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MOLECULAR AND MORPHOLOGICAL CHARACTERISATION OF DIGENEANS OF THE FAMILY STRIGEIDAE RAILLIET, 1919 FROM ICELAND

Master thesis

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Annotation

This study applies molecular and morphological procedures to identify larval and adult stages of trematodes of the family Strigeidae in Iceland. Intermediate hosts (snails and fishes) and definitive host (birds) from 11 freshwater lakes were sampled and examined for the presence of trematodes. Recovered species were subjected to study of morphology, sequencing and phylogenetic analyses. A total of seven species of three genera were identified *via* phylogenetical analyses based on mitochondrial (*cox*1) and nuclear (28S) sequences, and morphological data. The life-cycle of *Apatemon gracilis* was fully elucidated in Iceland, and those of *Australapatemon burti* and *Australapatemon minor* in part (cercariae and adults). The relationship of *Cotylurus* sp. 'Lin. 1I' and *Cotylurus* sp. 'Lin. 2I' could not be resolved.

Declaration

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České Budějovice, 18 April 2018 Hynek Mazanec

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Introduction

Northern ecosystems

Iceland, a volcanic island in the sub-Arctic region has been considered, as all regions in northern circumpolar zones, to exhibit simple ecosystems with low diversity, short trophic chains, a low amount of pathogens and a limited capacity to adapt to environmental changes (Hoberg et al., 2012). Climate change is considered a key factor influencing Arctic freshwater ecosystems with major impact on regional distribution and abundance of species (Lemoine et al., 2007; Wrona et al., 2013). Recently, a rapid change in temperature has been recorded, implying that there might be significant changes affecting Arctic flora and fauna (Post et al., 2009).

The ecosystems in northern latitudes serve as promising models for studies of emerging diseases and factors influencing distribution, parasite-host associations and evolution of pathogens in wildlife populations (Hoberg et al., 2008). However, the lack of baselines for the diversity of parasites in the Arctic is a major obstacle, especially in freshwater habitats (Blasco-Costa et al., 2014). Therefore, to understand these ecosystems and to promote future comparative studies, it is important to precisely identify the species involved and assess their life-cycles. This is enabled by the integrative approach combining molecular and morphological methods; with its aid basic levels of diversity and distribution of parasites in Arctic wildlife can be delimited (Hoberg et al., 2008, 2012).

With the advancing development of molecular approaches an unexpected diversity of cryptic species in northern regions has been discovered in recent years (Aldhoun et al., 2009; Blasco-Costa et al., 2014; Faltýnková et al., 2014; Gordy et al., 2016, 2017; Soldánová et al., 2017). A detailed survey on trematode diversity in Norway (Soldánová et al., 2017) and in North-America (Gordy et al., 2016, 2017) revealed many species, whose life-cycles include birds. Among them, representatives of the family Strigeidae Railliet, 1919 such as species of *Apatemon* Szidat, 1928, *Australapatemon* Sudarikov, 1959 and *Cotylurus* Szidat, 1928 have proven to be frequent and many novel lineages have been discovered indicating a potentially higher species diversity than previously expected. The present study is a part of an ongoing monitoring of the diversity of digenean trematodes in freshwater ecosystems in Iceland, which have so far revealed a considerable species richness including cryptic species (see Georgieva et al., 2012, 2013a; Blasco-Costa et al., 2014; Faltýnková et al., 2014).

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Biodiversity in Iceland

Iceland, surrounded by the North Atlantic ocean, has been considered difficult to colonise, and is indeed characteristic for its depauperate diversity of free-living freshwater and terrestrial biota (Ministry for the Environment & The Icelandic Institute of Natural History, 2001). Five freshwater snail species have been recorded: *Anisus spirorbis* (L.), *Galba truncatula* (Müller), *Gyraulus laevis* (Alder), *Physella acuta* (Draparnaud) and *Radix balthica* (L.) (see Einarsson, 1977; Glöer, 2002; Skírnisson et al., 2009). There are five fish species native to Iceland occurring in freshwater, which are however all connected to the marine realm: *Anguilla anguilla* (L.), *Gasterosteus aculeatus* L., *Salmo salar* L., *Salmo trutta* L. and *Salvelinus alpinus* (L.). Rainbow trout (*Oncorhynchus mykiss* (Walbaum)) has been introduced to local hatcheries from where it escaped into the wild. Before human colonisation of Iceland, the only indigenous mammal present was the Arctic fox, which migrated there during the glacial period (Ministry for the Environment & The Icelandic Institute of Natural History, 2001).

The most species rich group of vertebrates in Iceland are birds, although they are less diverse than in continental Europe (Alerstam et al., 1990; Jóhannesdóttir et al., 2014). Since Iceland is located on the East Atlantic Flyway, a number of species of migratory birds stopover there during annual spring or autumn migrations between North America, Europe and Africa (Boere & Stroud, 2006; Dusek et al., 2014). Moreover, Icelandic ecosystems sustain internationally important bird populations breeding in wetlands (Jóhannesdóttir et al., 2014). Notably, birds function as important biological and mechanical carriers for free-living biota and for parasites including trematodes of which they are important definitive hosts (Borgsteede, 1997). Because of their motility, birds are a keystone factor of dispersion and maintaining diversity of numerous pathogens (Reed et al., 2003; Hubálek, 2004; Jourdain et al., 2007).

Trematodes and their life-cycles

Parasites are integral components of ecosystems because they represent a significant amount of species diversity and biomass, they influence the functioning of ecosystems and food web structure, and they can enhance trophic interactions of their hosts (Marcogliese, 2004; Kuris et al., 2008; Poulin, 2010). Digenean trematodes are characteristic for their complicated life-cycles which can comprise up to four hosts. The keystone-organisms in these trematode life-cycles are molluscs, the almost obligatory first intermediate hosts (Galaktionov &

Dobrovolskiy, 2003). Few marine species of the family Aporocotylidae Odhner, 1912, using annelids as first intermediate hosts, are an exception to this rule (Esch et al., 2001). In the first intermediate hosts the trematodes (sporocysts and/or rediae) reproduce asexually. Asexual reproduction results into the stage of cercariae which are usually equipped with a tail for active movement in water column, and with penetration gland-cells for penetration into second intermediate hosts (Galaktionov & Dobrovolskiy, 2003). Cercarial emergence and movement activity are stimulated by several factors (light, temperature, water current, gravity, season, etc.) to maximise the probability of reaching the time and space of the second intermediate host (Combes et al., 1994). Large amounts of emerging cercariae significantly increase the chance of infecting next hosts and also ensure dispersion in space (Combes et al., 1994). After penetration to the second intermediate host the cercariae encyst, forming metacercariae. In this inactive stage they may endure for a long time before they can infect the definitive host (Galaktionov & Dobrovolskiy, 2003). The variety of species serving as second intermediate or definitive hosts is substantially higher and differs for each digenean family (Galaktionov & Dobrovolskiy, 2003).

Trematodes in Iceland

The very first studies on Icelandic trematodes comprise surveys on the diversity of adult trematodes predominantly from marine fishes and birds (Rees, 1953; Brinkmann, 1956). Studies on trematodes from freshwater intermediate hosts (snails, fishes) have for long been scarce, the only data have been provided by Blair (1973, 1974, 1976) who reported seven trematode species from the pulmonate snail *Lymnaea peregra* (Müller) (presumably *Radix balthica*) and completed the life-cycle of *Apatemon gracilis* (Rudolphi, 1819) experimentally (Blair, 1974).

Freshwater metacercariae have been reported from fishes, but the species spectrum is limited to *Apatemon gracilis* and *Diplostomum* spp. (see Blair, 1973; Frandsen et al., 1989; Kristmundsson & Richter, 2009; Natsopoulou et al., 2012; Karvonen et al., 2013). Moreover, *Diplostomum* sp. should be regarded as a collective term because the species spectrum could not be assessed reliably in the past due to high morphological similarity of the metacercariae and because there were no molecular methods available at that time. Only two freshwater trematode species occurring as adults in fishes were recorded, *Crepidostomum farionis* (Müller, 1784) and *Phyllodistomum conostomum* (Olsson, 1876) in *Salvelinus alpinus* and *Salmo trutta* (see Brinkmann, 1956; Kristmundsson & Richter, 2009).

The first complex studies aimed at reliable species identification and consequent assessment of species diversity were those on bird schistosomes, triggered by the outbreak of cercarial dermatitis in bathing areas in Iceland (Kolářová et al., 1999; Skírnisson et al., 2009). Kolářová et al. (1999) first described several bird schistosome cercariae causing swimmer's itch in Iceland. This led to further examination of local freshwater ecosystems, especially lymnaeid snails, which serve as intermediate hosts for the trematodes. As a result, eight representatives of this family have been discovered, including new species to science (Kolářová et al., 2006, 2013; Skírnisson & Kolářová, 2008; Aldhoun et al., 2009). In recent years, studies focused on single families revealed new representatives of the family Echinostomatidae Looss, 1899 (Kostadinova & Skírnisson, 2007; Georgieva et al., 2013a) including the elucidation of the life-cycle of *Petasiger islandicus* Kostadinova & Skírnisson, 2007 in Iceland (Georgieva et al., 2012). Furthermore, studies focused on species composition of *Diplostomum* revealed an unexpected diversity of representatives of this group in snails and fishes completing their life-cycles in Iceland, including the well-known *Diplostomum spathaceum* (Rudolphi, 1819) and five putative new species of *Diplostomum* (see Blasco-Costa et al., 2014; Faltýnková et al., 2014).

The family Strigeidae Railliet, 1919

The family Strigeidae is a group of digenean trematodes infecting as adults birds and mammals (Dubois, 1968). Due to a relatively high abundance of birds in Iceland, strigeids could be expected to be one of the major parasitic groups in Iceland. Unlike the related family Diplostomidae, there have been no pathogenity reports of strigeid representatives. However, there is a report of a negative effect of metacercariae of *Apatemon gracilis* on heart performance of *Oncorhynchus mykiss* (see Tort, 1987). Strigeids have either a typical three-host life-cycle (see above) or a derived four-host life-cycle. In case of the latter, the parasitic stage of mesocercaria is put between the stage of cercaria and metacercaria. In history, identification of specimens to genera was mostly based on adult morphology as it contained the highest informative value, followed by cercariae and lastly by metacercariae.

The type-species of the genus *Apatemon*, *A. gracilis*, exhibits a high morphological variability, which led some authors to divide it to numerous subspecies (Dubois, 1968), whereas others considered it as a polymorphic species with a wide host range and cosmopolitan distribution (Beverley-Burton, 1961). This led to problems with delimiting *Apatemon* from other genera, especially *Australapatemon* due to their intraspecific variability combined with intergeneric/interspecific homogeneity (see Stunkard, 1941;

Dubois & Pearson, 1965; Yamaguti, 1971; Bell et al., 2002; Blasco-Costa et al., 2016). Although the representatives of the two genera differ in their life-cycles, i.e. *Apatemon* spp. uses fishes as second intermediate hosts (Dubois, 1968), while *Australapatemon* spp. utilise leeches (Sudarikov, 1959), their taxonomic status has been questioned several times and the genus *Australapatemon* has been often considered a subgenus of *Apatemon* (see Dubois & Pearson, 1965). Only the recent molecular data of Blasco-Costa et al. (2016) solidified the proof that *Apatemon* and *Australapatemon* are distinct genera.

The members of the genus *Cotylurus* exhibit a similar variability in morphology as those of the previously mentioned *Apatemon* that led to high interspecific variation (Dubois & Rausch, 1950). From the type-species, *Cotylurus cornutus* (Rudolphi, 1808), another species, *Cotylurus brevis* Dubois & Rausch, 1950 had been later delimited by Dubois & Rausch (1950), this was further confirmed by Nasir (1960) and Dubois (1968). Before that, *C. brevis* had been also associated with *Apatemon gracilis* (see Dubois & Rausch, 1950).

In the present study we provide novel data on strigeid trematodes in Iceland. The adult and larval stages (cercariae, metacercariae) are characterised molecularly and corresponding life-cycle stages are matched with the aid of molecular data. Also, detailed morphological descriptions of most lineages (without metacercariae) are provided.

Objectives of the Thesis

The aim of the study was the assesment of the diversity of digeneans of the family Strigeidae Railliet, 1919 in freshwater snails, fishes and birds in Iceland via:

i. Morphological characterisation and identification of the isolates of cercariae and adults.

ii. Generating partial sequences of the mitochondrial *c* oxidase subunit 1 and nuclear 28S rRNA gene.

iii. Conduction of phylogenetic analyses to aid molecular identification of the newly obtained isolates.

iv. Matching corresponding life-cycle stages of the strigeid trematodes with aid of phylogenetic analyses.

Materials and Methods

Collecting and processing of material

Trematodes from snails, fishes and birds were collected from 2009 to 2016 by K. Skírnisson, S. Georgieva, and J. Roháčová. A total of 1,488 *Radix balthica*, 375 *Physella acuta* and 145 *Gyraulus laevis* were collected from 10 lakes or ponds across Iceland (see Table 1 and Figure 1). Snails were identified following Glöer (2002). Three fish species, i.e. two salmonids: *Salmo trutta* (n = 19) and *Salvelinus alpinus* (n = 4), and one gasterosteid, *Gasterosteus aculeatus* (n = 59) were collected from Lake Hafravatn. A total of hundred birds of 19 species of seven families were dissected: Anatidae (3 *Anas platyrhynchos* L., 10 *Aythya fuligula* (L.), 7 *Aythya marila* (L.), 1 *Bucephala islandica* (Gmelin), 2 *Clangula hyemalis* (L.), 2 *Histrionicus histrionicus* (L.), 9 *Melanitta nigra* (L.), 5 *Mergus merganser* L., 6 *Mergus serrator* L. and 1 *Somateria mollissima* (L.)), Gaviidae (12 *Gavia immer* (Brünnich) and 2 *Gavia stellata* (Pontoppidan)), Laridae (4 *Larus marinus* L., 15 *Larus ridibundus* L., and 1 *Rissa tridactyla* (L.)), Podicipedidae (4 *Podiceps auritus* (L.)), Stercorariidae (1 *Stercorarius parasiticus* (L.)), Sternidae (14 *Sterna paradisaea* Pontoppidan), and Sturnidae (1 *Sturnus vulgaris* L.). The bird material was obtained from regional Icelandic authorities and through donation of the Natural History Museum of Reykjavík.

Snails were transferred to the lab, placed individually in cups and subjected to light to stimulate cercarial emergence. All snails with no emerging cercariae for three days were dissected to detect infections with sporocysts and/or rediae with immature cercariae, and metacercariae. Head of fish hosts were dissected and metacercariae were isolated from their eyes. Adult trematodes from birds were obtained by dissection of bird intestines. Preliminary identification of trematodes was attempted using relevant sources (Dubois, 1968; Combes, 1980; Gibson et al., 2002; Faltýnková et al., 2007, 2008). Upon preliminary identification, samples of larval and adult stages were fixed both in molecular-grade ethanol for DNA isolation and in cold 4% formaldehyde solution for subsequent morphological examinations. Cercarial isolates were fixed in large numbers (± 50) from each infected snail. All isolates intended for DNA isolation were photographed with the aid of a digital camera on an Olympus BX51 microscope and QuickPHOTO CAMERA 2.3 image analysis software. To substantiate the characterisation of each species, vouchers sensu Pleijel at al. (2008) were obtained, including hologenophores (an individual from which a part is cut and used for molecular studies and the rest is kept as a voucher) and paragenophores (a group of two or more specimens considered conspecific, sampled at the same time from the same host of which one is used for DNA isolation and the other is kept as a voucher) for metacercariae and adults, and isogenophores (specimens with an essentially clonal relationship to the studied specimens, i.e. asexually produced siblings, or an asexually produced progeny/parent relationship) for cercariae. Adult worms used as hologenophores were cut between the forebody and hindbody, i.e. at a region which does not hold any characters important for identification, and then this piece was used for DNA isolation.

Table 1 Locality with coordinates of the sampling sites in Iceland

Locality number	Locality name	Region	Coordinates
1	Akranes	Western Iceland	64°19'15"N, 22°04'16"W
2	Áshildarholtsvatn	Sauðárkrókur, Northern Iceland	65°43'50"N, 19°37'14"W
3	Family Park	Reykjavík, Southwestern Iceland	64°08'15"N, 21°52'03"W
4	Geirastaðir	Northern Iceland	66°07'53"N, 23°14'45"W
5	Hafravatn	Reykjavík, Southwestern Iceland	64°07'50"N, 21°39'54"W
6	Krínsjörn	Southeastern Iceland	64°19'42"N, 15°16'05"W
7	Landmannalaugar	Southern Iceland	63°59'02"N, 19°04'02"W
8	Lake Mývatn	Northern Iceland	65°38'04"N, 16°55'28"W
9	Nordic House	Reykjavík, Southwestern Iceland	64°08'19"N, 21°56'45"W
10	Oslandstjörn	Höfn, Southeastern Iceland	64°14'34"N, 15°12'29"W
11	Hrauntunsjörn	Reykjavík, Southwestern Iceland	64°10'38"N, 21°41'11"W
12	Rauðavatn	Reykjavík, Southwestern Iceland	64°06'27"N, 21°46'11"W
13	River Leirvogsá	Reykjavík, Southwestern Iceland	64°10'38"N, 21°41'11"W
14	Sýkið	Deildartunguhver, Western Iceland	64°39'46"N, 21°24'41"W

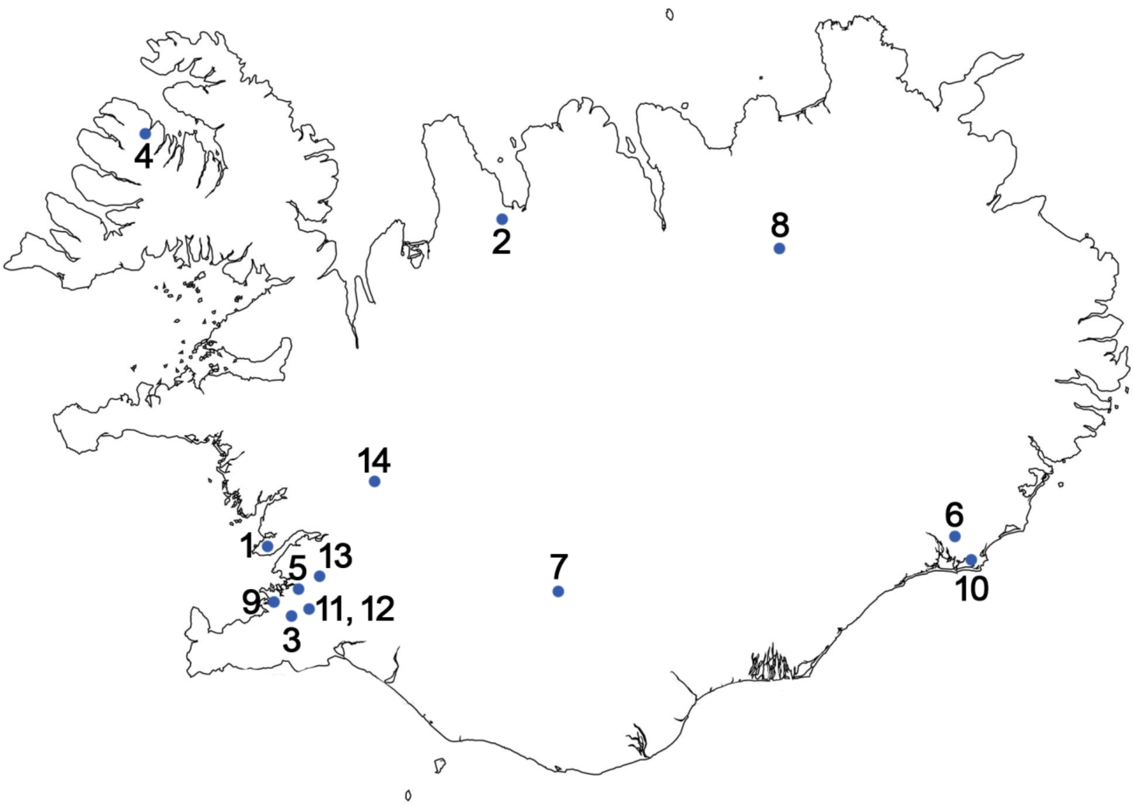

Figure 1 Sampling locations in Iceland. Numbers of sampling sites correspond to numbers in Table 1

Morphological examination

Vital stains (Neutral red and Nile blue sulphate) were used to improve visualisation of internal organs and the excretory system of cercariae. Sets of photomicrographs were taken for each isolate (live) with a digital camera on an Olympus BX51 microscope to document the morphology of each stage. Measurements were taken from digital images with the aid of QuickPHOTO CAMERA 2.3 image analysis software.

Some cercarial isolates fixed in cold formaldehyde solution were selected for scanning electron microscopy (SEM) observations; these were post-fixed in 2% osmium tetroxide for 2 hours, washed in 0.1 M phosphate buffer, dehydrated through an acetone series, critical point-dried and sputter-coated with gold. SEM examinations were performed using a JEOL JSM 7401-F scanning electron microscope at an accelerating voltage of 4 kV.

Adults used as hologenophores were photographed by a digital camera (see above) prior to cutting; subsequently, measurements of the whole body and non-collapsed eggs were taken from photomicrographs as above. Adult worms selected for morphological studies were stained using iron-acetocarmine, dehydrated through a graded ethanol series, cleared in dimethyl phtalate ester and mounted in Canada balsam as permanent mounts. Representative total mounts were used to prepare drawings of each lineage using an Olympus BX51 microscope with a drawing attachment.

The voucher material of adult worms is deposited in the Helminthological Collection of the Institute of Parasitology (IPCAS), Biology Centre of the Czech Academy of Sciences České Budějovice.

All measurements taken are in micrometres and given as the range and the mean in parentheses. Cercariae were measured from live photomicrographs and the following abbreviations were used: BL, body length; BW, body width; AOL, anterior organ length; AOW, anterior organ width; VSL, ventral sucker length; VSW, ventral sucker width; PHL, pharynx length; PHW, pharynx width; OESL, length of oesophagus; CAECAL, length of caecum; EYEL, eye spot length; EYEW, eye spot width; TSL, tail stem length; TSW, tail stem width; FL, furca length; FW, furca width; BL/TSL, body length to tail stem length ratio; TSL/FL, tail stem length to furca length ratio; AOW/VSW anterior organ width to ventral sucker width ratio. Adults were measured from total mounts and from photomicrographs; following abbreviations were used: BL, total body length; FBL, forebody length; FBW, maximum forebody width; HBL, hindbody length; HBW maximum hindbody width; OSL, oral sucker length; OSW, oral sucker width; VSL, ventral sucker length; VSW, ventral sucker width; HFL, length of holdfast lobe; PGL, proteolytic gland length; PGW, proteolytic gland width; PHL, pharynx length; PHW, pharynx width; ATL, anterior testis length; ATW, anterior testis width; PTL, posterior testis length; PTW, posterior testis width; OVL, ovary length; OVW, ovary width; MGL, Mehlis' gland length; MGW, Mehlis' gland width; VRL, vitelline reservoir length; VRW, vitelline reservoir width; GCL, genital cone length; GCW, genital cone width; HDL, length of hermaphroditic duct; TEND, length of posttesticular region, i.e. distance of posterior level of posterior testis to posterior extremity; OVAR, distance of ovary from anterior extremity of hindbody; EggL, EggW (wet mounts), length and width, respectively, of eggs from a fixed specimen mounted in water; EggL, EggW (total mounts), length and width, respectively, of eggs from a fixed specimen mounted in Canada balsam; Egg N, number of eggs; HBL/FBL, hindbody length to forebody length ratio; VSL/OSL, sucker length ratio; VSW/OSW, sucker width ratio; GCL/HBL %, genital cone length as a proportion of hindbody length; % TEND, proportional length of post-testicular region; % OVAR, proportional length of distance of ovary from anterior extremity of hindbody; SV/HBL %, proportion of hindbody length occupied by seminal vesicle.

Molecular data

Ethanol-fixed larval and adult stages were isolated using Chelex® extraction protocol. Specimens were placed in 200 µl of a 5% suspension of deionised water and Chelex® and 2 µl of 0.1 mg/ml of proteinase K and incubated at 56 °C overnight; this was followed by boiling at 90 °C for 8 min and centrifugation at 16,000x *g* for 10 min. Acquired DNA was amplified for two different fragments: the mitochondrial cytochrome *c* oxidase subunit 1 (*cox*1) and the nuclear 28S rRNA gene. Polymerase chain reaction (PCR) amplifications were performed for *cox*1 in a total volume of 20 µl containing 10 µl 2× MyFi™ Mix (Bioline, USA), 1.6 µl of each PCR primer (5 pmol/µl), 1.8 µl of dH_2O and 5 µl (*c*. 50 ng) of genomic DNA supernatant; for 28S they differed in 3.8µl of dH_2O and 3µl of template DNA. Primer sets used and thermocycling conditions are detailed in Table 2 and Figure 2.

PCR amplicons were visualised on 1% agarose gel stained with GelRed™ fluorescent nucleic acid dye and purified with QIAquick PCR purification kit (Qiagen Ltd, UK) following the manufacturer's instructions. DNA quantification (ng/µl) was performed with NanoDrop 1000 Spectrophotometer using the programme ND1000. PCR amplicons were sequenced using the same primer sets as during the PCR amplification directly from both strands with ABI BigDye chemistry (ABI Perkin-Elmer), alcohol-precipitated, and run on an

ABI Prism 3130xl or 3730xl automated sequencers. Contiguous sequences were assembled, edited and aligned in MEGA v. 7 (Kumar et al., 2016). Sequence identity of the newly generated sequences was verified by the Basic Local Alignment Tool (BLAST). (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastn&PAGE_TYPE=BlastSearch&LINK_LOC=blasthome).

Alignments and phylogenetic analyses

Newly generated sequences for the *cox*1 and 28S rRNA genes (see Table 3) were aligned in two separate datasets. Published sequences of the Strigeidae (see Table 4 and 5) available from GenBank were included in the alignments. Datasets were aligned using MUSCLE (Edgar, 2004a, b) implemented in MEGA v. 7. Outgroups were chosen based on previous studies (Blasco-Costa et al., 2016). Extremes of the alignments were trimmed to match the shortest sequence prior to phylogenetic analyses. The alignment for the mitochondrial *cox*1 gene included no gaps or insertions and was aligned with reference to the amino acid translation, using the echinoderm mitochondrial code (Telford et al., 2000). (Translation table; https://www.ncbi.nlm.nih.gov/Taxonomy/Utils/wprintgc.cgi#SG9).

Alignment 1 for the protein-coding *cox*1 gene (345 nt positions; 134 sequences) included 81 newly generated sequences and 53 sequences retrieved from GenBank of the family Strigeidae. *Tylodelphys clavata* (von Nordmann, 1832) (Diplostomidae Poirier, 1886) was used as an outgroup for the *cox*1 alignment. Alignment 2 for the partial nuclear 28S rDNA sequences (975 nt positions; 39 sequences) included 19 newly generated and 20 sequences retrieved from GenBank, following the same approach as in Alignment 1. *Diplostomum phoxini* (Faust, 1918) (Diplostomidae) was used as an outgroup for the 28S alignment.

Molecular identification of the parasite isolates sequenced was achieved using Bayesian inference (BI) and Maximum likelihood (ML) phylogenetic analyses. Prior to analyses, appropriate models were selected for both alignments (*cox*1 HKY+I+G; 28S GTR+I+G) with jModelTest 2.1.1 (Guindon & Gascuel, 2003, Darriba et al., 2012) to estimate the best fitting model under Akaike Information Criterion with correction for small sample sizes (AICc) (Sugiura, 1978). Bayesian inference analyses were run on MrBayes v. 3.2.2 (Ronquist et al., 2012) as online execution on the Cipres Science Gateway v. 3.1 (http://www.phylo.org/sub_sections/portal/) (Miller et al., 2010), using MrBayes (3.2.6) on XSEDE. Maximum likelihood analyses were conducted using online platform ATGC (http://www.atgc-montpellier.fr/phyml/) (Guindon et al., 2010). Trees were visualised using FigTree v.1.4.2 (Rambaut, 2014).

Naming scheme of unresolved species follows the same principle as Faltýnková et al. (2014) using lineage number plus the country of provenance, Iceland (abbreviated as ‘Lin. 1I’, ‘Lin. 2I’ in the text).

Table 2 Primer sets used for PCR amplifications and sequencing reactions

Gene	**Primer name**	**Direction**	**Sequence (5'–3')**	**Source**
*cox*1	Plat-diploCOX1F	F	CGTTTRAATTATACGGATCC	Moszczynska et al. (2009)
	Plat-diploCOX1R	R	AGCATAGTAATMGCAGCAGC	
	MplatCOX1dF	F	TGTAAAACGACGGCCAGTTTWCITTRGATCATAAG	
	MplatCOX1dR	R	CAGGAAACAGCTATGACTGAAAYAAYAIIGGATCICCACC	
28S rRNA	LSU-5	F	TAGGTCGACCCGCTGAAYTTAAGCA	Olson et al. (2003)
	ZX-1	F	ACCCGCTGAATTTAAGCATAT	Bray et al. (2009)
	1500R	R	GCTATCCTGAGGGAAACTTCG	Tkach et al. (2003)
	900F*	F	CCGTCTTGAAACACGGACCAAG	Olson et al. (2003)
	300*	R	GTTCATGGCACTCCCTTTCAAC	Lockyer et al. (2003)
	ECD2*	R	CTTGGTCCGTGTTTCAAGACGGG	Littlewood et al. (2000)

* Internal sequencing primers; abbreviations: F, forward; R, reverse.

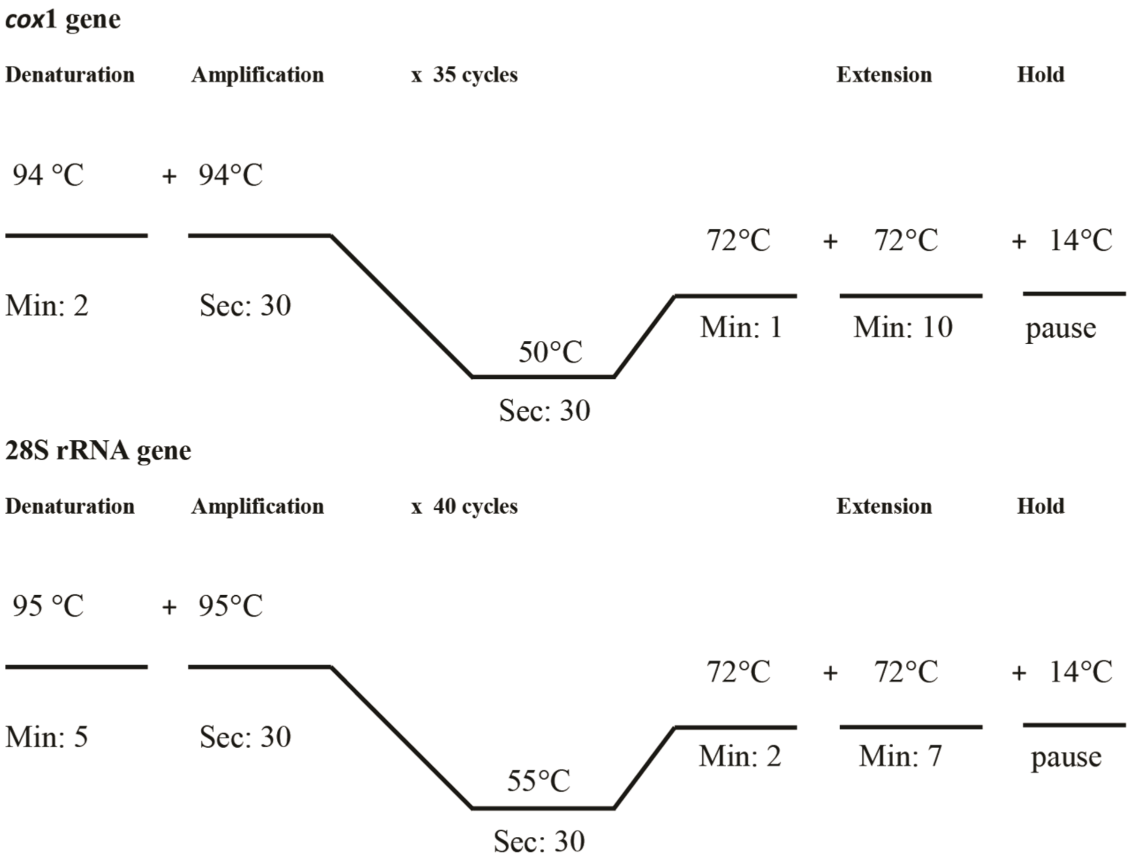

Figure 2 PCR thermocycle profiles used for amplification of the two genetic markers

Table 3 Summary data for the sequences provided in the present study

Species	Life-cycle stage*	Host species	Locality	Gene	
				***cox*1**	**28S**
Strigeidae					
Apatemon gracilis	C	*Radix balthica*	Lake Mývatn	Ge166	
Apatemon gracilis	C	*Radix balthica*	Lake Mývatn	Ge167	
Apatemon gracilis	C	*Radix balthica*	Lake Mývatn	Ge168	
Apatemon gracilis	C	*Radix balthica*	Lake Mývatn	Ge169	
Apatemon gracilis	S	*Radix balthica*	Lake Mývatn	Ge170	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge155	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge156	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge157	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge158	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge159	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge160	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge161	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge162	Ge706
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge163	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge164	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge165	
Apatemon gracilis	C	*Radix balthica*	Lake Nordic House	Ge206	
Apatemon gracilis	C	*Radix balthica*	Lake Raudavatn	Ge207	
Apatemon gracilis	C	*Radix balthica*	Lake Raudavatn	Ge1146	
Apatemon gracilis	MTC	*Salmo trutta*	Lake Hafravatn	Ge219	Ge711
Apatemon gracilis	MTC	*Salvelinus alpinus*	Lake Hafravatn	Ge220	
Apatemon gracilis	A	*Gavia immer*	Akranes	Ge1093	
Apatemon gracilis	A	*Melanitta nigra*	Lake Mývatn	Ge1096	
Apatemon gracilis	A	*Mergus serrator*	River Leirvogsá	Ge1086	
Apatemon gracilis	A	*Mergus serrator*	River Leirvogsá	Ge1087	
Apatemon gracilis	A	*Mergus serrator*	River Leirvogsá	Ge1088	
Apatemon gracilis	A	*Mergus serrator*	River Leirvogsá	Ge1089	
Apatemon gracilis	A	*Mergus serrator*	River Leirvogsá	Ge1090	
Apatemon gracilis	A	*Mergus merganser*	Hrauntunstjörn	Ge1091	
Apatemon gracilis	A	*Mergus merganser*	Hrauntunstjörn	Ge1092	
Apatemon gracilis	A	*Mergus merganser*	-		Ge1229
Apatemon gracilis	A	*Somateria mollissima*	Lake Mývatn	AK134	
Apatemon gracilis	C	*Radix balthica*	Lake Family Park	AK135	
Apatemon gracilis	C	*Radix balthica*	Lake Family Park	AK136	
Apatemon sp. 'Lin. 1I, bulbocauda'	C	*Gyraulus laevis*	Lake Nordic House	Ge582	Ge714
Australapatemon sp.	C	*Radix balthica*	Lake Nordic House	Ge574	Ge708
Australapatemon minor	C	*Radix balthica*	Lake Nordic House	Ge572	
Australapatemon minor	C	*Radix balthica*	Lake Nordic House	Ge578	
Australapatemon minor	C	*Radix balthica*	Lake Nordic House	Ge580	Ge707
Australapatemon minor	A	*Melanitta nigra*	Lake Mývatn	Ge1094	
Australapatemon minor	A	*Melanitta nigra*	Lake Mývatn	Ge1095	
Australapatemon burti	C	*Radix balthica*	Lake Family Park	Ge567	
Australapatemon burti	C	*Radix balthica*	Lake Family park	Ge575	
Australapatemon burti	C	*Radix balthica*	Lake Family Park	Ge1140	
Australapatemon burti	C	*Radix balthica*	Lake Family Park	AK131	
Australapatemon burti	C	*Radix balthica*	Lake Family Park	AK132	
Australapatemon burti	C	*Radix balthica*	Lake Family Park	AK133	
Australapatemon burti	C	*Radix balthica*	Lake Nordic House	Ge576	
Australapatemon burti	C	*Radix balthica*	Lake Nordic House	Ge577	Ge709
Australapatemon burti	C	*Radix balthica*	Lake Nordic House	Ge579	
Australapatemon burti	C	*Radix balthica*	Lake Nordic House	Ge581	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge631	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge632	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge633	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge634	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge635	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge636	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge637	

Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge1098	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn	Ge1099	
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn		Ge1233
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn		Ge1234
Australapatemon burti	A	*Melanitta nigra*	Lake Mývatn		Ge1237
Cotylurus sp.	C	*Lymnaea stagnalis*	Czech Republic	AK22	Ge1265
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge208	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge209	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge210	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge564	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge565	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge566	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge568	Ge1264
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge569	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge1141	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge1142	Ge1263
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Family park	Ge1145	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Nordic House	Ge573	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Nordic House	Ge1143	
Cotylurus sp. 'Lin. 1I'	C	*Radix balthica*	Lake Nordic House	Ge1144	
Cotylurus sp. 'Lin. 1I'	MTC	*Radix balthica*	Lake Family park		Ge710
Cotylurus sp. 'Lin. 2I'	A	*Aythya fuligula*	Lake Mývatn	Ge628	
Cotylurus sp. 'Lin. 2I'	A	*Aythya fuligula*	Lake Mývatn	Ge629	
Cotylurus sp. 'Lin. 2I'	A	*Aythya fuligula*	Lake Mývatn		Ge1238
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Landmannalaugar	Ge623	Ge713
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Landmannalaugar	Ge624	
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Landmannalaugar	Ge625	
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Landmannalaugar	Ge626	
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Mývatn	Ge1097	
Cotylurus sp. 'Lin. 2I'	A	*Aythya marila*	Lake Mývatn		Ge1239
Cotylurus sp. 'Lin. 2I'	A	*Melanitta nigra*	Lake Mývatn		Ge1230
Cotylurus sp. 'Lin. 2I'	A	*Melanitta nigra*	Lake Mývatn		Ge1236

*Life-cycle stages: A, adult; C, cercaria; MTC, metacercaria; S, sporocyst

Table 4 Summary data for the sequences retrieved from Genbank for *cox*1 analysis

Lineage	**Host**	**Locality**	**GenBank ID**	**Source**
Apatemon gracilis	*Radix balthica*	Norway, Takvatn	KY513216	Soldánová et al. (2017)
Apatemon sp. SAL-2014	*Gasterosteus aculeatus*	Norway	KM212028	Kuhn et al. (2015)
Apatemon sp. SAL-2014	*Gasterosteus aculeatus*	Norway	KM212029	Kuhn et al. (2015)
Apatemon sp. 1 SAL-2008	*Etheostoma nigrum*	Canada, Ontario	HM064633	Locke et al. (2010)
Apatemon sp. 1x SAL-2010	*Etheostoma nigrum*	Canada, Ontario	HM064635	Locke et al. (2010)
Apatemon sp. 1x SAL-2010	*Etheostoma nigrum*	Canada, Quebec	HM064636	Locke et al. (2010)
Apatemon sp. 1 SAL-2008	*Etheostoma nigrum*	Canada, Quebec	FJ477183	Moszczynska et al. (2009)
Apatemon sp. 4 SAL-2008	*Ambloplites rupestris*	Canada, Quebec	HM064647	Locke et al. (2010)
Apatemon sp. 4 SAL-2008	*Ambloplites rupestris*	Canada, Quebec	FJ477186	Moszczynska et al. (2009)
Apatemon sp. 'jamiesoni'	*Potamopyrgus antipodarum*	New Zealand	KT334181	Blasco-Costa et al. (2016)
Apatemon sp. 'jamiesoni'	*Gobiomorphus cotidianus*	New Zealand	KT334182	Blasco-Costa et al. (2016)
Apatemon sp. MAG-2016	*Stagnicola elodes*	Canada	KT831359	Gordy et al. (2017)
Apatemon sp. 3 SAL-2008	*Ambloplites rupestris*	Canada, Quebec	HM064645	Locke et al. (2010)
Apatemon sp. 3 SAL-2008	*Ambloplites rupestris*	Canada, Quebec	FJ477185	Moszczynska et al. (2009)
Apharyngostrigea cornu	*Ardea alba*	Mexico, Panuco	JX977777	Hernández-Mena et al. (2014)
Apharyngostrigea cornu	*Ardea herodias*	Canada	JF769450	Locke et al. (2011)
Apharyngostrigea cornu	*Ardea herodias*	Canada	JF769451	Locke et al. (2011)
Apharyngostrigea pipientis	*Rana pipiens*	Canada, Quebec	HM064884	Locke et al. (2011)
Apharyngostrigea pipientis	*Rana pipiens*	Canada, Quebec	HM064885	Locke et al. (2011)
Australapatemon burti	*Stagnicola elodes*	Canada	KT831351	Gordy et al. (2016)
Australapatemon burti	*Anas diazi*	Mexico	JX977727	Hernández-Mena et al. (2014)
Australapatemon mclaughlini	*Anas acuta*	Canada	KY587405	Gordy et al. (2017)
Australapatemon mclaughlini	*Anas acuta*	Canada	KY587406	Gordy et al. (2017)
Australapatemon niewiadomski	*Anas platyrhynchos*	New Zealand	KT334177	Blasco-Costa et al. (2016)
Australapatemon niewiadomski	*Anas platyrhynchos*	New Zealand	KT334178	Blasco-Costa et al. (2016)
Australapatemon sp. Lin1	*Stagnicola elodes*	Canada	KY207548	Gordy et al. (2017)
Australapatemon sp. Lin3	*Stagnicola elodes*	Canada	KY207577	Gordy et al. (2017)
Australapatemon sp. Lin4	*Aythya collaris*	Canada	KY587397	Gordy et al. (2017)
Australapatemon sp. Lin5	*Stagnicola elodes*	Canada	KY207597	Gordy et al. (2017)
Australapatemon sp. Lin6	*Physella gyrina*	Canada	KY207616	Gordy et al. (2017)
Australapatemon sp. Lin8	*Physella gyrina*	Canada	KY207622	Gordy et al. (2017)
Australapatemon sp. Lin9	*Stagnicola elodes*	Canada	KY207550	Gordy et al. (2017)
Cardiocephaloides medioconiger	*Larus* sp.	Mexico, Campeche	JX977782	Hernández-Mena et al. (2014)
Cardiocephaloides medioconiger	*Larus* sp.	Mexico, Campeche	JX977783	Hernández-Mena et al. (2014)
Cardiocephaloides medioconiger	*Larus occidentalis*	Mexico, Guerrero negro	JX977784	Hernández-Mena et al. (2014)
Cotylurus gallinulae	*Stagnicola elodes*	Canada	KT831347	Gordy et al. (2016)
Cotylurus cornutus	*Radix balthica*	Norway, Takvatn	KY513234	Soldánová et al. (2017)
Cotylurus cornutus	*Radix balthica*	Norway, Takvatn	KY513235	Soldánová et al. (2017)
Cotylurus gallinulae	*Aythya affinis*	Mexico, La Esperanza	JX977781	Hernández-Mena et al. (2014)
Ichthyocotylurus pileatus	*Perca flavescens*	Canada, Quebec	HM064720	Locke et al. (2010)
Ichthyocotylurus pileatus	*Perca flavescens*	Canada, Quebec	HM064721	Locke et al. (2010)
Ichthyocotylurus sp. 2 SAL-2008	*Perca flavescens*	Canada, Quebec	HM064728	Locke et al. (2010)
Ichthyocotylurus sp. 2 SAL-2008	*Perca flavescens*	Canada, Quebec	FJ477205	Moszczynska et al. (2009)
Ichthyocotylurus sp. 3 SAL-2008	*Notropis hudsonius*	Canada, Ontario	HM064729	Locke et al. (2010)
Ichthyocotylurus sp. 3 SAL-2008	*Notropis hudsonius*	Canada, Ontario	HM064730	Locke et al. (2010)
Parastrigea cincta	*Eudocimus albus*	Mexico, Caimanero	JX977757	Hernández-Mena et al. (2014)
Parastrigea diovadena	*Eudocimus albus*	Mexico, Caimanero	JX977729	Hernández-Mena et al. (2014)
Parastrigea plataleae	*Platalea ajaja*	Mexico, Topolobampo	JX977761	Hernández-Mena et al. (2014)
Strigeidae sp.	*Gasterosteus aculeatus*	Norway	KM212056	Kuhn et al. (2015)
Strigeidae sp.	*Gasterosteus aculeatus*	Norway	KM212057	Kuhn et al. (2015)
Strigeidae sp. 2	*Perca flavescens*	Canada, Quebec	FJ477184	Moszczynska et al. (2009)
Strigeidae sp. 7	*Porichtys notatus*	Canada, Quebec	FJ477189	Moszczynska et al. (2009)
Tylodelphys clavata	*Radix auricularia*	Germany, Hengsteysee	JX986908	Georgieva et al. (2013b)

Table 5 Summary data for the sequences retrieved from Genbank for 28S analysis

Lineage	**Host**	**Locality**	**GenBank ID**	**Source**
Apatemon gracilis	*Gasterosteus aculeatus*	Norway, Takvatn	KY513177	Soldánová et al. (2017)
Apatemon sp. AK-2017	*Gasterosteus aculeatus*	Norway, Takvatn	KY513178	Soldánová et al. (2017)
Apatemon sp. AK-2017	*Gasterosteus aculeatus*	Norway, Takvatn	KY513179	Soldánová et al. (2017)
Apatemon sp. 'jamiesoni'	*Phalacrocorax punctatus*	New Zealand, Otago Harbour	KT334169	Blasco-Costa et al. (2016)
Apharyngostrigea cornu	*Ardea cinerea*	Ukraine, Kherson region	AF184264	Tkach et al. (2001)
Apharyngostrigea pipientis	*Nycticorax nycticorax*	USA, Northern Great Plains	JF820597	Pulis et al. (2011)
Apharyngostrigea pipientis	*Lithobates sylvaticus*	USA, Northern Great Plains	JF820598	Pulis et al. (2011)
Australapatemon burti	*Helisoma trivolvis*	Canada	KY207625	Gordy et al. (2017)
Australapatemon niewiadomski	*Barbronia weberi*	New Zealand, Lake Hayes	KT334164	Blasco-Costa et al. (2016)
Australapatemon niewiadomski	*Anas platyrhynchos*	New Zealand, Balclutha	KT334165	Blasco-Costa et al. (2016)
Australapatemon sp.	*Oxyura jamaicensis*	Canada, Manitoba	MF124269	Gordy et al. (2017)
Australapatemon sp.	*Anas acuta*	Canada, Manitoba	MF124270	Gordy et al. (2017)
Cardiocephaloides longicollis	*Larus ridibundus*	Ukraine	AY222171	Olson et al. (2003)
Cotylurus cornutus	*Radix balthica*	Norway, Takvatn	KY513180	Soldánová et al. (2017)
Cotylurus cornutus	*Gyraulus acronicus*	Norway, Takvatn	KY513181	Soldánová et al. (2017)
Cotylurus cornutus	*Gyraulus acronicus*	Norway, Takvatn	KY513182	Soldánová et al. (2017)
Ichthyocotylurus erraticus	*Coregonus autumnalis*	United Kingdom, Northern Ireland	AY222172	Olson et al. (2003)
Nematostrigea serpens	*Pandion haliaetus*	Russia, Karelia	KF434762	Lebedeva & Yakovleva (2016)
Strigeidae sp.	*Turdus naumanni*	Japan, Yamagata	LC011455	Sato & Iwaki (Unpublished)
Diplostomum phoxini	*Phoxinus phoxinus*	United Kingdom, Wales	AY222173	Olson et al. (2003)

[,,následující pasáž o rozsahu 20–66 (46) stran je obsažena pouze v archivovaném originále diplomové práce uloženém na Přírodovědecké Fakultě Jihočeské Univerzity'']

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