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Myxidium finnmarchicum n. sp. (Myxosporea: Myxidiidae) from the gall bladder of whiting *Merlangius merlangus* (L.) (Pisces: Teleostei) in North Norway

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Abstract

A new species of myxosporean is described from the gall bladder of whiting *Merlangius merlangus* (L.) (Pisces: Teleostei) caught at the northernmost extremity of the range of this fish off the northwest coast of Finnmark county, North Norway. The new species, *Myxidium finnmarchicum*, is described morphologically and genetically and compared with other similar species of *Myxidium* reported from the gall bladders of gadid fish in the North Atlantic - *M. sphaericum*, *M. gadi* and *M. bergense*. Both the morphological and molecular descriptions support the status of *Myxidium finnmarchicum* as a new species. *Myxidium sphaericum* is a parasite of whiting in the North Sea, but the two species are separated geographically by an intervening area in the northern North Sea north of 58° N where no whiting has been found infected with any species of *Myxidium*. Based upon 18S rRNA analysis, *M. finnmarchicum* shows closest sequence identity to *M. gadi*. The confusion in the literature regarding the validity and host specificities of *M. sphaericum*, *M. gadi*, *M. bergense* and *M. incurvatum* is highlighted and discussed. We suggest that a more detailed investigation of the range of morphological and molecular variation in these parasites from their various reported host species is required.

Key words: *Myxidium finnmarchicum* **n. sp.**, *Merlangius merlangus*, North Norway

Introduction

Whiting, *Merlangius merlangus* (L.), is a gadid fish with a geographical distribution in the northeast Atlantic from the southern Barents Sea and Iceland to Portugal, and in the Black, Adriatic and Aegean Seas (Froese & Pauly, 2009). During a cruise of the University of Tromsø research vessel *Jan Mayen* along the coast of Finnmark in North Norway in 1999, we had the opportunity to examine whiting caught at the northern extremity of the range of the species. We found the gall bladders to be infected with a myxosporean parasite of the genus *Myxidium*, which came as a surprise because MacKenzie & Kalavati (1995) and MacKenzie *et al.* (2005) had reported that the common *Myxidium* species infecting the gall bladders of whiting, *Myxidium sphaericum* Thélohan 1895, was found only in whiting caught south of 58º N in the North Sea and did not appear in any of the North Sea samples taken north of this latitude. Closer examination revealed that the *Myxidium* from Finnmark showed consistent morphological differences when compared to *M. sphaericum* and to *Myxidium bergense* Auerbach, 1909, another species infecting cod *Gadus morhua* L. and haddock *Melanogrammus aeglefinus* (L.) off Finnmark. These differences suggested the presence of a different, possibly new, species. In November 2008 and October 2009 we returned to the coast of Finnmark and collected further material. In this paper the new species is described morphologically and genetically and compared with other species of *Myxidium* infecting gadid fish in the North Atlantic—*M. sphaericum*, *M. bergense* and *Myxidium gadi* Georgèvitch, 1916.

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Material and methods

Sample collection. Whiting were caught by trawl in the southern Barents Sea off western Finnmark and in the southern North Sea off Flamborough Head (54° 10´ N, 0° 5´ E), dissected aboard ship, and the gall bladders removed for examination. For Barents Sea whiting, fresh smears were made from a drop of bile fluid and a scraping from the internal wall of each gall bladder, and examined aboard ship by phase-contrast microscopy at magnifications of x250 – 400. Fresh spores and vegetative stages of the myxosporeans were photographed and samples were collected and stored, some in 4% formaldehyde solution for later morphological examination, and some in 100% ethanol for molecular analyses. Twenty gall bladders from southern North Sea whiting were placed directly into ethanol and later examined in the laboratory for *Myxidium* infections. The specific identity of the *Myxidium* specimens from these whiting could not be confirmed morphologically because preservation in ethanol causes distortion of the spores and vegetative stages. For comparative purposes we also sequenced samples from single infected gall bladders identified morphologically as *M. bergense* from cod caught by rod and line at Brønnøysund (65° 30´ N, 12° 5´ E) and Kvarøy (66° 27´ N, 12° 28´ E) off the west coast of Norway. The volume of ethanol was 5 to 10 times greater than the volume of gall bladder plus contents in all cases.

For detailed morphological examination, formaldehyde-fixed material was examined at magnifications of up to x1000 under bright-field and phase-contrast illumination. Air-dried smears were refixed in either methyl alcohol, Carnoy's fluid or Schaudinn's fluid and stained with Giemsa, Feulgen/Light Green or Heidenhein's haematoxylin to highlight details of spore morphology, from which measurements were taken. Drawings were made with the aid of Camera Lucida and measurements are given in micrometres. The description follows the guidelines of Lom & Arthur (1989). Collection numbers quoted refer to specimens deposited, as stained slides, in The Natural History Museum, London, UK.

Molecular analysis. Samples for molecular analysis were taken from a single infected Barents Sea whiting collected on 1 October 2009 from off the Coast of Finnmark (see Results for precise location) and a single infected Brønnøysund cod, collected in June 2008. Further samples were analysed from two infected cod from Kvarøy, one collected in June 2007 and one in September 2007, and from three infected whiting from the southern North Sea, all collected in January 2009.

Extraction of DNA. Infected gall bladders in 100% ethanol were removed from their collection tubes and transferred to a Petri dish. Using a glass pipette, about 50 µl ethanol containing myxozoans was removed from the inner surface of each infected gall bladder and placed in a 1.75ml Eppendorf tube. The tube was placed open in an oven at 80 ºC and left for approximately 15 minutes to allow ethanol to evaporate. DNA was extracted from the dried material using the DNeasy Blood and Tissue Kit (Qiagen) following manufacturer's instructions and eluted in 100 µl buffer.

PCR amplification of 18S rRNA. 18S rRNA PCR products were generated using a number of different primers and two different reaction conditions (Table 1).

TABLE 1. Primers and PCR conditions used to amplify 18S rRNA from *Myxidium* spp. samples collected from whiting and cod and from different geographical areas.

Host	Origin	PCR*	Forward primer	Reverse primer	References (primers)	PCR product ~(bp)	Accession No.
Whiting	Barents Sea	I	18e	Myxgen4r	Hillis & Dixon, 1991; Kent *et al.*, 2000	1444	GQ890672
			18e	Myxgp5r	Hillis & Dixon, 1991; Kent *et al.*, 2000	460	
Whiting	Southern North Sea	II	MyxospecF	ERIB10	Barta *et al.*, 1997; Fiala, 2006	1454	GQ890675
Cod	Kvarøy	I	18e	Myxgen4r	Hillis & Dixon, 1991; Kent *et al.*, 2000	1407	GQ890673 GQ890674
Cod	Brønnøysund	II	MyxospecF	MyxospecR	Fiala, 2006	775	GQ890676

*: PCR conditions I and II are detailed in the text.

PCR reaction condition I consisted of 50 µl reaction mix containing 1x NH_4 buffer, 2mM $MgCl_2$, 0.2mM dNTPs, 0.5 mM forward and reverse primers (Table 1), 2.5 units Taq polymerase (BioTaq, Bioline, UK), 2 µl eluted DNA and PCR grade water to reach a final volume of 50 µl. PCR thermocycling consisted of a single cycle of 94 ºC for 3 min, 40 cycles of 94 ºC for 1 min, 52 ºC for 1 min and 72 ºC for 2 min, and a final extension at 72 ºC for 10min.

PCR reaction condition II consisted of 1 µl eluted DNA added to a 50 µl reaction mix containing 1x NH_4 buffer, 1.5mM $MgCl_2$, 0.25mM dNTPs, 0.4 mM forward and reverse primers (Table 1), 1 unit Taq polymerase (BioTaq, Bioline, UK), and PCR grade water. PCR thermocycling consisted of 95 ºC for 4 min, 40 cycles of 95 ºC for 1 min, 55 ºC for 1 min and 72 ºC for 2.2 min, and a final extension at 72 ºC for 10 min. Cod and whiting host DNA was amplified alongside *Myxidium* DNA under the same conditions in an attempt to identify non-specific products originating from host tissue. Triplicate PCR reactions were performed from each DNA sample when fewer than three infected hosts were available from a given location. Single PCR reactions were performed on DNA samples from three individual hosts where three or more infected hosts from the same site were available.

PCR products were run alongside molecular size markers (Invitrogen) on agarose gels and visualised under UV light.

Purification and sequencing of PCR products. PCR products were excised from gel and purified using the MinElute gel purification Kit (Qiagen) and eluted in approximately 20 µl of elution buffer. Purified product was run on agarose gels alongside known molecular weight markers to estimate DNA concentration. PCR products obtained from *Myxidium* sp. from the Barents Sea were cloned using the TOPO TA cloning Kit (Invitrogen) and TOP 10 competent cells (Invitrogen). Plasmids were purified using the Miniprep plasmid purification Kit (Qiagen). Sequencing reactions for all products were performed using the GenomeLab DTCS Quick Start kit (Beckman Coulter), according to manufacturer's instructions, using 4 µl reaction mix, 1.5 µl sequencing reaction buffer, 0.5 µM primer as used in original PCR or M13 primers where cloned products were sequenced. Approximately 30 ng to 60 ng DNA and 200 ng DNA was used for PCR or cloned products respectively in sequencing reactions. The sequencing reactions were run on a CEQ 8800 Sequencher (Beckman Coulter).

Sequence analysis. Sequences were analysed initially using Sequencher software (Intelligenetics/Gene Codes Corporation) and NCBI's MEGABLAST algorithm was used to identify *Myxidium* spp. from the sequence data (Zhang *et al*. 2000). Sequences representative of all marine myxozoan clades, as defined in Fiala (2006), were retrieved from the database and were aligned with *Myxidium* spp sequences generated from cod and whiting. The 5' and 3' ends were trimmed and pairwise genetic distances were calculated over 1400 nucleotides of 18S rRNA sequence from the *Myxidium* spp. from whiting from the Barents Sea. Sequences were aligned using the ClustalW function in BioEdit v7.0.5.3 (Hall, 1999), followed by manual editing of alignments. PAUP vers. 4.0B10 PPC (Swofford, 1999) was used to calculate pairwise genetic distances, excluding gaps and ambiguous nucleotides, using the Kimura 2 parameter distance model.

Results

Family Myxidiidae Thélohan, 1892

Genus *Myxidium* Bütschli, 1882

Myxidium finnmarchicum n. sp.

(Figs. 1–4)

Material studied.

Host: Merlangius merlangus (L.)

Site of infection: gall bladder

Locality, dates and depths: (1) Off Sørøya, North Norway, 24 October, 1999, 70˚ 47′ N, 22˚ 58′ E, 137m;

(2) Coast of Finnmark, North Norway, 25–28 November, 2008, 71° 17´ N, 24° 30´ E, 290m; (3) Coast of Finnmark, North Norway, 1 October, 2009, 71° 15´ N, 27° 14´ E, 135m. (4) Coast of Finnmark, North Norway, 6 October, 2009, 70° 00´ N, 23° 80´ E, 67m.

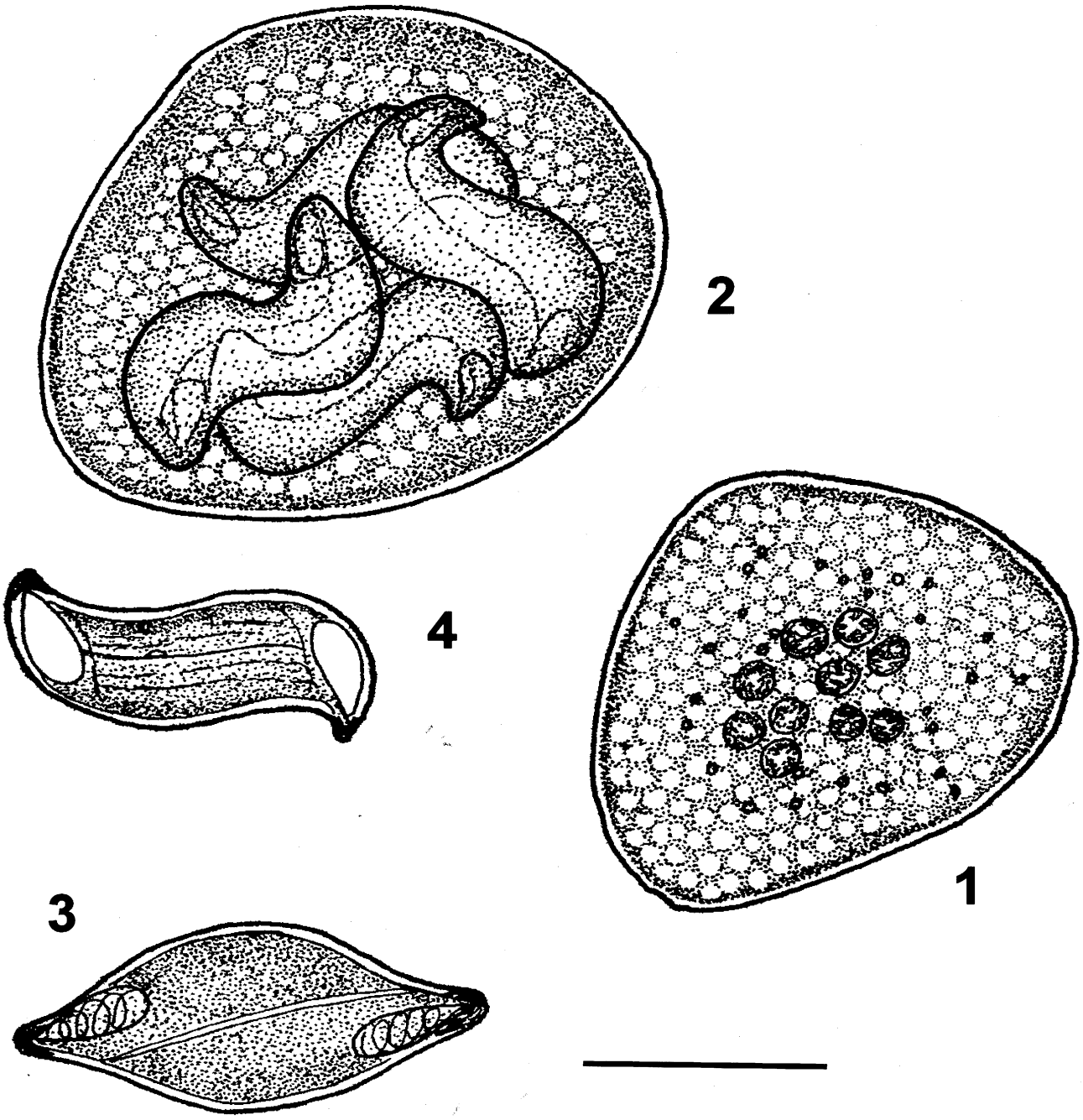
Type locality: (1).

Prevalence: (1) 60% (18 of 30); (2) 58% (21 of 36); (3) 77% (23 of 30); (4) 93% (13 of 14).

Host length range: 24 – 45 cm.

Collection numbers: 2009:11:9:1; 2009:11:9:2; 2009:11:9:3; 2009:11:9:4.

Morphological description. Trophozoite (Figs. 1, 5) spherical or ovoid. No pseudopodia observed. Ectoplasm and endoplasm clearly differentiated. Plasmodium (Fig. 2, 6) di- or tetra-sporous. Dimensions, based on 10 fixed specimens: 40–50 x 30–36.



FIGURES 1–4. Line drawings of *Myxidium finnmarchicum* **n. sp.** 1. Trophozoite, stained with Giemsa. 2. Plasmodium, unstained fixed specimen. 3. Spore, sutural view, stained with Giemsa. 4. Spore, valvular view, unstained fixed specimen. *Scale bar:* 10μm.

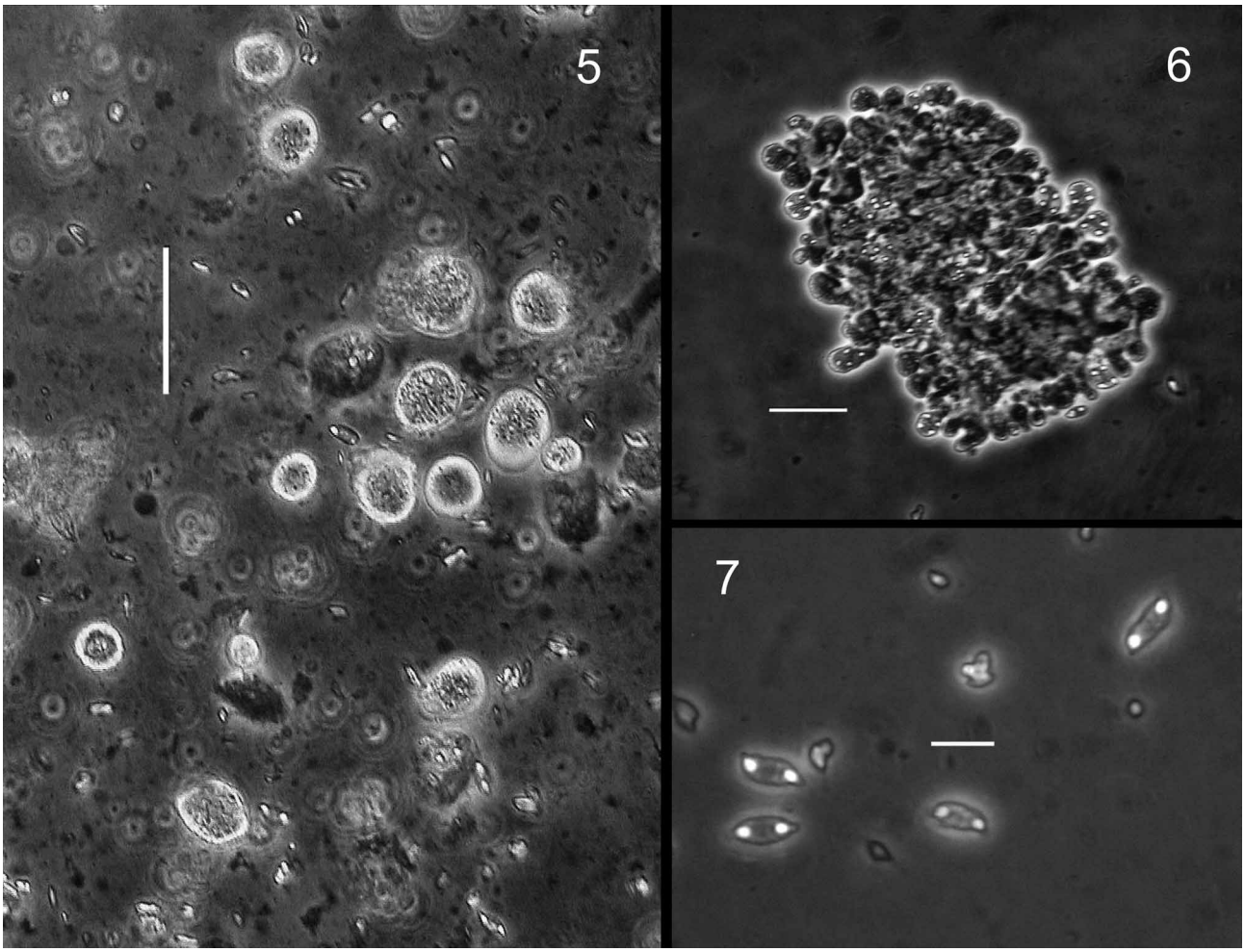


FIGURE 5. *Myxidium finnmarchicum* **n. sp.** Fresh trophozoites under phase-contrast. *Scale-bar:* 50µm.
FIGURE 6. *Myxidium finnmarchicum* **n. sp.** Fresh plasmodia under phase-contrast. *Scale-bar:* 50µm.
FIGURE 7. *Myxidium finnmarchicum* **n. sp.** Fresh spores under phase-contrast. *Scale-bar:* 20µm.

Spore (Figs. 3, 4, 7) fusiform with bluntly pointed club-shaped extremities in both sutural and valvular views. Ends markedly thickened. Sutural line distinct and curved. Spore valves S-shaped, thin, with 4–6 fine longitudinal striations. Polar capsules pyriform, with broad bases, sub-terminal, on different but parallel long axes. Polar filament with 4–5 coils. Sporoplasm binucleate and intercapsular. Dimensions, based on 30 fixed spores, as ranges with means ± SD in parentheses: spore length 17.6–22.4 (19.2 ± 1.6); spore width 6.4–9.6 (7.6 ± 1.0); length of polar capsule 4.8–6.4 (5.6 ± 0.6); width of polar capsule 3.2–4.8 (3.7 ± 0.3); polar capsule length: spore length = 1: 3.2–4.1; spore width: spore length = 1: 2.1–2.8.

Table 2 compares the main diagnostic features of *M. finnmarchicum* with those of three other similar species of *Myxidium* reported from gadid hosts in the North Atlantic. The new species shows features similar to all three, but in most features it resembles *M. sphaericum* and *M. bergense* more than *M. gadi.* A fourth species, *M. oviforme,* is not considered here as it is very different morphologically from the other species.

Molecular results: *Myxidium finnmarchicum*. PCR amplification using all primer pairs apart from MyxospecF/ERIB10 amplified contaminating host DNA alongside *Myxidium* DNA under the conditions used.

Myxozoan 18S rRNA PCR products of approximately 450bp and 1500bp were obtained using the primer pairs 18e/Myxgp5r and 18e/Myxgo4r respectively from the single infected whiting from the Barents Sea. Products from three individual PCR reactions per primer pair were cloned and sequences were obtained from six clones, one clone per PCR reaction. No nucleotide differences were observed between sequences (Accession GQ890672). MEGABLAST analysis revealed that this was a novel sequence differing from other

TABLE 2. A comparison of the morphological diagnostic features of *Myxidium finnmarchicum* n. sp. with those of other similar species of *Myxidium* described from gadid hosts in the North Atlantic by MacKenzie & Kalavati (1995).

Feature	*Myxidium* species			
	***M. sphaericum* (from whiting)**	***M. bergense* (from haddock)**	***M. gadi* (from saithe)**	***M. finnmarchicum***
Trophozoite	Spherical or ovoid with many small lobose pseudopodia.	Amoeboid, with one long lobose pseudopodium, the tip of which is sometimes branched.	Irregularly shaped, usually with 5-6 small lobose pseudopodia.	Spherical or ovoid. No pseudopodia observed.
Plasmodium	Usually di-, rarely mono-sporous. 25-30 x18-24	Poly-, di- or mono-sporous. 48-68 x 20-50.	Spherical, polysporous, containing up to 48 spores. 22.5-45.0 x 25.0-40.0.	Tetra- or di-sporous. 40-50 x 30-36.
Spore	Fusiform, broad in mid region with fairly blunt ends in valvular view, S-shaped in sutural view. Sutural line thin and faint. 15.0-20.0 x 5.0-10.0.	Fusiform, convex in middle region, ends pointed in valvular view, S-shaped in sutural view. Sutural line distinct and curved. 17.5-20.0 x 6.2-7.5.	Fusiform in valvular view, S-shaped in sutural view with pointed extremities. Sutural line thin, slightly curved. 12.0-15.0 x 5.0-7.5.	Fusiform, with bluntly pointed club-shaped ends in both sutural and valvular views. Sutural line distinct and curved. 17.6-22.4 x 6.4-9.6.
Spore valves	Thin and smooth.	Thin and smooth.	Thin and smooth.	Thin and finely striated.
Polar capsules	Pyriform, terminal on long axis of spore. 3.0-5.0 x 2.5-5.0.	Pyriform, terminal, parallel to spore valve but on different long axes. 4.0-6.0 x 2.5-3.7.	Pyriform, terminal, lying along sutural line. 2.5-4.5 x 2.5-4.0.	Pyriform, sub-terminal, with broad base, parallel to spore valve but on different long axes. 4.8-6.4 x 3.2-4.8.
Polar filament	3-4 coils.	5-6 coils.	5-6 coils.	4-5 coils.
Spore width: spore length	1: 1.8-3.2.	1: 2.5-3.0.	1:1.2-1.4.	1: 2.1-2.8.
Polar capsule length: spore length.	1: 4.0-4.5.	1: 3.5-4.0.	1: 2.2.	1: 3.2-4.1.

myxozoan sequences currently available in the public databases and showing closest sequence identity to *M. gadi* (DQ377711), followed by *M. bergense* (DQ377702). Pairwise comparisons of 18S rRNA showed fewest nucleotide differences between that of *M. finnmarchicum* and *M. gadi*, estimated at 4.9 %. *M. finnmarchicum* showed 6.9 % difference with *M. bergense*, while percentage difference between *M. gadi* and *M. bergense* was 3.9%.

Molecular results: other *Myxidium* spp. A number of different sized PCR products were obtained using the different primer pairs, the shortest product from Brønnøysund cod *Myxidium* sp. giving a sequence of 731 nucleotides. *Myxidium* spp.18S rRNA PCR products were amplified, in three independent PCR reactions per host, from the single infected cod specimen from Brønnøysund and from each of the two infected cod from Kvarøy. Sequence data were obtained directly for PCR products from each reaction. Sequence data were obtained from single PCR reactions from 3 infected whiting caught in the southern North Sea off Flamborough Head.

Sequence data obtained for *Myxidium* sp. material from Brønnøysund cod (Accession No.GQ890676) and Kvarøy cod (Accession Nos.GQ890673 and GQ890674) and southern North Sea whiting (Accession No. GQ890675) were identical to each other and to the sequence of *M. gadi* infecting saithe (*Pollachius virens*) (DQ377711) (Fiala, 2006). The *Myxidium* sp. from Kvarøy cod and the *M. gadi* from saithe (DQ377711) differed from *M. gadi* from haddock (DQ377707) (Fiala, 2006) at a single nucleotide position, with the haddock *M. gadi* having an "A" and all others having a "G" at position 351 (relative to the DQ377711 sequence). The sequences obtained for southern North Sea whiting and Brønnøysund cod did not extend over this polymorphic site to allow comparison. The *M. gadi* from haddock also differed from the others at a number of nucleotide positions at the extreme 3' – end of its NCBI sequence. However, as differences in this position may be due to sequencing artefacts, the sequence region was not included in further analysis.

Discussion

MacKenzie & Kalavati (1995) found whiting infected with a *Myxidium* species they identified and redescribed as *M. sphaericum* in the North Sea south of about 58° N, but they found no whiting infected with *Myxidium* in the northern North Sea between 58 and about 61° N. *Myxidium finnmarchicum* was found only at 70 – 71° N, but as far as we are aware, no-one has examined the gall bladders of whiting caught between latitudes 61 and 70° N. So, we do not know the extent of the area in which whiting are apparently free from *Myxidium* infection. However, MacKenzie & Kalavati (1995) did find haddock and saithe in the northern North Sea infected with *M. bergense* and *M. gadi* respectively.

Noble (1957) suggested that *M. bergense* and *M. sphaericum* may be conspecific because of the great deal of variation he observed in the form of the trophic stages, plus the lack of evidence for two distinct forms of spore within the size ranges of the two species. His proposal to reduce *M. bergense* to synonymity with *M. sphaericum* was accepted by Kabata (1967), Shotter (1970) and Moser *et al.* (1989), but was rejected by MacKenzie & Kalavati (1995), who redescribed both species and found significant differences between them in morphological features and geographical distributions.

The molecular results in the present study appear to contradict the morphological identifications in that they show the sequence data obtained for the *Myxidium* spp. material from Kvarøy and Brønnøysund cod (identified morphologically as *M. bergense*), and that from southern North Sea whiting, to be identical to the published *M. gadi* sequence from saithe. The material from southern North Sea whiting was collected in ethanol, which causes distortion of myxosporean spores and vegetative stages, so morphological identification was not possible, and no genetic data currently exist for *Myxidium* spp. morphologically identified as *M. sphaericum*. Although MacKenzie & Kalavati (1995) reported only *M. sphaericum* from whiting, *M. gadi* was identified from whiting in the Black Sea by Schepkina & Yurakhno (2008), and one of us (KM) recently identified *M. gadi* on morphological features from whiting off the southeast coast of Scotland (unpublished data).

Another species within the marine *Myxidium* clade - *Myxidium incurvatum* Thélohan, 1892 - must also be considered here. Moran *et al.* (1996) reported *M. incurvatum* from the gall bladders of the sharp-beaked redfishes *Sebastes fasciatus* and *S. mentella* caught in the Gulf of St. Lawrence, Canada, and commented that their material was "undoubtedly identical" to that recorded as *M. sphaericum* from *Sebastes* spp. and other fishes in the northwest Atlantic by Khan *et al.* (1986). Although *M. incurvatum* has not been reported from a gadid host, it has been reported from about 50 other teleost hosts of different orders throughout the North Atlantic. However, it is doubtful that all these records are really of the same species, especially considering the wide range of spore dimensions reported (Lom & Dyková, 1992).

It is clear from the above account that a great deal of confusion and doubt exists regarding the validity and host specificities of *M. sphaericum*, *M. gadi*, *M. bergense* and *M. incurvatum*. Although *M. finnmarchicum* appears to be closest to *M. gadi* of the species for which we have sequence data, morphologically it has more features similar to *M. sphaericum* and *M. bergense* than to *M. gadi*. Obviously a more detailed investigation of the range of morphological and molecular variation in these parasites from their various reported host species is required. Meanwhile, we consider *M. finnmarchicum* to be sufficiently different in its molecular sequence, morphology and geographical distribution to be considered a new species.

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