to be more widely distributed, such as *G. macronychus* on *P. phoxinus* in the UK, *P. cf. morella* in Czech Republic, *Phoxinus* sp. 7 in Finland, Norway, and the UK, *P. ujmonensis* in Mongolia, *P. isetensis* in Russia, and *P. septimaniae* in Spain (Cruz et al., 2022; Ergens, 1976; Ergens & Dulmaa, 1967; Dorovskikh & Stepanov, 2008; Grano-Maldonado et al., 2011; Matějsová et al., 2000; Pettersen et al., 2016; Ziętara &

Lumme, 2003). Such wide ranges of distribution may be the result of (1) cross-countries transfer of hosts and parasite species, (2) a wide host spectrum of these parasites, or (3) undetected cryptic diversity of these parasites on *Phoxinus* minnows arising from the exclusive use of morphological criteria before the advent of molecular methods. The highest diversity of *Gyrodactylus* has so far been recorded from *Phoxinus* sp. 7, with 13 known species from *P. isetensis* (10 species), *P. ujmonensis* (9 species), and *P. phoxinus* (7 species). No *Gyrodactylus* were reported from *P. csikii* and *P. lumaireul*, which more likely results from *Gyrodactylus* not being the focus of studies concerning these *Phoxinus* species than from an absence of *Gyrodactylus*. Compiled studies regarding *P. lumaireul* addressed the immunological and cellular response to the infection by the Nematoda *Raphidascaris acus* (Bloch, 1779) and studies conducted on *P. csikii* focused on several Platyhelminthes species, mostly *D. phoxini*. The diversity of *Gyrodactylus* was thus likely overestimated in *P. phoxinus* but is most probably underestimated in the genus *Phoxinus* at the Eurasian scale.

Co-speciation studies would be of interest to explore the common evolutionary history of *Gyrodactylus* and their *Phoxinus* hosts and may allow the detection of host-switching or hybridization events. The identification of *Gyrodactylus* species and haplotypes combined with host-specific determination could furthermore be a useful tool in retracing their hosts' dispersion routes, whether natural or anthropogenic. Parasites, and especially Monogenea, have already been used successfully to gain insights on the historical distribution and routes and vectors of introduction of their host: the origin of *Limnothrissa miodon* (Boulenger, 1906) (Clupeidae) in Lake Kariba, Zimbabwe, was clarified by examining its *Kapentagyryus* (Dactylogyridae) (Kmentová et al., 2019); contemporary contacts among North American Leuciscidae and historical contact with their European counterparts were revealed through the use of their host-specific Dactylogyridae (Šímková et al., 2022); and the lack of *Gyrodactylus* on the round goby

Neogobius melanostomus (Pallas, 1814) allowed Huyse et al. (2015) to suggest an introduction via ballast water for this fish in Belgium.

4.2 | *Diplostomum* spp.: Implications for animal health

Several Diplostomidae are recorded on *Phoxinus* minnows: *Diplostomum commutatum* (Diesing, 1850) and *Hysteromorpha triloba* (Rudolphi, 1819) were found on *P. septimaniae* in Spain, and *Posthodiplostomum cuticola* and *Tylodelphys clavata* (von Nordmann, 1832) were found on *P. phoxinus* in the UK and *P. septimaniae* in Spain (Cruz et al., 2022; Hockley, 1935; Kennedy, 1974; Nicoll, 1924). One of the most widespread parasites of *Phoxinus* minnows, *D. phoxini* (reported under this name and synonyms in the literature, Table 1), a Diplostomidae (Platyhelminthes: Digenea), whose metacercariae parasitize the brain of *Phoxinus* minnows, is reported from *P. phoxinus* in Ireland and the UK, *Phoxinus* sp. 7 in Finland, Norway, the UK, and Russia, *P. csikii* in Switzerland, and *P. septimaniae* in Spain (Ballabeni, 1994; Cruz et al., 2022; Kekäläinen, Lai, et al., 2014; Kortet et al., 2015; Kristoffersen & Teigland, 1997; Lebedeva et al., 2021; Rees, 1955; Schwelm et al., 2021). However, Lebedeva et al. (2021) showed that Fennoscandian and Mongolian *Phoxinus* minnows were hosts to different *Diplostomum* species, with a correlation of each line of brain Diplostomidae with a specific *Phoxinus* lineage, thus supporting the conclusion of a high specificity of brain *Diplostomum* toward their host. This conclusion is in agreement with the cross-infection experiment conducted by Ballabeni and Ward (1993), which showed that *D. phoxini* originating from two close Swiss lakes were more infective to their sympatric hosts than to allopatric hosts. Moreover, analysis conducted in North America revealed a wide and previously undetected diversity of Diplostomoidea using barcoding and showed that parasites of this group occurring outside of the eyes are highly host specific (Locke et al., 2010). These elements suggest cryptic diversity among the brain flukes reported as *D. phoxini* with potentially several host-specific species parasitizing the numerous *Phoxinus* species. Gathering data about this parasite may be of veterinary importance as it caused fatal enteritis in chicks of the vulnerable *Fratercula arctica* (Linnaeus, 1758) kept in captivity (Hoby et al., 2022). Moreover, members of the genus *Diplostomum* are pathogenic to their intermediate fish host. *D. phoxini* disrupts brain tissue integrity and necrosis of the layer surrounding the larvae (Dezfuli, Capuano, et al., 2007).

4.3 | *Phoxinus* as valuable hosts for conservation biology of the endangered freshwater mussel *Unio crassus*

A systematic molecular identification of *Phoxinus* minnows in parasitological studies may also be of interest from a conservation biology perspective. *Unio crassus* is an endangered freshwater mussel (Gastropoda: Bivalvia), with conservation status assessments ranging from “extinct in the wild” (Lithuania and the Netherlands) to “least

concern” (Kazakhstan and Russia) (Bolotov et al., 2020; Lopes-Lima et al., 2017; Soroka et al., 2021). Unionidae mussels have the particularity of having an obligatory parasitic glochidium stage living attached to gills of freshwater fish. Glochidia larvae of freshwater mussel were recovered in the wild only from France (*P. phoxinus* and *P. csikii*) and Sweden (*Phoxinus* sp. 7) for *U. crassus* Philipsson, 1788 and from Spain (*P. septimaniae*) for an unidentified Unionidae (Cruz et al., 2022; Lamand et al., 2016; Schneider et al., 2019), and experimental infections were successful also for *Anodonta anatina* (Linnaeus, 1758) (Beggel & Geist, 2015; Kekäläinen, Pirhonen, & Taskinen, 2014). According to the literature, *P. phoxinus* has been found to be a primary host for *U. crassus*. However, except in France, where this parasite was found in the wild on this host in the Seine and Rhine river basins, the experimental infestations were conducted in Czech Republic and Germany, where the host species’ reassignment is uncertain (*P. phoxinus*, *P. csikii*, *P. cf. morella*, *P. cf. morella*, or *P. marsilii* depending on the origin) (Douda et al., 2012; Douda, 2015; Lamand et al., 2016; Schneider et al., 2017; Taeubert, Gum et al., 2012; Taeubert, Martinez et al., 2012). Molecular identification of the *Phoxinus* hosts would be of interest to gain a better understanding of these organisms’ host range and specificity. It is known that compatibility between mussel strains and fish hosts is essential in the parasite–host interaction, and thus for the conservation and management of *U. crassus* (Schneider et al., 2017). *U. crassus* has a wide distribution range in Eurasia, but records of its glochidia on *Phoxinus* minnows are comparatively relatively few. There could thus be preferences of the glochidia toward one or several *Phoxinus* species, which would be difficult to assess without molecular identification of the host. For this reason, a reliable identification of *Phoxinus* hosts could provide valuable information for the conservation and management of endangered freshwater mussels.

5 | CONCLUSION

Phoxinus minnows are hosts to a wide variety of Protozoa and Metazoa parasites, which, until recently, was attributed to *P. phoxinus* as a result of this genus’ unresolved taxonomy and cryptic diversity. *Phoxinus* taxonomy is undergoing an urgently needed clarification, with great progress made, especially in western Europe (Corral-Lou et al., 2019; Denys et al., 2020; De Santis et al., 2021; Kottelat, 2007; Palandačić et al., 2015, 2020, 2022), and also in southern and eastern Europe (Bogutskaya et al., 2020, 2023) and Asia (Cheng et al., 2022). This progress has allowed the reassignment of parasite records gathered in the present survey to their *Phoxinus* host species. Barcoding of *Phoxinus* minnows should be conducted when studying their parasites, as a reliable identification of the host is vital in parasitology research. Increasing the parasitological research effort toward the so-far neglected *Phoxinus* species, such as, *P. lumaireul*, *P. colchicus*, *P. bigerri*, *P. karsticus*, or *Phoxinus krkae*, will most likely increase the parasite diversity known for the genus *Phoxinus*. There is little doubt that in the upcoming years, molecular methods should help unravel previously unknown host specificities for parasites of *Phoxinus*

minnows. Studying these parasites could be important regarding the elucidation of introduced *Phoxinus*' origin, the health of fish populations, and the conservation of endangered species such as *U. crassus*.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Data collection and analysis were performed by Anaïs Esposito, Gaël P.J. Denys, and Yann Quilichini. The first draft of the manuscript was written by Anaïs Esposito, and all authors had commented on the previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no financial or proprietary interests in any material discussed in this article.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available within the article and its supplementary material. Raw data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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