

Remarks to the validity of Genbank sequences of *Myxobolus* spp. (Myxozoa, Myxosporidae) infecting Eurasian fishes

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Abstract

Of the 850 known *Myxobolus* spp., 89 named species have DNA (in most cases 18S rDNA) sequences deposited in the Genbank. Only a part of the deposited sequences represent well identified samples collected from adequate organs of the original hosts. Some of the samples were collected from additional hosts or from fishes genetically far standing from the type-host. In the paper, reliability of sequences of some best known *Myxobolus* spp., deposited in the Genbank from freshwater fishes of Eurasia's Palaearctic Region, are surveyed. Genbank sequences are classified into three groups. Sequences obtained from morphologically well characterised *Myxobolus* spp., which were collected from the type hosts, compose the group of valid sequences. To the group of probable valid sequences belong samples from spores morphologically corresponding to the original description, but collected from fishes closely related to the type-host; while sequences obtained from hosts genetically far standing from the type-hosts represent the category of the un-valid group.

Keywords

Myxobolus spp., Eurasian fishes, Genbank, revisions

Introduction

Up to the present time, about 850 *Myxobolus* species have been described. Although in general the shape, size, structure, and molecular pattern of *Myxobolus* spores of the known species show great variations, it occurs infrequently that spores with similar or identical morphological characters are found in genetically distant fishes from different habitats and continents. As the host specificity of *Myxobolus* spp. has not been adequately clarified, in the case of some very early described species, authors designated more than one, very often genetically dissimilar, hosts. The number of infected organs grew in a similar way. The most commonly and earliest known *Myxobolus* sp., *M. muelleri* e.g. was described by Bütschli (1882) from the gill filaments. Subsequent authors, however, thought it to occur in different organs. Recent papers (Molnár 1994, Cone and Overstreet 1998, Lom and Dyková 2006, Dyková and Lom 2007, Ferguson *et al.* 2008) suggested that development of a given *Myxobolus* sp. is mostly restricted to a specific organ and tissue and when

finding different host-, organ- and tissue tropism, species with morphologically similar spores must be identified as different species. A final, effective method for identification of *Myxobolus* spp. became only possible after introduction of molecular methods into *Myxobolus* research (Andree *et al.* 1999). By this time, DNA (in most cases 18S rDNA) sequences of 95 *Myxobolus* species have been deposited in the Genbank. Today Genbank data represent well identified *Myxobolus* spp. However, regardless that molecular methods can precisely elucidate identity of a given species studies of the 18S rDNA of some *Myxobolus* spp. (Bahri *et al.* 2003, Molnár *et al.* 2006) indicated that morphologically similar or identical spores, which had been collected from genetically distant hosts, seem to correspond to different, presumably un-described species.

In the present paper, the validity of some *Myxobolus* sequences deposited in the Genbank from fishes of the Palaearctic Region of Eurasia are surveyed. The major question of the manuscript is, whether DNA sequences in the Genbank correspond to correctly identified species.

Table I. Data on the validity of Genbank sequences of some *Myxobolus* spp. described from fishes of Eurasia's Palaearctic Region

Names of <i>Myxobolus</i> spp.	Type hosts	Reliability of sequences deposited in Genbank			
		valid	uncertain	invalid	remarks
<i>Myxobolus muelleri</i> Bütschli, 1882	<i>Leuciscus cephalus</i>	DQ439806 AY325284		AY129314	1
<i>M. dujardini</i> Thélohan, 1892	<i>Scardinius erythrophthalmus</i> , <i>Rutilus rutilus</i>		DQ439803 DQ439804		2
<i>M. ellipsoides</i> Thélohan, 1892	<i>Tinca tinca</i>			AF085178 DQ439812 DQ439813	3
<i>M. cycloides</i> Gurley, 1893	<i>Rutilus rutilus</i>		DQ439810		4
<i>M. obesus</i> Gurley, 1893	<i>Alburnus alburnus</i>	AY325286			
<i>M. exiguus</i> Thélohan, 1895	<i>Abramis brama</i> , <i>Mugil chelo</i> , <i>M. capito</i>	AY129316 AY129317			5
<i>M. pfeifferi</i> Thélohan, 1895	<i>Barbus barbus</i>		to be submitted		6
<i>M. cyprini</i> Doflein, 1898	<i>Cyprinus carpio</i> , <i>Rutilus rutilus</i> , <i>Tinca tinca</i> , <i>Abramis brama</i>	AF466657 AF380140			7
<i>M. cerebralis</i> Hofer, 1903	<i>Oncorhynchus mykiss</i>	42 sequences			8
<i>M. cyprinicola</i> Reuss, 1906	<i>Leuciscus waleckii</i> , <i>Cyprinus</i> <i>carpio</i>	DQ439805			9
<i>M. bramae</i> Reuss, 1906	<i>Abramis brama</i>	AF507968		AF085177	10
<i>M. sandrae</i> Reuss, 1906	<i>Sander lucioperca</i> , <i>Sander</i> <i>volgensis</i>	EU346379		AF085181	11
<i>M. musculi</i> Keysselitz, 1908	<i>Barbus barbus</i>	AF466658 AF380141			
<i>M. squamae</i> Keysselitz, 1908	<i>Barbus barbus</i>	to be submitted			
<i>M. rotundus</i> Nemeček, 1911	<i>Gobio gobio</i> , <i>Abramis brama</i>	EU710583 FJ851447 FJ851448 FJ851449		AY165179	12
<i>M. carassii</i> Klokacheva, 1914	<i>Carassius carassius</i>	DQ452012			
<i>M. toyamai</i> Kudo, 1915	<i>Cyprinus carpio</i>	FJ710802			
<i>M. koi</i> Kudo, 1920	<i>Cyprinus carpio</i> , <i>Acanthorhodeus asmussi</i> , <i>Squaliobarbus curriculus</i>	FJ710800 FJ841887			13
<i>M. branchialis</i> (Markevich, 1932)	<i>Barbus barbus</i>	to be submitted			
<i>M. pseudodispar</i> Gorbunova, 1936	<i>Rutilus rutilus</i>	EF466088. AF380142 AF380145			14
<i>M. dogieli</i> Bykhovskaya- Pavlovskaya et Bykhovskiy, 1940	<i>Phoxinus phoxinus</i> , <i>Tinca tinca</i> etc.			EU003977 EU003978	15
<i>M. hungaricus</i> Jaczó, 1940	<i>Abramis brama</i>	AF448444			
<i>M. kubanicus</i> Bykhovskaya- Pavlovskaya et Bykhovskiy, 1940	<i>Carassius auratus gibelio</i> , <i>Cyprinus carpio</i>		AY165183		16
<i>M. drjagini</i> (Akhmerov, 1954)	<i>Hypophthalmichthys molitrix</i>		AF085179		
<i>M. pavlovskii</i> (Akhmerov, 1954)	<i>Hypophthalmichthys</i> <i>molitrix</i>	AF507973 HM991164			
<i>M. rotundatus</i> Akhmerov, 1956	<i>Cyprinus carpio</i>		AY165180		16
<i>M. artus</i> Akhmerov, 1960	<i>Cyprinus carpio</i>	FJ710799			
<i>M. arcticus</i> Pugachev et Kokhlov, 1979	<i>Thymallus arcticus</i> , <i>Salvelinus neiva</i>		9 sequences		17

<i>M. diversicapsularis</i> Slukhai, 1966	<i>Rutilus rutilus</i>	GU968199	
<i>M. elegans</i> Kashkovski, 1966	<i>Rutilus rutilus</i> , <i>Leuciscus idus</i>	AF448445	
<i>M. impressus</i> Miroshnichenko, 1980	<i>Barbus tauricus</i> , <i>Leuciscus cephalus</i>		AF507970 18
<i>M. alburni</i> Donec, 1984	<i>Alburnus alburnus</i> , <i>Alburnus filippi</i>	EU567313	
<i>M. bliccae</i> Donec et Tozzyakova, 1984	<i>Blicca bjoerkna</i> , <i>Abramis brama</i> , <i>Abramis sapa</i> , <i>Scardinius erythrophthalmus</i> , <i>Rutilus rutilus</i> , <i>Chondrostoma nasus</i>	HM138770 HM138771 HM138772	19
<i>M. rutili</i> Donec et Tozzyakova, 1984	<i>Rutilus rutilus</i>	GU968201	
<i>M. leuciscini</i> Gonzales-Lanza et Alvarez-Pellitero, 1985	<i>Chondrostoma polylepis</i> , <i>Leuciscus cephalus</i> , <i>Rutilus arcasi</i>	DQ439811	20
<i>M. wulii</i> (Wu et Li, 1986)	<i>Carassius auratus</i>	EF690300	
<i>M. portucalensis</i> Saraiva et Molnár, 1990	<i>Anguilla anguilla</i>	AF085182	
<i>M. cultus</i> Yokoyama et al., 1995	<i>Carassius auratus</i>	AB121146	
<i>M. margitae</i> Molnár, 2000	<i>Alburnus alburnus</i>	EU598803	
<i>M. parviformis</i> Kallert et al., 2005	<i>Abramis brama</i>	AY495704 AY836151	
<i>M. gayerae</i> Molnár et al., 2007	<i>Leuciscus cephalus</i>	DQ439809	

Materials and methods

Of the *Myxobolus* sequences deposited in the Genbank, the author selected data concerning *Myxobolus* spp. infecting fishes of the Palaearctic-Eurasian fauna region (Table I). He compared genetic relation of host fishes, from which DNA sequences of the obtained myxospores were received, with type hosts and considered probability whether deposited sequences really correspond to the given species. Deposited sequences were rated as valid, when the studied *Myxobolus* spores were collected from the type hosts. They were rated as uncertain when sequences derived from adequate organs of closely related fishes, whereas sequences were regarded as false identifications (invalid), when the studied material was received from fishes genetically distant from the type hosts.

Remarks to Table I

(1) When Bütschli (1882) described spores of *Myxobolus muelleri*, he designated them to occur in large plasmodia in the gill filaments of different cyprinid fishes without indicating a type host. Thélohan (1892) collected similar spores of this species from two cyprinids, from the gills of *Leuciscus cephalus* and from the ovary of *Phoxinus phoxinus*, as well as from the eyes of a marine fish *Crenilabrus melops*. In Kudo's (1919) monography already 13 hosts and in Donec and Shulman's book (1984) as many as 82 fish species were designated

as hosts of *M. muelleri*. As this species was described by Bütschli (1882) from cyprinids and from the gills, Landsberg and Lom (1991) suggested regarding *Leuciscus cephalus* as the type host. Of the 5 different 18S rDNA sequences deposited to the Genbank, only DQ439806 and AY325284 meet the required criteria. Sequences from spores of *Mugil* spp. identified as *M. muelleri* seem to be sequences of a new, undescribed species.

(2) Sequences with Genbank-numbers DQ439803 and DQ439804 derive from *Leuciscus cephalus*, a cyprinid fish closely related to the type hosts *Scardinius erythrophthalmus* and *Rutilus rutilus*. The validity of deposited sequences seems to be uncertain.

(3) *M. ellipsoides* was described by Thélohan (1892) from *Tinca tinca*. 18S rDNA sequences with acc. numbers AF085178 from *Rutilus rutilus* and DQ439812 and DQ439813, however, were obtained from *Leuciscus cephalus*. The latter two fish species are genetically distant from *Tinca tinca*, therefore the parasite sequences seem to correspond to sequences of undescribed *Myxobolus* spp.

(4) *M. cycloides* was described by Gurley (1993) from *Rutilus rutilus*. DNA sequences obtained from spores collected from the closely related *Leuciscus cephalus* seem to correspond to the species.

(5) *M. exiguus* was described by Thélohan (1895) from the freshwater fish *Abramis brama* and from the marine fishes *Mugil* spp. simultaneously. Due to the relatively strict host-specificity of *Myxobolus* spp., the occurrence of *M. exiguus*

in two different fish groups could be excluded. Sequences deposited to the Genbank under numbers AY129316, AY157011 and AY129317 cover myxospores from *Mugil* spp. and correspond to the original description. Furthermore, I suggest omitting *Abramis brama* from the hosts of *M. exiguus*.

(6) The type host of *M. pfeifferi* is common barbel *Barbus barbus*. Sequences deposited in the Genbank were received from myxospores collected from Ibèrian barbel *Luciobarbus bocagei*. The occurrence of the species in the two closely related fish species is uncertain.

(7) Myxospores from plasmodia developing in muscle cells of different cyprinid fishes show a close morphological similarity. Lom and Dyková (1992) thought that they all corresponded to *M. cyprini*. Molnár *et al.* (2002), however, found that the molecular sequences of myxospores from *Cyprinus carpio*, identified as *M. cyprini* differed from the myxospores of other cyprinid fishes, and identified spores from *Barbus barbus* as *M. musculi*, while spores from *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Abramis brama* and *Blicca bjoerkna* were regarded as belonging to *M. pseudodispar*.

(8) A large number of 18S rDNA sequences of *M. cerebralis* from different salmonid fishes have been deposited to Genbank. *M. cerebralis* seem to be a species with a relatively wide host range.

(9) The 18S rDNA sequence of *M. cyprinicola* deposited in Genbank under DQ439805 derived from one of the type hosts *Cyprinus carpio*. The chance that this species occurs in *Leuciscus waldeckii*, a genetically distinct fish is scarce. I suggest omitting this latter fish from hosts.

(10) The 18S rDNA sequence of *M. bramae* was deposited in Genbank under acc. number AF085177 by Andree *et al.* (1999) and later by Eszterbauer (2004) under acc. number AF507968. The two DNA sequence, however, differs from each other in 28.4%. Myxospore samples were collected in both cases by the present author. Differences between the two DNA sequences might be caused by a contamination appeared in the course of the spore collection. The myxospore samples sequenced by Andree might be composed of myxospores from small-sized and large-sized plasmodia of *M. bramae* (Molnár and Székely 1999). Recent studies (Molnár *et al.* 2009, Székely *et al.* 2009), however, pointed out that *M. bramae* develops only in large plasmodia of the gill filaments, while small plasmodia of the gill lamellae correspond to *M. rotundus* species. It is suggested, therefore, that 18S rDNA sequence of AF507968 isolated from more carefully selected myxospores should be regarded as valid DNA sequence of *M. bramae*.

(11) Ferguson *et al.* (2008) found that sequence AF085151 is very likely invalid, replacing it with EU346379.

(12) *M. rotundus* was described by Nemeček (1911) from two cyprinid fishes, *Gobio gobio* and *Abramis brama*. The species was frequently found in the latter cyprinid fish (Molnár *et al.* 2009, Székely *et al.* 2009). 18S rDNA sequences of *M. rotundus* deposited in the Genbank on acc. number

GU574808 from goldfish *Carassius auratus gibelio* from China do not correspond to sequences received from the type host *Abramis brama* (Molnár *et al.* 2009, Székely *et al.* 2009). Realizing the above ambiguity, Zhang *et al.* (2010) described the latter parasite species as *M. turpisrotundus*, a novel species infecting the allogenic gibel carp *Carassius auratus gibelio* and goldfish *Carassius auratus auratus*.

(13) *M. koi* was described from three cyprinid fishes. Of them the common carp *Cyprinus carpio* should be regarded as the type host. Both sequences deposited in the Genbank were received from myxospores infecting the common carp. It is suggested to omit *Acanthorhodeus asmussi* and *Squaliobarbus curriculus* from the list of the hosts.

(14) *M. pseudodispar* Gorbunova, 1936 is a very common parasite in muscle cells of the typical host *Rutilus rutilus* and in some closely related cyprinids. DNA sequences from *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Blicca bjoerkna* and *Abramis brama* showed close similarity to each other, but they were somewhat more different from *M. cyprini* of *Cyprinus carpio* and *M. musculi* of *Barbus barbus* having morphologically similar spores. *M. pseudodispar* seems to be a species with relatively wide host range.

(15) *M. dogieli* Bykhovskaya-Pavlovskaya et Bykhovskiy, 1940 has originally been described from several cyprinids, therefore the designation of a type host is rather difficult. It seems likely that the name covers several non-segregated *Myxobolus* spp. infecting the heart of cyprinid fishes. Bauer *et al.* (1991) regarded common carp, *Cyprinus carpio* as type host. In Hungary, myxospores corresponding to *M. dogieli* in morphology as well as in their location were isolated from the heart of *Abramis brama*, and the 18S rDNA sequences obtained from this material were deposited in the Genbank under the acc. numbers EU003977 and EU003978.

(16) No host records are attached to Genbank data.

(17) Genbank data suggest a wide range of hosts for *M. arcticus*. DNA sequences are deposited to Genbank from myxospores collected from *Oncorhynchus alpinus*, *O. nerca* and are found later *O. keta*, *Salvelinus alpinus*, *S. leucomaensis*, but there are no data on myxospores from *Thymallus arcticus*.

(18) The 18S rDNA sequence of *M. impressus* (AF507970) in Genbank represents myxospores collected from the gills of *Abramis brama*. Type hosts, *Barbus tauricus* and *Leuciscus cephalus* belong to genetically distant genera.

(19) *M. bliccae* DNA sequences derived from two closely related cyprinids, the white bream *Blicca bjoerkna* (HM138770, HM138771), and the vimba bream *Vimba vimba* (HM138772), show 99.6% similarity and can be regarded as the same species. On the other hand, *Scardinius erythrophthalmus*, *Rutilus rutilus*, *Chondrostoma nasus* belonging to the Leuciscinae subfamily do not seem to be hosts of this species.

(20) Type hosts given by Gonzalez-Lanza and Alvarez-Pellitero (1985) for *M. leuciscini* are distant members of the Leuciscinae subfamily. Of them, Genbank sequences were received from *Leuciscus cephalus*.

Discussion

Until the relatively strict host-, organ- and tissue specificity of *Myxobolus* spp. were recognized, several *Myxobolus* spp. were described only by the morphological characters of their spores, and different organs of the host fishes were designated as the place of plasmodial development. Recent studies (Molnár 1994, Hedrick *et al.* 1999, Blazer *et al.* 2004, Easy *et al.* 2005, Ferguson *et al.* 2008), however, proved that *Myxobolus* spp. are either strictly specific parasites of a given fish species, or they develop only in some closely related fishes. *M. pavlovskii* e.g. is a common parasite of the closely related *Hypophthalmichthys molitrix* and *Aristichthys nobilis* (Molnár 1979), and Genbank sequences from the two species correspond to each other in 100% (Eszterbauer 2004). Of *M. drjagini*, however, it is known that its plasmodia develop only in *H. molitrix* (El-Mansy and Molnár 1997). A relatively wide host range characterizes *M. cerebralis*, *M. arcticus* and *M. pseudodispar* spp. *M. cerebralis*, a parasite of salmonid fishes infects fishes of *Salmo* and *Oncorhynchus* genera, but fishes of the *Salvelinus* genera are refractory to infection (Blazer *et al.* 2004). *M. arcticus*, however, was detectable from fishes of both *Oncorhynchus* and *Salvelinus* genera (Urawa *et al.* 2009). It is also known (Molnár *et al.* 2002), that *M. pseudodispar* might infect at least 4 cyprinids belonging to closely related genera of the Leuciscinae subfamily. In case of *M. cerebralis* Whipps *et al.* (2004) emphasized that besides SSU rDNA also the ITS-1 sequences from different fish hosts were well conserved proving a recent introduction of this species. In the above cases, DNA sequences of myxospores isolated from different fishes and deposited in the Genbank differed from each other only in a few base pairs. On the other hand, in some cases, Genbank sequences of myxosporeans obtained from non-related fishes, e.g. DNA sequences of *M. muelleri* or *M. rotundus* spp., significantly differed from each other. In the latter case, false species identifications might happen, due to the fact, that for *Myxobolus* spp. described very early in history, there were no type hosts designated and spores found in different hosts were erroneously identified. Sometimes, the original hosts can easily be traced out, while in some other cases, the problem comes from the fact that the describer of the species designated different fishes as host. In the description of *M. muelleri*, e.g. Bütschli (1882) failed to designate a type host, but refers in general to the infection of the gill filaments of different cyprinid fishes. As Thélohan (1892) found two cyprinid species infected with *M. muelleri*, but gill plasmodia were found only in *Leuciscus cephalus*, Landsberg and Lom (1991) suggested to accept this latter cyprinid fish as a type host of *M. muelleri*. Thélohan (1892) thought *M. muelleri* spores were also found in marine fishes, but this was a false diagnosis, and in a similar way, DNA sequences deposited in the Genbank as *M. muelleri* from *Mugil cephalus* (Bahri *et al.* 2003) must represent another *Myxobolus* species.

Similarly, DNA sequences of *M. rotundus* deposited in the Genbank under the number GU574808 from *Carassius auratus gibelio* from China do not correspond to the DNA sequence received from the type host *Abramis brama* (Molnár *et al.* 2009, Székely *et al.* 2009). In the case of *M. ellipsoides* the type host is *Tinca tinca*. Sequences deposited in the Genbank, however, were derived from another host *Leuciscus cephalus*. Both fish species belong to Cyprinidae but the wide genetic difference which exists between Tincinae and Leuciscinae subfamilies suggests the chance of improper diagnosis of the deposited material. Considering this problem authors labelled their sequences as *M. ellipsoides* ex *Leuciscus*. In this latter case the correct answer could only be given after a study on the *Myxobolus* infection of tench, a fish which is less studied in this respect. The situation is more complicated for *M. dogieli*. Bykhovskaya-Pavlovskaya and Bykhovskiy (1940) thought this species was found in several cyprinid and non-cyprinid fishes. It is supposed, however, that only the common carp is the valid host of this species (Bauer *et al.* 1991). Including this possibility, sequences from myxospores morphologically corresponding to *M. dogieli* but collected from *Abramis brama* have also been deposited in the Genbank as *M. dogieli* ex *Abramis brama*.

Until, however, at the above mentioned fishes some of the Genbank deposited sequences correspond to un-described *Myxobolus* spp., in case of *M. dujardini*, *M. cycloides* and *M. pfeifferi* it is not excluded that sequences, obtained from infection of other fishes than the type hosts, correspond to those ones infecting the type host. In the latter case sequenced samples of the given *Myxobolus* sp. derived from hosts belonging to the same subfamilies as the type host. In these cases a decision on the valid or invalid stage of a sequence can be done only after sequences of the species from the type host have been obtained. The situation is even more difficult when sequences of a species are sent to the Genbank without naming the host fish.

In most cases, the describer correctly designated a single, well defined typical host but later studies enriched the number of additional hosts. In this case, most of the latter recorded hosts should be disregarded and only the host mentioned in the original description can be accepted as type-host. If in the original description of a *Myxobolus* sp. more than one host were described, the subsequent designation of a type host is more difficult. For these cases the following solutions are suggested:

1. Only one of the hosts should be accepted as type-host.
2. If the hosts in the original descriptions are genetically closely related fishes, generally the first-mentioned fish species is suggested for designating as type-host and the last-mentioned should be regarded as additional host.
3. When the species is described from systematically distant hosts (e.g. from a marine fish and a freshwater fish) by the original describer, only one of the hosts (generally the first mentioned) should be accepted as type-host and the other should be omitted from the range of hosts.

4. In case, however, when abundant data concerns the *Myxobolus* sp. from the second mentioned fish host and the actual *Myxobolus* sp. from the first fish species is less studied (see: example of *M. exiguus*), the latter host might be designated as type host and then the first one should be omitted from the list of the hosts.

Acknowledgements. The study was rendered possible by a grant of the Hungarian Scientific Research Fund (project no. K71837). The author thanks K. Andree IRTA-Sant Carles de la Rapita, Spain for reviewing and critically commenting the manuscript. The author is also thankful to his colleagues Edit Eszterbauer and Csaba Székely for their suggestions.

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(Accepted May 16, 2011)