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Freshwater trematodes in Iceland and the surrounding north – current advances and questions

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Review Article

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Abstract

Iceland is an isolated, sub-Arctic, oceanic island of volcanic origin in the northern North Atlantic. With a limited faunal diversity and being the most northern point in the distributional range for some species, it is an intriguing model region to study parasite biodiversity and biogeography. Since 2006, there has been a history of intense biodiversity discoveries of freshwater trematodes (Trematoda, Digenea), thanks to the use of integrative taxonomic methods. The majority of digeneans (28 out of 41 known) were characterised with molecular genetic methods and morphological analyses, with some of their life-cycle stages and geographical distribution assessed. A surprising diversity has been discovered, comprising species of the families Allocreadiidae, Cyclocoeliidae, Diplostomidae, Echinostomatidae, Gorgoderidae, Plagiorchiidae, Notocotylidae, Schistosomatidae, and Strigeidae. Many of the recorded species complete their life cycles within Iceland, with three snail species (*Ampullaceana balthica*, *Gyraulus parvus*, *Physa acuta*) known as intermediate hosts. No trematodes endemic for Iceland were found; they appear to be generalists with wide geographical ranges dispersed mainly by migratory birds. Interestingly, fish trematodes recorded in Iceland were found in mainland Europe, indicating that they might be dispersed by anadromous fishes, by human activity, or by migratory birds carrying intermediate hosts. The trematode fauna is mainly Palaearctic, with few species recorded in North America. We highlight the ongoing need for precise species identification via integrative taxonomic methods, which is a baseline for any further ecological studies and adequate epidemiological and conservation measures. Also, there is still a need of obtaining well-preserved vouchers of adults for definite species delimitation.

Introduction

Iceland is an oceanic island in the sub-Arctic located in the Northeast Atlantic. It is of volcanic origin with multiple glacial events in the past (Bolotov *et al.* 2017; Downes 1988). Iceland was last covered by the Weichselian ice sheet, which ended 12,000 years ago (Norðdahl *et al.* 2008). There have been controversial views on whether Iceland was recolonised after the last glaciation (*tabula rasa* hypothesis) or if there were glacial refuge areas where some organisms could survive (Bingham *et al.* 2003; Habel *et al.* 2010; Rundgren 2007). The current view is that post-glacial colonisation is the main contributor to recent Icelandic fauna arriving from northwestern Europe (Downes 1988; Panagiotakopulu 2014). However, there is still some support for glacial refugia in Iceland and other northern parts of Europe (Habel *et al.* 2010).

The flora and free-living fauna are considered more Palaearctic (European) than Nearctic (Gíslason 2005, 2021). Nowadays, a relatively species-poor fauna with a very low degree of endemism is known from Iceland (Brochmann *et al.* 2003; Cortés-Guzmán *et al.* 2024; Downes 1988; Gíslason 2021; Lindegaard 1979). Nevertheless, the aquatic ecosystems in Iceland are among the unique wetlands of global value (on the Ramsar List) and support internationally important bird populations (with 21 species breeding in Iceland – mainly seabirds, waders, and waterfowl) including significant proportions of the entire world populations of some species (Jóhannesdóttir *et al.* 2014; Wetlands International 2006).

Sub-Arctic freshwater ecosystems are considered sentinel systems, as changes in temperature are most pronounced in these regions compared to areas in lower latitudes (Rolls *et al.* 2017). Iceland is sensitive to changes in atmospheric and oceanic circulation through time (Geirsdóttir *et al.* 2009; Mackintosh *et al.* 2002), rendering it a good model to monitor the impact of global

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warming on biodiversity, including metazoan parasites. Advancing climate change not only brings changes in temperature but also includes shifts in faunal distribution, and there is evidence for a poleward shift of some species (Jeppesen *et al.* 2010; Parmesan and Yohe 2003). Changes in species distributions can be disproportionate as invaders can appear faster than resident species are declining, which could result in higher species diversity in some areas, a state which might be only transient (Walther 2001). For a better understanding of how organisms in different locations respond to climate perturbations, it is necessary to have a species inventory and databases of the regions of interest (Davidson *et al.* 2011).

Parasites are ubiquitous components of ecosystems, having an impact on food webs and the structure of host populations and communities (Kuris *et al.* 2008; Mouritsen *et al.* 2018; Wood *et al.* 2007). Trematodes (Trematoda, Digenea) with their complex life cycles including multiple host species reflect the diversity of the free-living fauna; indeed, they are viewed as indicators of functioning trophic linkages and bioindicators of diversity and abundance of animal communities in ecosystems (Gardner and Campbell 1992; Hechinger *et al.* 2007; Hechinger and Lafferty 2005; Hudson *et al.* 2006; Kuris *et al.* 2008; Marcogliese and Cone 1998). Transmission of infective stages from host to host is highly temperature-dependent, which renders them sensitive to climate fluctuations (Marcogliese 2001; Mouritsen and Poulin 2002; Poulin 2006). The sub-Arctic region is considered as the northern distributional limit for freshwater trematodes, as further north, their life cycles cannot be completed due to lack of suitable hosts (Galaktionov 1996). Therefore, trematodes could be considered as particularly sensitive to poleward shifts of faunal distribution.

The host-parasite systems in the north have been considered as relatively simple, with short trophic linkages and low species diversity with limited capacity for adaptation to environmental changes (Dobson *et al.* 2015; Hoberg *et al.* 2012; Kutz *et al.* 2009). Therefore, we might expect to find a depauperate trematode fauna in the sub-Arctic, where a limited number of free-living species could be used as hosts. Blair (1973) also questioned whether trematode life cycles could be completed under the harsh climatic conditions in Iceland, when he first investigated larval trematodes from Icelandic freshwater snails. In the last two decades in Iceland, the advance of molecular genetic methods led to the discovery of an unexpected diversity of trematode fauna and revealed previously unconsidered patterns of species distribution.

Our aim is to summarise the current knowledge on trematodes in Iceland and recent advances, as well as prevailing gaps in knowledge of the trematode species diversity and distribution. The present text was written as an outcome of a presentation of the topic at the inaugural international meeting for trematodology, Trematodes, Brisbane, September 8–13 2024, Australia (Martin *et al.* 2024).

The species diversity of snails and other hosts for trematodes in Iceland

As mentioned above, the diversity of free-living animals acting as potential hosts for trematodes is much lower in Iceland than in mainland Europe, and most of the groups seem to have colonised Iceland during the Holocene (Cortés-Guzmán *et al.* 2024; Panagiotakopulu 2014). There are fewer species of all respective groups, and members of some classes are missing completely (i.e., amphibians and reptiles) (Biological Diversity in Iceland 2001).

In the trematode life cycles, molluscs, particularly snails (Gastropoda), are considered the most important group because with some exceptions, they are always used as the first intermediate hosts (Cribb *et al.* 2003). In Iceland, few species of aquatic snails were reported by Mandahl-Barth (1938) and Einarsson (1977), and summarised by, e.g. Glöer (2019). Of lymnaeid snails, *Ampullaceana balthica* (L.) (originally *Radix balthica* (L.)) and *Galba truncatula* (O. F. Müller) were recorded, and from planorbid snails, *Anisus spirorbis* (L.), *Gyraulus laevis* (Alder), *G. parvus* (Say) and *Bathyomphalus contortus* (L.) were found in few localities (Glöer 2019; own observations). In a pond at Nordic House, Vatnsmýri in Reykjavík, *Physa acuta* Draparnaud was found (Skírnisson and Schleich, unpublished, Pantoja *et al.* 2021). Of bivalves, *Pisidium* spp. are common in Iceland, and so far, 11 species were recorded (Hallgrímsson 1990; Kuiper *et al.* 1989).

Ampullaceana balthica is the most common and widespread snail in Iceland, occurring in all types of water bodies and tolerating elevated temperature in hot springs (Bolotov *et al.* 2017). Phylogeographic analyses by Bolotov *et al.* (2017) suggest that *A. balthica* colonised Iceland after the last glaciation rather than surviving in glacial refugia. Identification of *A. balthica* largely benefited from molecular genetic methods, as this snail species is variable in its shell characters and has been frequently confused with related species in mainland Europe (*Ampullaceana lagotis* Schrank, *Peregriana labiata* (Rossmässler), *P. peregra* (O. F. Müller)) and it was previously reported under different names, such as *Radix* (*Lymnaea*) *peregra* (O. F. Müller) or *R. ovata* (Draparnaud) (Huňová *et al.* 2012; Schniebs *et al.* 2011). Precise identification of the snail hosts has a substantial practical impact on parasitology, as different snail species might vary in susceptibility (Huňová *et al.* 2012).

Gyraulus parvus is widely distributed in North America. It is present up to south Greenland and is invasive in Europe (Glöer 2019). However, Lorencová *et al.* (2021) in their phylogenetic analyses based on DNA sequence data have revealed that *G. parvus* and *G. laevis*, the latter considered native in Europe, are in fact part of the same species-level clade and should be recognised as *G. parvus.* The Icelandic population of *Gyraulus* (or race; for details, see Lorencová *et al.* 2021) belongs to the one originally assumed to be *G. laevis.* This would imply that *G. parvus* expanded to Iceland via mainland Europe, indicating a possibly recent time of colonisation in the early to mid-Holocene (Lorencová *et al.* 2021). This might have further implications for the trematode species spectrum, as one of the trematode parasites (*Neopetasiger islandicus*) found in *G. parvus* in Iceland was recorded in several bird species in North America (Tkach *et al.* 2016).

Physa acuta is of American origin, and it is highly invasive. It can efficiently disperse via water, aquatic birds, and mammals, and it is present in almost all continents (Lorencová *et al.* 2021; van Leeuwen *et al.* 2013). It was described from France as a new species in 1805, and it further spread to Great Britain probably in the second half of the 19th century, either via human activity or bird transport (Anderson 2003; Vinarski 2017). *Physa acuta* was introduced to Iceland more than 40 years ago by human activity, and since then, there is a stable population in Nordic House, Vatnsmýri in Reykjavík (Skírnisson and Schleich, unpublished).

There are five native fish species in Iceland which live wholly or partly in freshwater: Atlantic salmon (*Salmo salar* L.), which is known to enter Icelandic rivers and lakes, Arctic charr (*Salvelinus alpinus* (L.)), brown trout (*Salmo trutta* L.), European eel (*Anguilla anguilla* (L.)), and three-spined stickleback (*Gasterosteus aculeatus* L.) (Biological Diversity in Iceland 2001). There are two non-native species: rainbow trout (*Oncorhynchus mykiss* (Walbaum)) which was introduced to Iceland with fish farming and escaped to the wild, and the Pacific pink salmon (*Oncorhynchus gorbuscha* (Walbaum)), which has been spreading since 1960 (Biological Diversity in Iceland 2001; Finnsson *et al.* 2025). Most of the fish species occur all over Iceland in rivers and lakes; only European eel is more common in the western and southwestern part of the island. The distribution of fishes in northern latitudes has been substantially influenced by glaciation events in the Pleistocene, and the current view is that fishes have rapidly recolonised Iceland after the last glaciation – for example, Arctic charr most probably diverging from one North Atlantic lineage (Bernatchez and Wilson 1998; Brunner *et al.* 2001; McKeown *et al.* 2010; Wilson *et al.* 2004). Currently, the native Arctic charr, brown trout, and Atlantic salmon are affected by climate warming, while the cold-adapted Arctic charr is the most vulnerable, and its populations have declined within the last 30 years (Jeppessen *et al.* 2010; Svenning *et al.* 2022).

Birds comprise the greatest faunal diversity in Iceland, with 88 species nesting regularly and about 424 species being recorded in total (Einarsson 2000; Lepage *et al.* 2014). They are assumed to be predominantly of European origin, breeding around the northern hemisphere or particularly in the North Atlantic region (Lepage *et al.* 2014). In Iceland, the most abundant are waterfowl, seabirds, and waders (Einarsson 2000). One of the most important nesting sites is Lake Mývatn (a designated Ramsar site), with all the waterfowl species known from Iceland breeding there (Biological Diversity in Iceland 2001; Einarsson 2000). Iceland is not only a major breeding region, but it is also an important stopover for migratory birds nesting in the Arctic (Canada, Greenland) and wintering further south (Einarsson 2000).

The mammalian fauna living in the wild in Iceland is considered to consist of four species. The Arctic fox (*Vulpes lagopus* (L.)) is the only native mammal species in Iceland, living in inland and coastal areas (Hersteinsson and MacDonald 1996). The Arctic fox colonised Iceland during the Little Ice Age, before humans arrived (Mellows *et al.* 2012). All other mammal species were introduced by humans – the wood mouse (*Apodemus sylvaticus* (L.)), reindeer (*Rangifer tarandus* (L.)), and mink (*Neogale vison* (Schreber)); completely bound to human settlements are *Mus musculus* L., *Rattus rattus* (L.), and *R. norvegicus* (Berkenhout) (Biological Diversity in Iceland 2001).

Icelandic literature collection and parasite-host records

To compile a comprehensive overview, we searched for published literature, locally published sources, and master/doctoral theses via Scopus, Science Direct, and Google Scholar. The key words we used for the search were 'Iceland AND Trematoda OR Digenea'. Further, we searched our personal library collections, particularly that of K. Skírnisson in Iceland.

We compiled a database of species-level distribution data consisting of a total of 48 relevant papers, published between 1956 and 2024, including articles published in Icelandic, conference abstracts, and two theses. The database comprises host-parasite locality records for trematode parasites of snails (three species), fishes (four species), birds (12 species), and mammals (one species) in freshwater habitats in Iceland. The database contains 222 records of 41 trematode species of 19 genera and 9 families (Table 1). The most frequently recorded families were Schistosomatidae, Diplostomidae, Strigeidae, Allocreadiidae, and Echinostomatidae. The most recorded species were *Diplostomum spathaceum*, *Crepidostomum farionis*, and *Trichobilharzia franki* "*peregra*". The snail species *Ampullaceana balthica* was recorded as the most commonly used first intermediate host by 21 trematode species of six families. Of the fishes, four species were found to be hosts for 13 trematode species of five families. The majority of fish records were as second intermediate hosts infected by metacercariae of *Diplostomum* and *Apatemon*. A total of 16 trematode species of six families were recorded in 12 species of birds (definitive hosts). Out of the 41 trematode species recorded, for five species (*Neopetasiger islandicus*, *Trichobilharzia anseri*, *T. franki* "*peregra*", *T. mergi*, and *T. regenti*), the whole life cycle was documented in Iceland. For *Apatemon gracilis* and *Diplostomum* spp., larval stages from both snails (cercariae) and fishes (metacercariae) were documented. For *Cotylurus cornutus*, *Echinoparyphium recurvatum* and *Echinostoma revolutum*, both larval stages and adults, were recorded; however, those were not linked using DNA sequence data.

Of the seven freshwater gastropod species known from Iceland, three species were found infected with trematodes: *Ampullaceana balthica*, *Gyraulus parvus*, and *Physa acuta*. *Galba truncatula*, an intermediate host for *Fasciola hepatica* Linnaeus, 1758, was recorded only at a few sites and was never found infected. *Ampullaceana balthica* was found as the first intermediate host of 21 trematode species, which by far exceeds all other snail species recorded and is comparable to *Lymnaea stagnalis* (L.) hosting 24 species in central Europe (Faltýnková *et al.* 2007). An explanation of this phenomenon might lie in the fact that *A. balthica* is one of the most widespread radicine snail species in mainland Europe, its distributional range reaching from north to south and extending eastwards to Siberia and Central Asia (Aksenova *et al.* 2018; Bolotov *et al.* 2017; Schniebs *et al.* 2011; Vinarski *et al.* 2021). Since it has been found to host a wide variety of trematode species in Europe (Kundid *et al.* 2024), we can infer that it is highly probable that trematodes using *A. balthica* in mainland Europe are able to complete their life cycles in Iceland as well, when they can find their susceptible snail host.

Of the planorbid snails, *G. parvus* was found infected with two trematode species, *N. islandicus* and *Apatemon* sp. 6. It is peculiar that both species possess cercariae with a large tail, mimicking prey to attract fish hosts (Faltýnková *et al.* 2023).

In *P. acuta*, one single species, *Echinoparyphium* sp. 2, was recorded by Pantoja *et al.* (2021), which is conspecific with material of Gordy and Hanington (2019) from Canada. The American origin of *P. acuta* might explain the presence of this American trematode species. There is a stable population of *P. acuta* in Nordic House, Vatnsmýri in Reykjavík, where the first echinostome and strigeid metacercariae were found in 2007 (Skírnisson and Schleich, unpublished), and cercariae of *Echinoparyphium* sp. 2 were recorded 14 years later by Pantoja *et al.* (2021).

Pisidium spp. so far have not been found infected, although they are known as intermediate hosts of allocreadiids and gorgoderids from, e.g. mainland Europe (Kristmundsson and Richter 2009).

Fish play an important role particularly as second intermediate hosts in trematode life cycles in Iceland. A total of 73% of the fish trematode records concern metacercariae of *Diplostomum* spp. or *Apatemon* spp., comprising 11 trematode species. Of trematodes using fishes as definitive hosts, four species were found from two genera (*Crepidostomum* and *Phyllodistomum*) in *Salmo trutta* and *Salvelinus alpinus*. *Anguilla anguilla* and *Gasterosteus aculeatus* were found to host only metacercariae. The highest number of trematode species was recorded in *G. aculeatus* (i.e., nine species (see Table 1)), which indicates that this fish species plays an important role in transmission of *Diplostomum* and *Apatemon* in Iceland and probably in other sub-Arctic areas (Blasco-Costa *et al.* 2014). In *S. trutta*, five trematode species were recorded, and in

Table 1. List of freshwater trematode species recorded in Iceland between 1956 and 2024 (order of families follows that of Olson *et al.* 2003)

Valid species name	Synonyms	Host (1., 2., D)*	Locality	Reference
Diplostomidae				
Diplostomum baeri Dubois, 1937	–	*Gasterosteus aculeatus* (2.)	Baulárvallavatn; Bretavatn; Heiðarvatn; Mývatn; Þingvallavatn	Karvonen *et al.* (2013); Natsopoulou *et al.* (2012)
Diplostomum spathaceum (Rudolphi, 1819)	–	*Gasterosteus aculeatus*, *Salmo trutta*, *Salvelinus alpinus* (2.)	Baulárvallavatn; Bretavatn; Elliðavatn; Hafravatn; Heiðarvatn; Family Park in Laugardalur, Reykjavík; Nordic House, Vatnsmýri, Reykjavík; Þingvallavatn	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014); Kristmundsson and Richter (2003); Natsopoulou *et al.* (2012); Richter (2003)
Diplostomum rauschi Shigin, 1993	*Diplostomum* sp. Lin. 2I	*Ampullaceana balthica* (1.); *Gasterosteus aculeatus*, *Salmo trutta* (2.)	Hafravatn; Nordic House, Vatnsmýri, Reykjavík; Rauðavatn	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014)
Diplostomum sp. Lin. 3I	–	*Salmo trutta*, *Salvelinus alpinus* (2.)	Hafravatn	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014)
Diplostomum sp. Lin. 4I	–	*Ampullaceana balthica* (1.); *Gasterosteus aculeatus* (2.)	Hafravatn; Nordic House, Vatnsmýri, Reykjavík	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014)
Diplostomum sp. Lin. 5I	–	*Salmo trutta*, *Salvelinus alpinus* (2.)	Hafravatn	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014)
Diplostomum sp. Lin. 6I	–	*Ampullaceana balthica* (1.); *Gasterosteus aculeatus* (2.)	Family Park in Laugardalur, Reykjavík; Nordic House, Vatnsmýri, Reykjavík	Blasco-Costa *et al.* (2014); Faltýnková *et al.* (2014)
Diplostomum spp.*	–	*Anguilla anguilla*, *Gasterosteus aculeatus*, *Salmo trutta*, *Salvelinus alpinus* (2.)	Elliðavatn; Frostastaðavatn; Hafravatn; Heiðarvatn; Mývatn; Steinsmýrarfljót (Þykkvabæjarklaustur); Þingvallavatn; Vífilsstaðavatn (Garðabær); River Ölfusá	Blair (1973); Frandsen *et al.* (1989); Kristmundsson and Helgason (2007); Kristmundsson and Richter (2009); Karvonen *et al.* (2013)
Strigeidae				
Apatemon gracilis (Rudolphi, 1819)	Furcocercaria 2 of Blair (1973)	*Ampullaceana balthica* (1.); *Gasterosteus aculeatus*, *Salmo trutta* (2.)	Elliðavatn; Hafravatn; Heiðarvatn	Blair (1973, 1976); Richter (2003)
Apatemon sp. 6	–	*Gyraulus parvus* (1.)	Mývatn	Faltýnková *et al.* (2023)
Apatemon sp.	*Apatemon* sp.	*Gasterosteus aculeatus*, *Salmo trutta*, *Salvelinus alpinus* (2.)	Baulárvallavatn; Bretavatn; Elliðavatn; Hafravatn; Heiðarvatn; Mývatn; Þingvallavatn	Karvonen *et al.* (2013); Kristmundsson and Richter (2003); Natsopoulou *et al.* (2012)
Australapatemon sp.	Furcocercaria 1 of Blair (1973)	*Ampullaceana balthica* (1.)	Bólstaður (fish farm, near Vík), ditch near Reynir (West of Vík)	Blair (1973)
Cotylurus cornutus (Rudolphi, 1808)	Furcocercaria 3 of Blair (1973)	*Ampullaceana balthica* (1., 2.); *Aythya marila*, *Clangula hyemalis*, *Melanitta nigra* (D)	Bólstaður (fish farm near Vík); Landmannalaugar; Mývatn; ditch near Reynir (West of Vík)	Blair (1973); Brinkmann (1956)
Strigea falconis Szidat, 1928	*Strigea* sp.	*Falco rusticolus* (D)	Vogastapi, Vatnsleysuströnd, Reykjanes; Önundarfjörður, Westfjords	Christensen (2013); Christensen *et al.* (2015); Faltýnková *et al.* (2024)
Schistosomatidae				
Allobilharzia visceralis Kolářová, Rudolfová, Hampl & Skírnisson, 2006	–	*Cygnus cygnus* (D)	Reykjavík, several sites in Iceland	Kolářová *et al.* (2006); Skírnisson and Kolářová (2008)
Dendritobilharzia sp.	–	*Anser anser* (D)	Reykjavík	Skírnisson and Kolářová (2008)
Trichobilharzia anseri Jouet, Kolářová, Patrelle, Ferté & Skírnisson, 2015	schistosome cercaria of Kolářová *et al.* (1999a); *Trichobilharzia* sp. of Kolářová *et al.* (1999b); *Trichobilharzia* sp. II of Skírnisson & Kolářová (2008); *Trichobilharzia* sp. 1 of Aldhoun *et al.* (2009)	*Ampullaceana balthica* (1.); *Anser anser* (D)	Family Park in Laugardalur, Reykjavík; Hrútafjörður; Mýrdalur; Reykhólar; Tjörnin; Reykjavík	Aldhoun *et al.* (2009); Jouet *et al.* (2015); Kolářová *et al.* (1999a, b); Skírnisson and Kolářová (2008)

(*Continued*)

Table 1. (*Continued*)

Valid species name	Synonyms	Host (1., 2., D)*	Locality	Reference
Trichobilharzia franki "*peregra*"	*Trichobilharzia franki* Müller & Kimmig, 1994; *Trichobilharzia* sp. III of Skírnisson & Kolářová (2008)	*Ampullaceana balthica* (1.); *Anas platyrhynchos* (D)	Botnsvatn; Hrísatjörn; Mývatn; Ósland; Rauðavatn; Family Park in Laugardalur, Reykjavík; Víkingavatn; Landmannalaugar	Aldhoun *et al.* (2009); Jouet *et al.* (2010b); Skírnisson and Kolářová (2008)
Trichobilharzia mergi Kolářová, Skírnisson, Ferté & Jouet, 2013	*Trichobilharzia* sp. 2, of Aldhoun *et al.* (2009); *Trichobilharzia* sp. V of Skírnisson & Kolářová (2008)	*Ampullaceana balthica* (1.); *Mergus serrator* (D)	Botnsvatn	Aldhoun *et al.* (2009); Kolářová *et al.* (2013); Skírnisson and Kolářová (2008)
Trichobilharzia regenti Horák, Kolářová & Dvořák, 1998	*Trichobilharzia* sp. I of Skírnisson & Kolářová (2008); *Trichobilharzia* sp. 3 of Aldhoun *et al.* (2009)	*Ampullaceana balthica* (1.); *Anas platyrhynchos*, *Anser anser* (D)	Landmannalaugar; Family Park in Laugardalur, Reykjavík	Aldhoun *et al.* (2009); Jouet *et al.* (2010a); Skírnisson and Kolářová (2008); Skírnisson *et al.* (2012)
A new yet undescribed species and genus	–	*Ampullaceana balthica* (D)	Ósland	Aldhoun *et al.* (2009)
Trichobilharzia sp. IV (visceral)	–	*Mergus serrator* (D)	Botnsvatn	Skírnisson and Kolářová (2008)
Trichobilharzia spp. (visceral and nasal) **	–	*Ampullaceana balthica* (1.); *Anas platyrhynchos*, *Anser anser*, *Cygnus cygnus* (D)	Family Park in Laugardalur, Reykjavík; Tjörnin	Kolářová *et al.* (1999a, 2005)
Notocotylidae				
Notocotylus attenuatus (Rudolphi, 1809)	Monostomes of Blair (1973)	*Ampullaceana balthica* (1., 2.†)	Bólstaður (fish farm, East of Vík); Heiðarvatn; Reynir (West of Vík); ditch near Reynir (West of Vík)	Blair (1973)
Notocotylus imbricatus (Looss, 1893)	*Notocotylus seineti* Fuhrmann, 1919	*Anas platyrhynchos*, *Aythya marila*, *Clangula hyemalis* (D)	Mývatn	Brinkmann (1956)
Catatropis verrucosa (Fröhlich, 1789)	–	*Somateria mollissima* (D)	Skerjafjörður	Skírnisson (2015)
Echinostomatidae				
Echinoparyphium recurvatum (Linstow, 1873)	–	*Ampullaceana balthica* (1., 2.); *Melanitta nigra* (D)	Áshildarholtsvatn; Mývatn; Rauðavatn; ditch near Reynir (West of Vík); Nordic House, Vatnsmýri, Reykjavík	Blair (1973); Brinkmann (1956); Pantoja *et al.* (2021)
Echinoparyphium sp. 2	–	*Physa acuta*	Nordic House, Vatnsmýri, Reykjavík	Pantoja *et al.* (2021)
Echinostoma revolutum (Frölich, 1802)	–	*Ampullaceana balthica* (1.); *Clangula hyemalis*, *Melanitta nigra* (D)	Mývatn; Nordic House, Vatnsmýri, Reykjavík	Brinkmann (1956); Georgieva *et al.* (2013b); Pantoja *et al.* (2021)
Echinostoma sp. IG	–	*Ampullaceana balthica* (1.)	Áshildarholtsvatn; Nordic House, Vatnsmýri, Reykjavík	Georgieva *et al.* (2013b); Pantoja *et al.* (2021)
Hypoderaeum conoideum (Bloch, 1782)	–	*Ampullaceana balthica* (2.)	Ditch near Reynir (West of Vík)	Blair (1973)
Neopetasiger islandicus (Kostadinova & Skírnisson, 2007)	–	*Gyraulus parvus* (1.); *Gasterosteus aculeatus* (2.); *Podiceps auritus* (D)	Áshildarholtsvatn; Mývatn	Georgieva *et al.* (2012); Kostadinova and Skírnisson (2007); Pantoja *et al.* (2021)
Echinostomes of Blair (1973)	–	*Ampullaceana balthica* (1.)	Bólstaður (fish farm, East of Vík)	Blair (1973)
Cyclocoeliidae				
Cyclocoelum mutabile (Zeder, 1800)	–	*Fulica atra* (D)††	Grindavík	Brinkmann (1956)
Gorgoderidae				
Phyllodistomum umblae (Fabricius, 1780)	*Phyllodistomum conostomum* (Olsson, 1876)	*Salmo trutta*, *Salvelinus alpinus* (D)	Elliðavatn; Hafravatn	Faltýnková *et al.* (2020); Kristmundsson and Richter (2009)

(*Continued*)

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Table 1. (*Continued*)

Valid species name	Synonyms	Host (1., 2., D)*	Locality	Reference
Phyllodistomum sp.	–	*Salmo trutta*, *Salvelinus alpinus* (D)	Elliðavatn; Hafravatn	Kristmundsson and Richter (2003)
Allocreadiidae				
Crepidostomum brinkmanni Faltýnková, Pantoja, Skirnisson & Kudlai, 2020	–	*Salmo trutta* (D)	Hafravatn	Faltýnková *et al.* (2020)
Crepidostomum farionis (O.F. Müller, 1780)	–	*Salmo trutta*, *Salvelinus alpinus* (D)	Elliðavatn; Hafravatn; Mjóavatn; Mývatn; Þingvallavatn; Ytra-Hólavatn	Brinkmann (1956); Faltýnková *et al.* (2020); Frandsen (1989); Kristmundsson and Richter (2009)
Crepidostomum pseudofarionis Faltýnková, Pantoja, Skirnisson & Kudlai, 2020	–	*Salvelinus alpinus* (D)	Hafravatn; Þingvallavatn	Faltýnková *et al.* (2020)
Crepidostomum sp.	–	*Salmo trutta*, *Salvelinus alpinus* (D)	Elliðavatn; Hafravatn	Kristmundsson and Richter (2003)
Plagiorchiidae				
Plagiorchis avium (Brinkmann, 1956)	*Paralepidauchen avium* Brinkmann, 1956	*Chroicocephalus ridibundus* (D)	Mývatn	Brinkmann (1956)
Plagiorchis elegans (Rudolphi, 1802)	–	*Vulpes lagopus*, *Falco rusticolus* (D)	Eyjafjörður; not specified	Christensen *et al.* (2015); Clausen and Gudmundsson (1981); Skírnisson *et al.* (1993)
Plagiorchis sp. 1 *sensu* Soldánová *et al.* (2017)	–	*Ampullaceana balthica* (1.)	Family Park in Laugardalur, Reykjavík; Rauðavatn	Kudlai *et al.* (2021)
Plagiorchis sp. 2 *sensu* Soldánová *et al.* (2017)	–	*Ampullaceana balthica* (1.)	Mývatn; Rauðavatn	Kudlai *et al.* (2021)
Plagiorchis sp. 3 *sensu* Soldánová *et al.* (2017)	–	*Ampullaceana balthica* (1.)	Mývatn; Rauðavatn	Kudlai *et al.* (2021)
Plagiorchis sp. 7 *sensu* Soldánová *et al.* (2017)	–	*Ampullaceana balthica* (1.)	Family Park in Laugardalur, Reykjavík	Kudlai *et al.* (2021)
Plagiorchis sp. 8 *sensu* Kudlai *et al.* (2021)	–	*Ampullaceana balthica* (1.)	Nordic House, Vatnsmýri, Reykjavík	Kudlai *et al.* (2021)
Xiphidiocercariae	–	*Ampullaceana balthica* (1.)	Heiðarvatn (near Vík)	Blair (1973)

*abbreviations for hosts: 1. – first intermediate host; 2. – second intermediate host; D – definitive host

**none of the records were identified to species level, and we assume there were more species involved

†empty shells with adolescariae (metacercariae encysted in the environment) were used for experimental obtaining of adults

††*Fulica atra* does not breed in Iceland; via drift migration, non-indigenous birds enter Iceland and might carry parasites with no connections to Iceland

S. alpinus, four. The populations of the mentioned salmonids can be truly landlocked, resident, or anadromous (Brunner *et al.* 2001), and it is likely that migration of the fish might be responsible for spreading of the parasites (i.e., *Crepidostomum* and *Phyllodistomum*). Also, in Hafravatn, it was recorded that *Salmo salar* is entering this lake (Kristmundsson and Richter 2009), which might further contribute to dispersion of trematodes between Iceland and mainland Europe.

Although birds are the group of organisms probably most contributing to the trematode diversity in Iceland, there are fewest records of them as definitive hosts. This can be due to ethical and practical reasons, as it is more difficult to obtain birds for dissections. In Iceland, birds of the Anatidae, Podicipedidae, Laridae, and Rallidae were examined and were found to harbour 16 trematode species. Most records comprise bird schistosomes (Schistosomatidae) because they occur at high prevalences in Icelandic birds (Skírnisson and Kolářová 2008), and researchers focused on this group of trematodes, as they are of medical importance. Judging from the records, the trematode diversity in birds is understudied, and many trematode species found in snails (e.g., *Diplostomum*, *Plagiorchis*) surely could be found in birds as well.

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Sampling locations in Iceland

We found records of 50 locations in Iceland from where material was obtained; they were predominantly lakes, of which most are of volcanic origin, or ponds; to a lesser extent, rivers or small brooks, and areas near the shore, were included (Figure 1). There was likely bias in the selection of sampling locations, as the central part of Iceland is largely covered with glaciers and is poorly accessible. Among the most sampled locations were those in Reykjavík (Nordic House, Vatnsmýri; Family Park in Laugardalur) and lakes in its proximity (Rauðavatn, Hafravatn, Elliðavatn). In SW Iceland, it was Lake Þingvallavatn, the largest lake in Iceland, from where fishes were obtained for ecological studies. In the North, the most sampled lake was Mývatn, which is eutrophic, with thermal vents and a high density of nesting birds (Einarsson 2004). Some of the lakes are connected with the sea and can be entered by anadromous salmonid fishes or catadromous eels (*Anguilla anguilla*), which could be responsible for spreading parasites originating from areas outside Iceland (Faltýnková *et al.* 2020).

In search for causative agents of cercarial dermatitis (bird schistosomes) affecting people bathing in water, a large number of localities were visited to collect snails or birds, the most famous being Landmannalaugar and Botnsvatn (Skírnisson *et al.* 2009). Those surveys extended the number of locations examined for trematodes; however, mostly only bird schistosomes were recorded there. Anyway, in most of the localities (i.e., 34), single trematode species were recorded. Lake Mývatn was identified as a hotspot for trematode diversity, with 13 species recorded. And a total of 10 species were found in each of Nordic House, Vatnsmýri in Reykjavík, and Hafravatn; the first site is a bird reserve, and both sites have been quite intensively sampled. Only a few sampling localities (7) had no trematodes recorded.

Historical accounts of trematode discovery in Iceland

The very first mention of a trematode from Iceland was that of Odhner (1902, 1905), which was a marine record (*Lepidophyllum steenstrupi* Odhner, 1902, from the spotted wolffish, *Anarhichas minor* Olafsen). The first comprehensive parasite study focused on different host groups from Iceland was that of Brinkmann (1956), who examined mammals (2 species), birds (16 spp.), and fishes (18 spp.) from Reykjavík, Neskaupstaður, Lake Mývatn, and Húsavík. Brinkmann (1956) found 24 species of trematodes, of which most were new records for Iceland. Many of the recorded species were marine, and Brinkmann (1956) assumed some to be introduced by migratory birds. Interestingly, Brinkmann (1956) reported that no zoogeographically Arctic group of fishes could

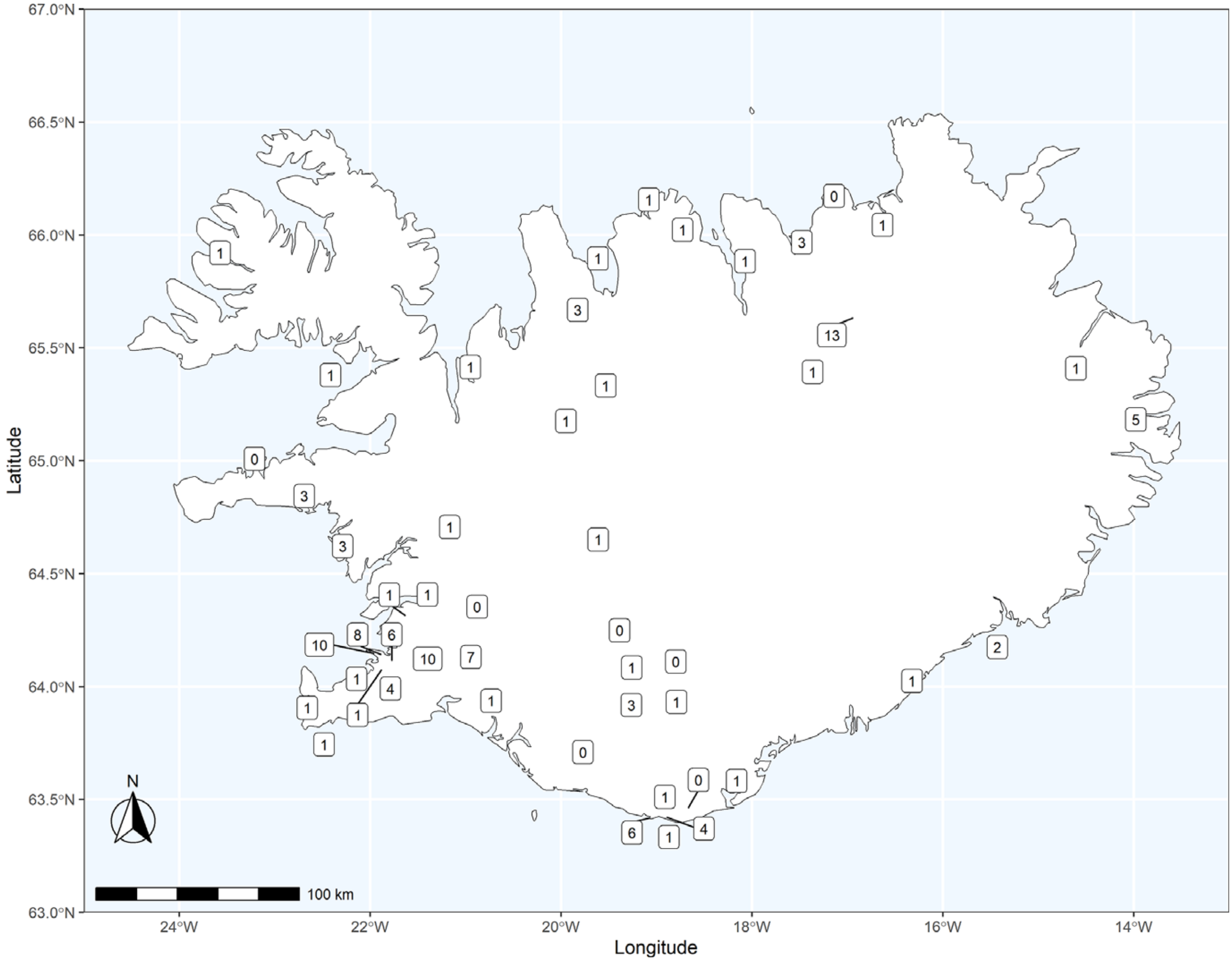

Figure 1. Localities in Iceland where sampling was done. Numbers in squares indicate how many trematode species were recovered; places with no findings are also included.

be distinguished, and consequently, no specifically Arctic trematodes were recovered. His conclusion was that the species were rather boreo-Arctic. The same was stated before by Odhner (1905) for those from the marine environment; both studies revealed a wider distribution of trematodes in the northern regions than previously expected.

The first study on larval trematodes from freshwater snails and fishes in Iceland was conducted by Blair (1973), who, during the Glasgow expedition in 1972, examined *Ampullaceana balthica* (by that time reported as *Lymnaea peregra*), *Galba truncatula*, *Oxyloma elegans groenlandica* (Møller) (= *Succinea groenlandica* Møller) (terrestrial snail of the family Succineidae), and *Gasterosteus aculeatus* from south Iceland. Blair (1973) found a diverse spectrum of strigeid, echinostome, and notocotylid cercariae/metacercariae in *A. balthica* and diplostomid and strigeid metacercariae in *G. aculeatus*. The identity of some of those species was verified experimentally by completing their life cycles (see also Blair 1976, 1977). No digeneans were found in *O. elegans groenlandica* or in *G. truncatula*. Blair (1973) was the first who proved that trematode larval stages are present in intermediate hosts in Iceland and that trematode life cycles are likely to be completed there.

In the following years, the attention of Icelandic researchers was mainly focused on ecology of fish trematodes and their health impact on fish populations of *Salvelinus alpinus*, *Salmo trutta*, and *G. aculeatus* (Frey *et al.* 2022; Karvonen *et al.* 2013; Kristmundsson and Richter 2003, 2009; Natsopoulou *et al.* 2012; Richter 1982, 2003). Frandsen *et al.* (1989) examined the degree of parasitism in different fish morphs of *S. alpinus* in Þingvallavatn and found an ecological segregation affecting the parasite transmission pathways. Parasites of European eels were examined by Kristmundsson and Helgason (2007), who discovered a species-poor freshwater parasite fauna compared to other parts of Europe, and *Diplostomum* spp. were the most prevalent helminth species.

Since the 1990s, most trematode research was directed on bird schistosomes (family Schistosomatidae), which cause cercarial dermatitis, an inflammatory reaction of the skin in humans (Horák *et al.* 2002). A massive outbreak of this serious rash was recorded in a recreational area in Reykjavík from 1995 to 1997 (Skírnisson *et al.* 1999, Skírnisson and Kolářová 2002, 2009; Kolářová *et al.* 1999a). Since then, bird schistosomes have been the best documented group in Iceland in the attempt to identify their species and to study their life cycles, biology, and distribution.

With the advance of molecular genetic methods, since 2006 in Iceland, an unexpected diversity of trematode species was discovered and characterised both genetically and morphologically. This led to descriptions of new species and the discovery of a wealth of previously cryptic species with unexpected connections to other regions in Europe and North America. Mainly species of the groups Diplostomidae, Strigeidae, Schistosomatidae, Echinostomatidae, Plagiorchiidae, Allocreadiidae, and Gorgoderidae were recorded, which are detailed below.

Bird schistosomes and cercarial dermatitis (Schistosomatidae)

Bird schistosomes are cosmopolitan trematodes parasitising aquatic birds and using mostly pulmonate snails as intermediate hosts in a two-host life cycle (Horák *et al.* 2002). In Iceland, the occurrence of cercarial dermatitis in humans caused by bird schistosomes can be traced back to 1925. At that time in Sýkið, a geothermally heated shallow pond in the vicinity of Deildartunguhver, and the largest thermal spring in Iceland, a skin rash was observed on wading children (see Skírnisson *et al.* 2009). The first scientifically documented record of the causative agent of cercarial dermatitis, the cercaria, is that of Kolářová *et al.* (1999a). The cercariae were obtained from snails (*Ampullaceana balthica*) in a recreation area in Reykjavík (pond in Family Park in Laugardalur), where in summer of 1995–1997, a skin rash was documented in children wading in the pond (Kolářová *et al.* 1999a, b; Skírnisson and Kolářová 2002). The authors described the cercariae morphologically (*Cercaria* sp.) and showed that they probably belong to the genus *Trichobilharzia*. However, they were not successful in obtaining adults experimentally, which at that time was the only way to identify the species; and no DNA sequences could be obtained.

Further cases of cercarial dermatitis were recorded in geothermally heated water bodies, which attract people for bathing, and where snails and birds necessary for completion of the life cycle were present. A severe outbreak of cercarial dermatitis was documented in Landmannalaugar (Skírnisson and Kolářová 2005; Skírnisson *et al.* 2009), which is a famous geothermally heated bathing site. Infected *A. balthica* and mallards (*Anas platyrhynchos* L.) were recovered at that site even in winter months; after finding the causative agents, the presence of cercariae in snails could be eliminated by preventing the birds from breeding at that site (Skírnisson *et al.* 2009). Another lake was Botnsvatn, from where two species of the genus *Trichobilharzia* were documented (see Table 1) and where one of the highest prevalences of bird schistosomes in *A. balthica* was found (Skírnisson and Kolářová 2008; Skírnisson *et al.* 2009).

Since the first case in Family Park, several studies followed which aimed to identify the causative agents of cercarial dermatitis and to assess its prevalence, therefore, freshwater snails and aquatic birds have been screened intensively (see Kolářová and Skírnisson 2000; Kolářová *et al.* 1999b; Kolářová *et al.* 2005; Skírnisson and Kolářová 2002, 2004). The methodology used to collect and examine snails and aquatic birds has been summarised by Kolářová *et al.* (2010). Waterfowl (*A. platyrhynchos*, *Anser anser* (L.) and *Cygnus cygnus* (L.)) were found infected with nasal and visceral species of bird schistosomes, whereas the examined specimens of *Anas penelope* (L.), *Bucephala islandica* (Gmelin), *Mergus serrator* L., and *Somateria mollissima* (L.) were free of infection (Kolářová *et al.* 2005). In 2006, the first study focused on Icelandic samples was published using integrative taxonomic methods (phylogenetic analyses of DNA sequence data in combination with morphology), and a new species and genus of bird schistosomes, *Allobilharzia visceralis*, was described by Kolářová *et al.* (2006) from whooper swans (*C. cygnus*). To identify the material of bird schistosomes found in 2002–2007 from *A. balthica* and anseriform birds, Aldhoun *et al.* (2009) analysed the samples using molecular genetic methods (based on the entire 18S-ITS1-5.8S-ITS2-28S sequence) and could distinguish five species/lineages of two different genera, of which some were identical to species found in mainland Europe. Skírnisson and Kolářová (2008) examined the morphology and dimensions of eggs of bird schistosomes and could distinguish seven species occurring in Iceland. A considerable number were classified provisionally, and only in recent times, some could be assigned to species via integrative analyses using various molecular markers in combination with morphology. Among them was the nasal species, *Trichobilharzia regenti*, which was proved as common in Iceland, and Jouet *et al.* (2010a) and Skírnisson *et al.* (2012) improved the knowledge of its morphological variation and host use by providing molecular and morphological data obtained from wildlife, as the species was originally only described from limited experimental material of adults in the Czech Republic (Horák *et al.* 1998).

Jouet *et al.* (2010b) attempted to clarify the status of *T. franki* and its haplotypes, which turned out to comprise two clades using two different snail species as intermediate hosts. The outcome was that *T. franki* using *Radix auricularia* (L.) is distributed in mainland Europe and corresponds to the original species described by Müller and Kiming (1994), whereas a different species (tentatively named *T. franki* "*peregra*" by Jouet *et al.* 2010b) using *A. balthica* is present in Europe and Iceland, and its status has yet to be clarified. Kolářová *et al.* (2013) described a new species, *T. mergi*, from *Mergus serrator* from Botnsvatn corresponding to the material of small eggs (*Trichobilharzia* sp. V) isolated by Skírnisson and Kolářová (2008) (Table 1); via DNA matching of cercariae, they revealed that the intermediate host was *A. balthica.* It was shown that the life cycle is being completed in Lake Botnsvatn, as both adults and cercariae originated from host samples collected at this lake. Since *M. serrator* is a migratory species, it is expected that *T. mergi* might have a Holarctic distribution; so far, it was reported from France and Belarus (Kolářová *et al.* 2013). Jouet *et al.* (2015) described *T. anseri* from *A. anser* in Family Park, Laugardalur in Reykjavík; the species is identical to that first documented by Kolářová *et al.* (1999a) as the causative agent of cercarial dermatitis, and to the material of eggs (*Trichobilharzia* sp. II) isolated from *A. anser* by Skírnisson and Kolářová (2008). *Trichobilharzia anseri* was also recorded from France (Jouet *et al.* 2015) (see Figure 2).

There is a considerable species diversity of bird schistosomes documented in Iceland, despite the fact that only one snail species (*A. balthica*) was recorded as the first intermediate host (Aldhoun *et al.* 2009). So far, eight species of three genera (*Allobilharzia*, *Dendritobilharzia*, and *Trichobilharzia*) of bird schistosomes have been reported (see Table 1), with at least one species of *Trichobilharzia* still to be formally described and one species probably belonging to a new genus (Aldhoun *et al.* 2009; Skírnisson 2010). Anseriform birds serve as definitive hosts, including three species which overwinter in Iceland (*A. platyrhynchos*, *A. anser*, and *M. serrator*), and *C. cygnus* which leaves Iceland for wintering grounds on the British Isles or western Norway (Skírnisson and Kolářová 2008; Skírnisson *et al.* 2009). This indicates that the life cycles of most of the bird schistosomes are being completed in Iceland, except for *A. visceralis*, which was only found in adult whooper swans after their arrival from wintering grounds outside Iceland (Skírnisson *et al.* 2009). Meanwhile, *A. visceralis* has been reported from North America ex *Cygnus columbianus* (Ord) and from Japan ex *C. cygnus* (Brant 2007; Hayashi *et al.* 2017). Swans have a Holarctic circumpolar distribution and could overlap in their breeding range, which might explain the geographical distribution of *A. visceralis* (Brant 2007) (see Figure 2). However, its intermediate snail host is still unknown; Brant (2007) assumed that it could be a brackish or marine snail from habitats where swans feed.

Trematode fauna of fish (Allocreadiidae, Gorgoderidae)

There is a long tradition of fish monitoring in Iceland (Petersen 2003), and thus, their parasite fauna has been studied to assess their health status since fishes are of substantial importance in ecosystems and are vital natural resources. Records of adult trematodes from freshwater fishes in Iceland range from 1956 to 2020, and four species of the family Allocreadiidae and Gorgoderidae have been discovered in *Salvelinus alpinus* and *Salmo trutta*, whereas no adult trematodes were found in *Gasterosteus aculeatus* and *Anguilla anguilla* (see also Table 1). Brinkmann (1956) recorded *Crepidostomum farionis* from *S. alpinus* and *S. trutta* and differentiated the species from *C. suecicum* Nybelin, 1933 (now a synonym of *C. metoecus* (Braun, 1900)), to which he considered the species most similar and provided a drawing but no thorough description. Richter (1982) briefly disclosed that adults of *C. farionis* and *Phyllodistomum conostomum* (Olsson, 1876) (a synonym of *P. umblae*) occur in Icelandic fishes. Further studies pursued ecological aspects of fish infection, but no taxonomic questions. Frandsen *et al.* (1989) examined the parasite burden in different ecological morphs of *S. alpinus* in Lake Þingvallavatn and found *C. farionis* in benthivorous fish morphs, which corresponds to the habitat of its intermediate hosts (clams, amphipods, ephemeropterans, which live in shallow littoral zones). Another brief review by Kristmundsson and Richter (2003) reported on the occurrence of *Crepidostomum* sp. and *Phyllodistomum* sp. in Arctic charr, however, with no specific identification. A detailed survey of the parasite fauna of the resident Arctic charr and brown trout was undertaken by Kristmundsson and Richter (2009) who reported *C. farionis* as a common parasite in both fish species, while *P. umblae* was more prevalent in *S. alpinus*; intermediate hosts for these species have not yet been documented in Iceland.

By the use of integrative taxonomy, Faltýnková *et al.* (2020) identified four species of trematodes in freshwater fishes in Iceland, the already known *C. farionis* and *P. umblae*, and two more species of *Crepidostomum*: *C. brinkmanni* and *C. pseudofarionis* (see also Table 1). The two latter species are morphologically highly similar to their genetically closest species (*C. metoecus* and *C. oschmarini* Zhokhov & Pugacheva, 1998; and *C. farionis*, respectively). Therefore, the use of integrative taxonomy is required in future studies, as species of both *Crepidostomum* and *Phyllodistomum* possess too few distinguishing morphological features and high plasticity of

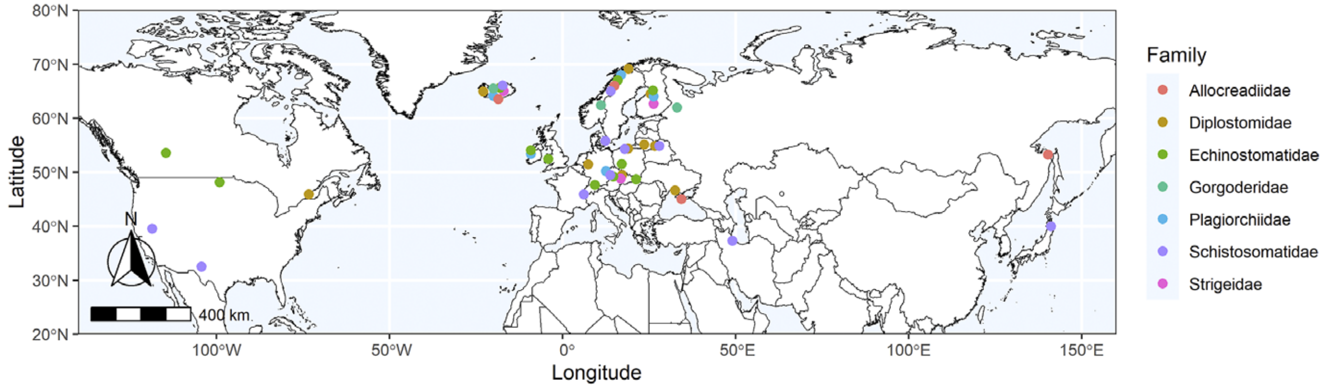

Figure 2. Selected trematode families and their distribution in Iceland and other countries. Only records confirmed by DNA sequence data are included.

characters. Moreover, for correct assessment of the distributional range and host specificity of these species, more material processed by an integrative taxonomic approach from different geographical areas, including North America, is still needed.

Interestingly, prior to their formal species description, *C. brinkmanni* and *C. pseudofarionis* had their life cycles deciphered molecularly by Soldánová *et al.* (2017) and Petkevičiūtė *et al.* (2018) in Norway. Both *C. brinkmanni* and *C. pseudofarionis* have a three-host life cycle involving clams of the genera *Sphaerium* and *Pisidium* as first intermediate hosts and mayflies (Ephemeroptera) and stoneflies (Plecoptera) as second intermediate hosts (Kristmundsson and Richter 2009). The life cycle of *P. umblae* was molecularly characterised by Petkevičiūtė *et al.* (2015) using material from Norway (cystocercous cercariae from *Euglesa parvula* (Westerlund) (=*Pisidium hibernicum* Westerlund) and *Sphaerium corneum* (L.); adults from *Thymalus thymallus* (L.) and *Coregonus albula* (L.)). From the common occurrence of *Crepidostomum* spp. and *P. umblae* in fishes in Iceland, we infer that their life cycles are completed there, as sphaeriid clams (*Pisidium*, first intermediate hosts) and mayflies, stoneflies, and crustaceans (second intermediate hosts) are present in Icelandic lakes, although their species diversity is much lower than in Europe (Kristmundsson and Richter 2009; Lindegaard 1979).

It is confirmed now by molecular genetic methods that *Crepidostomum* spp. and *P. umblae* have been found outside Iceland; that is, *C. brinkmanni*, *C. farionis*, and *C. pseudofarionis* were recorded in Norway by Soldánová *et al.* (2017) and Petkevičiūtė *et al.* (2018), and *C. brinkmanni* was found by Petkevičiūtė *et al.* (2018) in Ukraine. *Crepidostomum farionis* was found in the Russian Far East by Atopkin and Shedko (2014) (see Figure 2). The connection of Iceland with mainland Europe might be explained by the fact that Lake Hafravatn, from where the Icelandic material was recovered, is connected to the sea, and andromous Atlantic salmon, *Salmo salar*, which might carry infections of *Crepidostomum* or *Phyllodistomum* (Kennedy 1974), enter the lake (Kristmundsson and Richter 2009). Another way of dispersion could be via sphaeriid clams which have a high capacity for dispersion by migratory birds (Clewing *et al.* 2013; Figuerola and Green 2002). However, further sampling from a wider geographical scale is necessary to explain the distributional patterns of species of both *Crepidostomum* and *Phyllodistomum.*

Diplostomidae

Before the start of the molecular era, in Iceland, trematodes of the family Diplostomidae have been recorded frequently as metacercariae from the eyes of fishes (*Anguilla anguilla*, *Gasterosteus aculeatus*, *Salmo trutta*, and *Salvelinus alpinus*). At that time, reliable species identification was difficult, as metacercariae exhibit too few features suitable for identification. Therefore, the recovered metacercariae were mostly recorded as *Diplostomum spathaceum* or *Diplostomum* sp. by Frandsen *et al.* (1989), Kristmundsson and Richter (2003, 2009), and Richter (2003). Natsopoulou *et al.* (2012) reported *D. baeri* and *D. spathaceum* from *G. aculeatus.* The authors differentiated the site in the eye of the metacercariae; thus, Blair (1973) specified that he found *Diplostomum* in the eye lens, in the retina, and in the brain of *G. aculeatus* from different sampling places. Frandsen *et al.* (1989) noted that they found all metacercariae in the vitreous humour of the eyes of Arctic charr, whereas Karvonen *et al.* (2013) identified the species recovered from the eye humour as *D. baeri* and those from the eye lens as *Diplostomum* spp.

Frandsen *et al.* (1989) and Kristmundsson and Helgason (2007) reported *Diplostomum* sp. as the most prevalent of the helminths they recovered from fishes. Also, Kristmundsson and Richter (2009) reported a high prevalence of *Diplostomum* sp., with the intensity being higher in Arctic charr than in brown trout. However, since probably more species of *Diplostomum* were involved in those records (metacercariae tend to accumulate in their second intermediate hosts), the prevalence might have appeared higher than for single species.

More realistic estimates of the species diversity of *Diplostomum* in Iceland were provided by Blasco-Costa *et al.* (2014) and Faltýnková *et al.* (2014), who found a surprisingly high species richness within the genus *Diplostomum* in *Ampullaceana balthica*, Arctic charr, brown trout, and three-spined stickleback. In their complex analyses of the isolates of cercariae and metacercariae, integrating molecular, morphological, and ecological data, the authors revealed that there were *D. spathaceum* and five putative new species/lineages of *Diplostomum* present in Iceland (see Table 1). This diversity even exceeded that in central Europe reported by Georgieva *et al.* (2013a), who found fewer species in corresponding fish hosts (see Blasco-Costa *et al.* 2014). Except for *D. spathaceum*, all species/lineages were unknown to science, and despite the thorough molecular and morphological characterisation of their larval stages, they are awaiting formal description by matching with adults via molecular genetic analyses. Recently, Achatz *et al.* (2022) could match the Icelandic *Diplostomum* sp. Lin2I with *D. rauschi* from their material of adults from *Chroicocephalus genei* (Breme) and *Hydroprogne caspia* (Pallas) in Ukraine. However, so far, no adult diplostomids have been recorded from Iceland. The Icelandic species/lineages of *Diplostomum* corresponded to those from snails and fish in Finland, Germany, Lithuania, and Norway recorded by Behrmann-Godel (2013), Georgieva *et al.* (2013a), Soldánová *et al.* (2017), and Kudlai *et al.* (2024), and to those from Canada recovered by Galazzo *et al.* (2002) and Locke *et al.* (2010a, b) (see Figure 2).

Blasco-Costa *et al.* (2014) and Faltýnková *et al.* (2014) with their analytical approaches have set a solid framework for assessing the diversity and transmission patterns of *Diplostomum* spp. in high latitudes. They provided well-characterised and genetically distinct lineages linked to their morphological and ecological features (differing in size, microhabitat in eye, and host use), and thus, they aid to some degree identification based on microhabitat in fish eye. This highlights the importance to process diplostomid metacercariae in a live state from fresh fishes and to precisely record their site of infection in the eye (Faltýnková *et al.* 2022), a character already noticed by authors in the past (see above).

All of the *Diplostomum* spp. occurred at high prevalence and infection intensity in fishes, and those found as cercariae were all recovered in a single snail species, *A. balthica.* From the high prevalence and continuous occurrence in both snails and fishes throughout the years of sampling, it can be inferred that all species are completing their life cycles within Iceland.

Echinostomatidae

The first record of echinostomes was that of Brinkmann (1956), who reported *Echinostoma revolutum* and *Echinoparyphium recurvatum* in anatid birds from Lake Mývatn (see Table 1). Later, Blair (1973) recorded *E. recurvatum* and *Hypoderaeum conoideum* as metacercariae in *Ampullaceana balthica* from south Iceland, which he verified by experimental completion of their life cycles; also, he found echinostome cercariae in *A. balthica* which remained unidentified.

Much later, *Neopetasiger islandicus*, the first echinostome species described as new from the territory of Iceland by Kostadinova and Skírnisson (2007), was found in the grebe species, *Podiceps auritus* (L.), from Lake Mývatn. By that time, it was assumed that the occurrence of *N. islandicus* was restricted to the Icelandic population of *P. auritus* which was geographically isolated from those in North America (Boulet *et al.* 2005). The life cycle of *N. islandicus* was elucidated by Georgieva *et al.* (2012) using integrative taxonomy, and the life-cycle stages were matched via DNA sequence data.

Two cryptic species of the '*revolutum*' complex, *E. revolutum sensu stricto* and another species yet to be formally described, *Echinostoma* sp. IG, have been characterised via integrative taxonomy by Georgieva *et al.* (2013b) based on material from snails in Iceland and Germany. *Echinostoma revolutum s. str.* is well known from mainland Europe, where it occurs in *Lymnaea stagnalis* (L.), but also in other lymnaeid snails, thus having the widest first intermediate host range among the '*revolutum*' complex (Faltýnková *et al.* 2007; Georgieva *et al.* 2014). Georgieva *et al.* (2013b) proved that samples from North America, previously identified as *E. revolutum* by Detwiler *et al.* (2010), represent another cryptic species of the '*revolutum*' group, thus indicating that the supposed cosmopolitan distribution of '*E. revolutum*' might be a result of cryptic variation (Georgieva *et al.* 2013b).

To further contribute to the resolution of echinostome species diversity, Pantoja *et al.* (2021) examined freshwater snails in Iceland and in other northern regions in Europe and North America (Alaska). In Iceland, almost the same species spectrum as in the past was recorded, with one additional species not found before, *Echinoparyphium* sp. 2. ex *Physa acuta*, which was identical to an isolate from *Physa gyrina* Say in Alberta, Canada of Gordy and Hannington (2019). As echinostome cercariae have been found repeatedly in the lakes over the years, it can be assumed that their life cycles are well established in Iceland (Georgieva *et al.* 2012; Pantoja *et al.* 2021). Since Iceland lies on the East Atlantic flyway and is a nesting place for birds overwintering in Britain, Ireland, Norway, Netherlands, and other regions, it is unsurprising that the trematode species are shared with mainland Europe. On the other side, *N. islandicus* and *Echinoparyphium* sp. 2, using snails introduced from North America, might be of American origin.

Still, a more extensive assessment of the snail host-range of echinostomes via integrative taxonomy is needed and will possibly lead to more discoveries of trematode specificity and transmission pathways, further helping to reveal ecological patterns in these host-parasite interactions (Pantoja *et al.* 2021). Because of substantial interspecific homogeneity of morphological features of the life-cycle stages of the echinostomes, considerable taxonomic expertise is needed to distinguish the species morphologically, therefore, it is necessary to combine morphology with molecular genetic analyses for reliable identification (Faltýnková *et al.* 2015; Georgieva *et al.* 2014).

Plagiorchiidae

In Iceland, there have been scarce records of the Plagiorchiidae. Brinkmann (1956) found a plagiorchiid in the gull, *Chroicocephalus ridibundus* (L.), from Lake Mývatn and described it as new under the name *Paralepidauchen avium*, now a synonym of *Plagiorchis avium*. However, no further records of this species are known. From gyrfalcons (*Falco rusticolus* L.), *Plagiorchis elegans* was reported by Clausen and Gudmundsson (1981), Christensen (2013) and Christensen *et al.* (2015). The latter authors assumed that the infection with *P. elegans* could be postcyclic (i.e., that the gyrfalcons got infected by adult worms from their prey). This is more likely, as gyrfalcons prey upon birds and mammals (definitive hosts of *Plagiorchis* spp.), and plagiorchiids use small aquatic invertebrates as intermediate hosts (Krasnolobova 1987) which are an unlikely diet of gyrfalcons. Skírnisson *et al.* (1993) recorded *P. elegans* from the Arctic fox in a coastal area in northern Iceland. They assumed that the foxes could get infected from freshwater sources by ingesting aquatic invertebrates (e.g., snails) hosting plagiorchiid metacercariae; another option could be postcyclic infection as in gyrfalcons. Both options are possible, as Arctic foxes have a varied diet including invertebrates (molluscs, crustaceans, insects, echinoderms), birds, and mammals (Hersteinsson and MacDonald 1996).

A much greater diversity of *Plagiorchis* was found with the use of molecular genetic methods combined with morphology when examining snail first intermediate hosts. In *Ampullaceana balthica*, Kudlai *et al.* (2021) found five species of *Plagiorchis* new to Iceland, including one new to science (see Table 1). Interestingly, the recovered species are not unique to Iceland; four of them were reported before from Norway by Soldánová *et al.* (2017), and Kudlai *et al.* (2021) found that they occur also in Finland and Ireland (see Figure 2). Recently, two of those species were recorded in central Europe by Kundid *et al.* (2024). From the quite high prevalence (up to 70% in *A. balthica*, although variable between sampling sites; see Kudlai *et al.* 2021) over consecutive years and seasonal occurrence of *Plagiorchis* spp., it is obvious that their life cycles are being completed in Iceland. All recovered *Plagiorchis* spp. are using one single snail species, *A. balthica*, as the first and second intermediate host in Iceland. However, some species showed a wider host spectrum in mainland Europe – for example, *Plagiorchis* sp. 7 *sensu* Soldánová *et al.* (2017) was found also in *Myxas glutinosa* (O. F. Müller) in Finland.

No overlap in spatial distribution of species of *Plagiorchis* was noticed between Europe and North America; the records rather reflect a connection between Iceland, Norway, Ireland, and the British Isles within the East Atlantic bird flyway (Cramp and Simmons 1983; Kudlai *et al.* 2021). For *P. elegans*, which was reported before from North America (e.g., Rausch *et al.* 1990), Kudlai *et al.* (2021) found no match of their *cox*1 sequences to those from North America of Moszczynska *et al.* (2009), Rudko *et al.* (2018), and Gordy and Hannington (2019), indicating that this species is most probably restricted to the Palaearctic. *Plagiorchis elegans* was not found in snails in Iceland but was recorded in continental Europe in *Lymnaea stagnalis* (see Kudlai *et al.* 2021; Kundid *et al.* 2024). Thus, *P. elegans* might not complete its life cycle in Iceland, and the foxes and gyrfalcons (see above) could possibly have acquired their infections from migratory birds which got infected in mainland Europe. We cannot exclude that some of the species found by Kudlai *et al.* (2021) might represent *P. avium*, recorded before by Brinkmann (1956) (see above). However, further trematode sampling would be appropriate (including other hosts than snails) to assess the species diversity of *Plagiorchis* in Iceland at a finer scale.

Plagiorchiids are highly adaptable, with adults of low host specificity and a three-host life cycle involving a wide spectrum of second intermediate hosts (aquatic insects and their larvae, crustaceans, molluscs), thus being able to infect a wide spectrum of definitive hosts (birds, bats, and other insectivore mammals) (Krasnolobova 1987; Tkach *et al.* 2000). The recovered species are highly uniform in their morphology, and despite some variability within each species, identification based on morphology is highly unreliable; therefore, DNA sequence data are required to confirm the species identity.

Kundid *et al.* (2024), who investigated the species diversity of *Plagiorchis* in central Europe, found out that so far, the highest species diversity of this genus was recorded in northern Europe. However, in central and more southern Europe, data on trematodes are missing or are not supported by molecular genetic data. Therefore, sampling in more southern regions of Europe is necessary to assess the trematode diversity in lymnaeid snails to find out if the diversity of *Plagiorchis* spp. is specific to regions in the sub-Arctic or not.

Strigeidae

Adult strigeids of *Cotylurus cornutus* were recorded in anatid birds by Brinkmann (1956) from Lake Mývatn. Larval stages (cercariae and metacercariae) were found by Blair (1973) in *Ampullaceana balthica* and *Gasterosteus aculeatus* in southern Iceland (see Table 1). Blair (1973) verified the identity of his records by experimental completion of the trematode life cycles (i.e., he obtained adults with characters sufficient for identification, a time-costly task requiring meticulous work). In this way, Blair (1973) could identify cercariae and metacercariae of *Apatemon gracilis* and *C. cornutus.*

In surveys of fish parasites and investigations on their impact on fish health, strigeid metacercariae identified either as *A. gracilis* or *Apatemon* sp. have been recorded in *Anguilla anguilla*, *Gasterosteus aculeatus*, *Salmo trutta*, and *Salvelinus alpinus* by Richter (1982, 2003), Natsopoulou *et al.* (2012), Kristmundsson and Richter (2003, 2009), Karvonen *et al.* (2013), and Sæmundsdóttir (2023). Apart from *A. gracilis*, another species of *Apatemon*, *Apatemon* sp. 6 was found in planorbid snails of *Gyraulus parvus* by Faltýnková *et al.* (2023). The cercariae of *Apatemon* sp. 6 exhibited prey-mimetism (i.e., a morphological and behavioural adaptation to enhance transmission to the next intermediate fish host by mimicking its prey). The strong morphological adaptation of the cercariae precluded certain identification in the past, but with molecular genetic methods, it was found with certainty that this species belongs to the strigeid genus *Apatemon.*

The attention of Icelandic authors had been turned on the parasite fauna of gyrfalcons (*Falco rusticolus*), protected birds of prey, to examine their health state, and a trematode-poor fauna was recorded (Clausen and Gudmundsson 1981). Christensen (2013) and Christensen *et al.* (2015) carried out a large-scale survey of Icelandic gyrfalcons and found few marine species, and several specimens of *Strigea* sp., which by that time could not be further identified.

The identity of *Strigea* sp. found by Christensen (2013) and Christensen *et al.* (2015) was solved recently by integrative taxonomic methods when Faltýnková *et al.* (2024) obtained DNA sequence data linked to morphology and confirmed the species identity as *Strigea falconis.* Iceland is most probably the northernmost distributional range of *S. falconis*, which is a common parasite of birds of prey and is widely distributed in the Holarctic (Dubois 1968; Faltýnková *et al.* 2024; Heneberg *et al.* 2018). However, the occurrence of *S. falconis* in Iceland is surprising, as the gyrfalcon population is not leaving the territory of Iceland, and there are no second and third intermediate hosts (tadpoles, frogs, or reptiles) present to ensure completion of the trematode life cycle. The only plausible answer to this paradox is the annual presence of migratory birds potentially carrying metacercariae of *S. falconis* acquired in more southern regions of Europe (see Faltýnková *et al.* 2024). The record shows the versatility of this trematode with a complex four-host life cycle, with probably paratenic bird hosts included. However, it also points at Iceland as a dead-end locality for *S. falconis.* Moreover, gyrfalcons do not seem to be suitable hosts for trematodes because of their restricted range (Arctic, sub-Arctic) and their main diet being rock ptarmigan (*Lagopus muta* (Montin)), which is not a permissive host for trematodes (Christensen *et al.* 2015; Faltýnková *et al.* 2024).

So far, of the family Strigeidae, only for *S. falconis* and *Apatemon* sp. 6 DNA sequence data were provided which could be linked to morphological descriptions. Although *A. gracilis* seems to be a common species in Iceland, a precise identification based on integrative taxonomic methods is still pending. An exact delimitation is needed, as *A. gracilis* exhibits a high morphological variability and has a wide distributional range, which led to the dispute whether it consists of numerous subspecies or it is a cosmopolitan species with a polytypic morphology and a wide host range (Beverley-Burton 1961; Dubois 1968). Also, for species of the genera *Australapatemon* and *Cotylurus*, molecular genetic data are lacking, indicating that the species diversity of strigeids is not yet fully discovered.

Life cycles of trematodes in Iceland

The life cycles of trematodes are complex, typically involving sequential use of several hosts (vertebrate and invertebrate) linked together mostly by trophic interactions; due to this, trematode diversity and abundance observed in an ecosystem are inherently linked to host diversity and abundance and reflect the dynamics of the trophic interactions of the hosts (Hechinger and Lafferty 2005). From the data obtained in Iceland by, e.g. Kolářová *et al.* (2013), Blasco-Costa *et al.* (2014), Kudlai *et al.* (2021), or Pantoja *et al.* (2021), it is obvious that trematodes can complete their life cycles in freshwater ecosystems in the sub-Arctic. From our data, we have evidence that larval stages do overwinter in snails in Iceland, as there are infections found in snails in June, which is the start of the season, and before this, the water is not warm enough to ensure sufficient parasite development within snails.

Trematodes are highly adaptable, and despite the life-cycle bottleneck (i.e., low host diversity as outlined by Blasco-Costa *et al.* (2014)), they are abundant in Iceland. It can be inferred that this substantial trematode diversity is sustained by the definitive bird hosts. Iceland is an important nesting place for aquatic birds, which occur at high density during summer (Jóhannesdóttir *et al.* 2014; Wetlands International 2006), thus enhancing trematode transmission. Many of those birds are migratory, wintering in Norway, British Isles, Ireland, or France (Cramp and Simmons 1983), and this is reflected in the occurrence of conspecific trematode species (*Diplostomum*, *Plagiorchis*, and *Trichobilharzia*) in these countries (Jouet *et al.* 2010b; Kudlai *et al.* 2021; Pantoja *et al.* 2021; Soldánová *et al.* 2017) (see Figure 2). An interesting phenomenon is the use of predominantly one snail species, *Ampullaceana balthica*, as the first intermediate host by diverse trematode species. In other sub-Arctic regions in Canada and Norway, the same pattern of host use and higher-than-expected trematode species diversity was discovered by Gordy and Hanington (2019) and Soldánová *et al.* (2017).

In the sub-Arctic freshwater ecosystems, there is a high annual cyclicity of processes, and the free-living fauna are adapted to this by high food consumption and rapid conversion to storage of lipids during summer (Wrona and Reist 2013). We infer that in Iceland, trematodes are following this pattern, which manifests in intense growth and replication of larval trematode stages in snails during the summer season to match the high abundance of bird hosts, which lasts for a short time. We observed a high prevalence of trematode larval stages in *A. balthica*, reaching up to 70–80% in August; also, many double infections occur (our data, not shown). In *Plagiorchis* spp. we noted a tendency to abbreviate the life cycle (i.e., cercariae transform to metacercariae directly in sporocysts, while some cercariae still emerge from the snails). This could be an adaptation to the ephemeral presence of migratory birds stopping for a short time in some of the Icelandic lakes, or it could be an adaptation to a lower diversity/availability of invertebrates other than snails used as second intermediate hosts (Galaktionov and Blasco-Costa 2018; Kudlai *et al.* 2021).

However, there are records of trematodes from migratory birds where it is clear they do not circulate in Iceland as is the case of *Allobilharzia visceralis* (Kolářová *et al.* 2006). Also, some species, though recorded in Iceland, as is the case of *Strigea falconis*, cannot complete their life cycles because of the absence of intermediate hosts (see Faltýnková *et al.* 2024).

Conclusions

Knowledge on trematode parasites in Iceland has largely benefited from integrative taxonomic methods, and since 2006, there has been a history of intense biodiversity discoveries of freshwater trematodes. The majority of digeneans, 28 species out of 41 recorded, has been assessed using this approach. A surprising diversity has been discovered, comprising species particularly of the families Allocreadiidae, Diplostomidae, Echinostomatidae, Gorgoderidae, Plagiorchiidae, and Schistosomatidae. A total of six species were described as new from the territory of Iceland, and 14 lineages/putative new species are awaiting description/linking to known species. Still, the trematode diversity is lower than in mainland Europe, a pattern that complies with the island biogeography theory, where the number of species on islands decreases with increasing distance from mainland (Gíslason 2005, 2021; MacArthur and Wilson 1967).

Most records comprise trematodes using birds as definitive hosts. We assume this is because birds are the most abundant, species-rich, and vagile vertebrates in Iceland. We infer that the trematode species spectrum in Iceland has been mainly influenced by introductions via migratory birds (predominantly of European origin), and although some bird populations are sedentary, we assume that there is an ongoing circulation of trematodes between nesting and wintering places (see also Figure 2). This assumption is further supported by the fact that none of the trematode species recorded are endemic to Iceland; on the contrary, they are mostly generalists with a wide distributional range. This pattern again conforms with the island biogeography theory, but it also might indicate that Iceland was more likely colonised in post-glacial time during the Holarctic, as there are neither any free-living animals truly endemic to Iceland (Gíslason 2005). Moreover, the trematode fauna is mainly Palaearctic with few species (*Neopetasiger islandicus*, *Echinoparyphium* sp. 2) that might be considered North American. This is in accordance with the freshwater free-living fauna, which is also Palaearctic and predominantly boreal, related to the fauna in Great Britain and Norway (Gíslason 2005). On the contrary, the pre-ice age fauna was considered to be more similar to the North American fauna (Gíslason 2005).

When we return to Blair's (1973) question of whether trematode life cycles can be completed in Iceland, we can answer that now we know that many of them can, and that the trematode species spectrum is quite diverse. However, we have no answer to the question of whether this diversity might be due to a northward shift of originally more southern species, which could create temporarily higher parasite diversity (see Jeppesen *et al.* 2010; Parmesan and Yohe 2003). To answer this, we do not have enough data from the past (or only from a very short past), but surely it is of value to further monitor species occurrences to evaluate the ongoing changes and to be able to take appropriate measures for conservation.

At the trematode community diversity scale, molecular identification may shed light on parasite community patterns and host-parasite associations (Blasco-Costa *et al.* 2014); particularly the latter phenomenon remains understudied. For example, the question regarding why the snail *Ampullaceana balthica* hosts so many trematode species remains unanswered. Also, we have yet to evaluate if this snail species is being used as much in temperate regions where the species richness of other snails is much higher than in the sub-Arctic. However, there are currently too few data from mainland Europe to evaluate the host use at a finer scale. Moreover, there is an ongoing need for more records based on molecular genetic identification from Europe, as many of the surveys on trematode life-cycle stages were done without generating DNA sequence data (Faltýnková *et al.* 2007, 2008). Increasing availability of these data would shed light on the full distributional range for groups such as *Plagiorchis* spp., for which we do not know if the high species diversity within this genus is a feature typical for the sub-Arctic or if the situation is similar in more southern regions.

We still need precise species identification of parasites using integrative taxonomic methods, based on well-fixed vouchers linked to DNA sequence data (see Pleijel *et al.* 2008). These data provide a baseline for any further ecological studies and adequate epidemiological and conservation measures. For definite species descriptions in many trematode groups, adults are needed, which would allow matching DNA sequences with already known lineages and completing life-cycle data.

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