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REVIEW ARTICLE

An overview on the myxosporean parasites in amphibians and reptiles

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Abstract

An overview on the myxosporean species infecting amphibians and reptiles is presented. The characteristics of the species are reported, as well as the pathology, hosts and geographical range. The host specificity and life cycle are discussed on the basis of the data thus far.

Key words

Myxosporean parasites, amphibians, reptiles, pathology, geographical distribution

Introduction

Myxosporeans are common parasites of fish. Despite their occurrence in amphibians and reptiles these hosts are usually considered as uncommon. Thus far 19 species have been described from amphibians and reptiles belonging to the genera *Myxobolus*, *Myxidium*, *Hoferellus*, *Chloromyxum*, *Caudomyxum* and *Sphaerospora*. In addition, some myxosporeans have been reported in different hosts but not described to the specific level. Most of the studies refer to species descriptions and new host and location records, and some report the pathology of the infection. However, the biology of these parasites is poorly understood and details of their life cycle are completely unknown.

In this paper we present a review of the literature on the myxosporeans infecting amphibians and reptiles.

In the following list the measurements are given in µm. Unless stated otherwise the dimensions presented are length-breadth-thickness.

Genus *Myxobolus* Bütschli, 1882

Myxobolus fallax Browne, Scheltinga, Pomering et Mahony, 2002 infecting the testes of the anuran *Litoria fallax* from Australia. Spores ovoid in dorsal view, 13.4 (12.6–14.6) × 9.5 (8.3–10.6) × 6.8 (6.5–7.6); polar capsules broadly pyriform, equal in size, 4.2 (3.3–4.7) × 2.4 (2.1–2.8) with 7–8 coils in the polar filament, perpendicular to the longitudinal axis of the polar capsule; without intercapsular appendix.

Myxobolus hylae Johnston et Bancroft, 1918 infecting the testes, oviduct and kidneys of the anuran *Hyla aurea* from Australia. Spores oval or more or less egg-shaped, 8–10 in breadth and about 6 in thickness; some spores approximately circular, with a diameter of 7–8; polar capsules pear-shaped, equal in size, 4–5 × 2; without intercapsular appendix. Browne *et al*. (2002) attempted to describe the species more accurately from archival samples. These authors proposed the existence of two *M. hylae* spore types: type 1 spores much larger and more ovoid than those of type 2. The spores (types 1 and 2 in average) were 13.9 (8.8–15.5) × 9.1 (8.0–10.7) × 7.2 (6.7–7.8), and the polar capsules were 4.2 (3.3–5.2) × 2.6 (2.2–3.1).

Myxobolus bufonis Upton, Freed, Freed, McAllister et Goldberg, 1992 infecting the testes of the anuran *Bufo maculatus* from Cameroon. Spores disc-shaped, spherical to subspherical in one plane and more flattened when viewed end-on, 9.2 (8.8–9.6) × 8.9 (8.6–9.4) × 4.0 (3.6–4.4); polar capsules pyriform, equal in size, 4.1 (3.4–4.6) × 3.2 (2.0–3.4) with 3–4 coils in the polar filament; without intercapsular appendix.

Myxobolus ranae Guyénot et Naville, 1922 infecting the skin of the anuran *Rana temporaria* in Switzerland. Spores ovoid with pointed posterior extremity, 11–12 × 8–10; polar capsules equal in size, 4–5 × 2.5–3.5; without intercapsular appendix.

Myxobolus chimbuensis Ewers, 1973 infecting the testes of the anuran *Litoria darlingtoni* from New Guinea. Spores

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ovoid, slightly flattened without pointed ends, 11.9 (10–13) × 8.4 (8–9) × 6.2 (6–7); polar capsules pyriform, equal in size, 4.7 (4–6) × 2.2 (2–3); without intercapsular appendix.

Genus ***Myxidium*** **Bütschli, 1882**

Myxidium chelonarum Johnson, 1969 infecting the bile ducts and gall bladder of the turtle *Pseudemys scripta scripta* from U.S.A. Spores boat-, banana-, or spindle-shaped with bluntly pointed ends, almost round in cross-section; suture line indistinct; valves with 4–6 striae arranged obliquely across the long axis of the spore; 14.4 (12.5–16) × 4.5 (3–5) × 5.5 (4–7); polar capsules nearly spherical, 4.5 (2.5–5) × 2–3; polar filament forming 5–7 coils.

Myxidium serotinum Kudo et Sprague, 1940 infecting the gall bladder of the anurans *Rana pipiens* and *Rana* sp. from U.S.A. Spores ellipsoidal with equally broadly rounded extremities in both front and side views, 16–18 × 9; polar capsules nearly spherical, 5–5.5 in diameter; polar filament forming 3–5 coils; sutural ridge not straight, not reaching the extremities of the spore, but curving out some distance from the ends; sutural margin thickened into a ridge; 2–4 longitudinal ridges on each valve parallel to the sutural ridge, turning sharply when the suture curves outward and taking a transverse course between the sutural line and the extremities of the spore; 10–13 transverse ridges, most clearly seen in the front view of the spore, within the area marked by the longitudinal ridge that is furthest from the sutural line, these transverse ridges extending over the entire shell valve in all spores. There are, however, various irregularities with reference to the number and arrangement of the ridges: for example, certain of the transverse ridges near the suture may turn at one end and take a course parallel with the suture on one side of the spore, while on the other, end at a ridge parallel with the suture; a transverse ridge may be single at one end and bifurcated at the other.

Myxidium lesminteri Delvinquier, Markus et Passmore, 1992 infecting the gall bladder of the anurans *Tomopterna krugerensis*, *Bufo garmani* and *Heleophryne natalensis* from South Africa. Spores ovoid with smooth shells, 12.5 (9.5–15.0) × 6.5 (5.7–8.0) in *T. krugerensis*, 12.6 (11.0–13.0) × 5.7 (5.0–7.0) in *B. garmani*, and 13.9 (12.5–15.0) × 6.5 (6.0–7.0) in *H. natalensis*; polar capsules spherical.

Myxidium haldari Sarkar, 1982 infecting the gall bladder of the anuran *Hyla arborea* from India. Spores fusiform or cylindrobiconical in sutural view, circular in polar view, slightly bent in the middle; suture line almost straight, 8–10 longitudinal (end to end) striations on the spore wall; 10.3 (10.0–12.0) × 6.6 (6.5–7.0); polar capsules round, 3.6 (3.0–4.0) in diameter.

Myxidium americanum Kudo, 1919 infecting the lumen of urinary tubules of the kidney of the turtle *Trionyx spinifera* from U.S.A. Spores spindle-shaped, circular in cross-section, with the two pointed extremities stretched in opposite directions; sutural line straight, fine longitudinal striations on the shell, eight to ten on each valve; 15–16 × 5.5–6; polar capsules nearly spherical, 4 × 3.5; polar filament forming 3 coils.

Myxidium immersum Lutz, 1889 (syn. *Cystodiscus immersus* Lutz, 1889; *Myxidium lindoyense* Carini, 1932) infecting the gall bladder of the anuran *Bufo marinus* and *Leptodactylus ocellatus* from Brazil. Spores broadly fusiform with rounded extremities in front view, rectangular in lateral view, shell valves marked with two longitudinal and 7–9 transverse ridges, 12–14 × 9–10.

Myxidium mackiei Bosanquet, 1910 infecting the kidney of the turtle *Trionyx gangeticus* from India. Spores fusiform with rather pointed ends, 16–17 × 5 (many broader); shell finely striated.

Myxidium danilewskyi Laveran, 1897 infecting the kidney of the turtle *Emys orbicularis* from France. Spore elongated, fusiform, 12 × 3–4.

Genus ***Hoferellus*** **Berg, 1898**

Hoferellus anurae Mutschmann, 2004 infecting the kidneys, intestine and urinary bladder of the anuran *Afrixalus dorsalis* from Nigeria (also in the ureter of *Hyperolius concolor* and *Hyperolius* sp.). Spores laterally flat, pyramidal or “mitra-like” with a slightly elongated, rounded, anterior apex; posterior end flat having a saucer-shaped depression with either 2 small outgrowths from the lateral edges and sometimes one extra outgrowth from the suture line; 8.0 (7.0–8.9) × 7.9 (6.1–7.9) × 4.9 (4.5–5.2); spore surface with 8–10 longitudinal striations or ridges, starting at the anterior apex and occasionally extending to the short, brush-like, caudal filaments (length: 1.2–3.2); polar capsules pyriform, 3.8 (3.2–4.3) × 2.0 (1.8–2.1); polar filament forming 6–7 coils.

Genus ***Chloromyxum*** **Mingazzini, 1890**

Chloromyxum careni Mutschmann, 1999 infecting the kidney of the anuran *Megophrys nasuta* from Indonesia. Spore ovoid to ellipsoid, 8 (7.2–9.0) × 5 (4.8–5.9); valves with 6–8 external striations; 4 pyriform polar capsules located anteriorly, 2.8 (2.0–3.1) × 1.8 (1.1–2.3).

Chloromyxum salamandrae Upton, McAllister et Trauth, 1995 infecting the gall bladder of the caudata *Eurycea multiplicata griseogaster*, *E. multiplicata multiplicata* and *E. neotenes* from U.S.A. Spores subspherical 8.3 (7.8–8.8) × 7.7 (7.0–8.2); polar capsules pyriform, 4.0 (3.8–4.2) × 2.6 (2.4–2.8); polar filament forming apparently 4 coils; 10–12 external striations on each valve.

Chloromyxum protei Joseph, 1905 infecting the renal tubules of the caudata *Proteus anguineus* from Austria. Spores spherical, 10–13 in diameter, polar capsules 4–6 in length; horizontal and curved external striations densely disposed.

Genus ***Caudomyxum*** **Bauer, 1948**

Caudomyxum caudatum Upton, McAllister et Trauth, 1995 (*Chloromyxum caudatum* Thélohan, 1894) infecting the gall bladder of the caudata *Triton cristatus* from France. Spores ovoid with rounded posterior extremity, 18 × 6–7, with four polar capsules; one caudal projection, sometimes bifurcated, 10 µm long.

Genus ***Sphaerospora*** **Thélohan, 1892**

Sphaerospora ohlmacheri Desser, Lom et Dyková, 1986 (*Chloromyxum ohlmacheri* Whinery, 1893) infecting the renal tubules and the space of Bowman's capsule of tadpoles of *Rana catesbeiana* from Canada. Spore surface with roughly radial striations, making about 24 notches around the outline of each spore valve, 12.6 × 10.9 in average; polar capsules large, spherical, 4.4 in diameter; polar filament forming six coils oblique to the longitudinal axis of the capsule. According to Desser *et al*. (1986) *S. ohlmacheri* is identical with the species recorded from *Bufo lentiginosus* by Ohlmacher (1893) and Whinery (1893), and from *Rana catesbeiana* by Gurley (1894) in U.S.A., and named *Chloromyxum ohlmacheri* Whinery, 1893.

Besides these well established species, other forms, not classified to the specific level, were reported from different hosts and different locations. Ewers (1973) reported a *Myxobolus* species that infects *Litoria thesaurensis* from New Guinea, a form similar in size and shape to *M. chimbuensis* (probably the same species), but differing in some characteristics at the polar capsules. Ray (1933) reported for Indian hosts *Chloromyxum* sp. for the anurans *Rana tigrina* and *Bufo melanostictus*, and *Myxidium* sp. for the reptiles *Amyda granosa*, *Kachuga smithi* and *Nicoria trijuga*. All the parasites infected the gall bladder of the hosts. The author did not give any information or drawings on the characteristics of the spores. Théodoridès *et al*. (1981) described a *Myxobolus* sp. that infects the testes of *Bufo regularis* from Togo, and *Ptychadena maccarthyensis* from the Ivory Coast in Africa. The spore sizes were similar in both host species (10 × 8, polar capsules 4 × 2.5, and 10 × 9–10 for *B. regularis* and *P. maccarthyensis*, respectively) but differed in internal details, which suggests that two different species may be involved. Hill *et al*. (1997) described a *Myxidium* sp. infecting the gall bladder of *Litoria caerulea* from Australia. The spores were ovoidal, 14.6 (13.6–15.6) × 7.9 (7.0–9.0). Duncan *et al*. (2004) reported the occurrence of *Chloromyxum* sp. in the kidneys of some species of Asian horned frog, *Megophrys nasuta* imported into U.S.A. The spores were spherical to pyriform, 6–8 μm long, with four ellipsoid 2–3 μm long polar capsules containing polar filaments with four to five coils. The spore shell had seven to nine prominent external ridges on both sides of the suture line. Mubarak and Abed (2001) described the infection of the Egyptian toads *Bufo regularis* by *Myxobolus* sp. having spores 9.2–10.4 × 8.5–9.5, with equal polar capsules 3.1–3.9 × 2.3–2.5. Gioia *et al*. (1987) reported the occurrence of *Myxidium* sp. in the gall bladder of *Bufo paracnemis* from Brazil. The spores, elliptical in front view, laterally spindle-shaped, with 4–5 transverse ridge striations, measured 14.2 (13.3–15.8) × 9.8 (8.9–10.5). The polar capsules were 4.2 long, and the polar filament formed 4 coils.

The species *Leptotheca ranae* found in *Rana fusca* and *R. esculenta* in France by Thélohan (1894) without a suitable description must be considered a nomen nudum (Desser *et al*. 1986). The species *Leptotheca ranae* described by Morelle (1929) from the kidney tubules of *Rana temporaria* in Belgium was assigned provisionally to the genus *Wardia* due to its apparent differences from the genus *Leptotheca* – for discussion see Desser *et al*. (1986).

Ultrastructural scanning observations were provided for *Myxidium serotinum* (McAllister *et al*. (1995), *M. immersum* (Delvinquier 1986) and *M. lesminteri* (Delvinquier *et al*. 1992), and TEM descriptions were reported for *Myxobolus* sp. from *Bufo regularis* (Mubarak and Abed 2001), *Chloromyxum* sp. from *Megophrys nasuta* (Duncan *et al*. 2004) and *Myxidium mackiei* from *Lissemys punctata andersonii* (Helke and Poynton 2005).

Pathology

The reports on the pathology of the infection of amphibians and reptiles by myxosporeans are variable. Some authors did not find gross pathology associated with the infection and the host's health was apparently unaffected: *Chloromyxum salamandrae* in the gall bladder of *Eurycea multiplicata griseogaster*, *E. m. multiplicata* and *E. neotenes* (Upton *et al*. 1995), *Myxobolus fallax* in the testes of *Litoria fallax* (Browne *et al*. 2002), *Myxobolus bufonis* in the testes of *Bufo maculatus* (Upton *et al*. 1992), *Myxobolus* sp. in the testes of *Bufo regularis* and *Ptychadena maccarthyensis* (Théodoridès *et al*. 1981) and *Myxidium mackiei* in the kidney of *Lissemys punctata andersonii* (Helke and Poynton 2005) and in the kidney of *Trionyx gangeticus* (Bosanquet 1910).

In some cases moderate pathological changes were observed. *Litoria darlingtoni* infected by *Myxobolus chimbuensis* showed very few sperm and little meiotic activity, and the testes were enlarged and slightly discoloured (Ewers 1973). Small cellular changes in the epithelial cells of the renal tubules of *Megophrys nasuta* parasitized by *Chloromyxum careni* were reported by Mutschmann (1999). *Hyla aurea* infected by *Myxobolus hylae* appeared sickly and emaciated, and in cases of heavy infections the testes were swollen (Johnston and Bancroft 1918).

Severe changes in the testes of the Egyptian toad *Bufo regularis* were described by Mubarak and Abed (2001). In some cases the plasmodia of the parasites were so abundant that the plasmodia occupied almost all the testicular tissue. Disruption and complete destruction of the seminiferous tubules were observed; extensive haemorrhages were usually seen in the infected testes, and the interstitial cells were vacuolated and swollen.

In other cases severe pathological changes, which can lead to the death of the host, were described. Hill *et al*. (1997) reported severe hepatitis in farmed green tree frogs, *Litoria caerulea*, associated with the presence of *Myxidium* sp. trophozoites in the bile ducts, including distension and partial occlusion of bile ducts, together with peribiliary fibrosis and associated inflammation. According to these authors field investigations of declining frog populations should consider *Myxidium* sp. as potential pathogens and they suggested that infected specimens should be submitted for laboratory examination. Mutschmann (2004) described the pathology of kidney infections in frogs *Afrixalus dorsalis* and *Hyperolius con-*

color by *Hoferellus anurae*. In both host species there was extensive renal pathology which could lead to the loss of renal function and reduce vitality of the hosts. The author proposed for this condition the name "frog kidney enlargement disease" (FKED). Desser *et al*. (1986) studied the pathology of the infection of *Sphaerospora ohlmacheri* in the renal tubules of *Rana catesbeiana*. The parasites were associated with extensive dystrophic changes in the renal tubular epithelium. These changes were often characterised by the presence of large eosinophilic droplets containing a hyaline-like material in the cytoplasm of the host cell. The nuclei of affected cells were pycnotic, cell membranes were not clearly visible, and many cells appeared necrotic. Ohlmacher (1893) found a single specimen of *Bufo lentiginosus* with the kidney infected by an unidentified myxosporean. He observed generalised oedema, kidney enlarged about twice its normal size, and mechanical blocking of the kidney tubules. The death of the host was attributed to the parasite infection.

Duncan *et al*. (2004) recently described kidney infections in eight specimens of Asian horned frog, *Megophrys nasuta*, imported into U.S.A. In all the cases the parasite was judged to be the primary cause of death. Histological changes in the kidneys included varying degrees of renal tubular dilation and necrosis and mild to severe, nonsupurative intestinal nephrites associated with vegetative stages of myxosporidia. Five of the frogs also exhibited severe ulcerative dermatitis and cellulitis that contributed to their death. Severe hepatic pathology was also observed in five specimens.

Hosts and geographical distribution

At least 83 species of amphibians and 15 species of reptiles are known to be infected by myxosporeans belonging to several genera (*Myxidium*, *Myxobolus*, *Chloromyxum*, *Caudomyxum*, *Hoferellus* and *Sphaerospora*) (Table I). The occurrence of myxosporeans in reptiles is probably higher than the figures suggested by these data, and the low number of reptiles known to be infected is probably due to lack of research. The results of Johnson (1969) who found 14 of 21 species and subspecies of North American turtles infected with *Myxidium chelonarum* suggest that myxosporeans may be frequent parasites of aquatic reptiles.

The geographical distribution of the parasites is wide – the infection was reported in Europe, North and South America, Africa, Asia and Australia, and the majority of the hosts were reported from Australia (20) and U.S.A. (53). However, this fact does not necessarily means that infection is more abundant in some places, but probably that research was more intense there. It is important to note that a few researchers are responsible for most of the hosts reported so far (Johnson 1969; Delvinquier 1986; McAllister and Upton 1987; McAllister *et al*. 1989, 1995; Delvinquier *et al*. 1992; Upton *et al*. 1992, 1995; McAllister and Trauth 1995; McAllister and Freed 1996; Mutschmann 1999, 2004). A survey of the infection in other places would probably lead to the discovery of new hosts as well as new species of parasites including possibly other genera of myxosporeans not yet reported from amphibians and reptiles. Places worth investigating specifically include Central and South America, as well as Africa, where the diversity of amphibians (and aquatic reptiles) is higher, and very little research is currently being conducted. The same occurs in Europe – for this continent only *Myxobolus ranae* was described by Guyénot and Naville (1922) for *Rana temporaria* in Switzerland, *Caudomyxum caudatum* (Thélohan, 1894) Upton, McAllister and Trauth, 1995 from *Triturus cristatus* from France, *Myxidium danilewskyi* Laveran, 1897 from *Emys orbicularis* in France, and *Chloromyxum protei* Joseph, 1905 from *Proteus anguineus* from Austria (assuming that *Leptotheca ranae* Thélohan, 1894 is a nomen nudum).

At least in one case the geographical distribution of the parasites is likely to be partially explained by artificial movements of the host: the presence of *Myxidium immersum* in Australia was attributed to the artificial displacement of the host *Bufo marinus* (Delvinquier 1986). *Bufo marinus* was introduced in Australia in June, 1935 in an attempt to eradicate two species of beetles, *Lepidoderma albohirtum* and *Lepidota frenchi*, from the sugarcane fields. According to Delvinquier (1986) *M. immersum* was introduced into Australia with *B. marinus*, and this led to the infection of native Australian frogs including, in 1986, 12 species of *Litoria*, 4 species of *Limnodynastes*, one species of *Myxophyes*, one species of *Ranidella* and one species of *Litoria*.

The artificial transmission of fish myxosporeans, sometimes causing significant economic damages, is well known and documented for several species due to the trade of fish (Hoffman 1970) or the alternative hosts of the parasites (Lowers and Bartholomew 2003). However, this mechanism of dissemination is likely to be less important in the case of amphibians and reptiles due to a lesser extent of artificial movements.

Host specificity

The current information suggests that host specificity for myxosporeans infecting amphibians and reptiles, if any, is the exception rather than the rule. Some species were described from many hosts. For example, *Myxidium immersum* was reported from at least 34 different amphibian hosts, *M. serotinum* was reported from 37 amphibians, and *M. chelonarum* was observed in 14 species of reptiles. Clark and Shoemaker (1973) concluded that the salamander *Eurycea bislineata* was the "preferred" host for *Myxidium serotinum* and that anurans should be regarded as "incidental hosts". However, McAllister and Upton (1987) found contradictory results and stated that "there is little host specificity in amphibians for the Myxosporea". Several other species were also observed infecting several host species: *Myxidium lesminteri*, *Myxobolus chimbuensis*, *Hoferellus anurae* and *Chloromyxum salamandrae*.

In contrast, other species were reported from a single host species (see Table I): *Myxidium haldari*, *Myxobolus hylae*,

Table I. Myxosporean species infecting amphibians and reptiles: Hosts and geographical location

Host	Location	Reference
	***Myxidium immersum* Lutz, 1889**	
Anura		
Bufonidae		
Bufo arenarum	Uruguay	Cordero (1919)
Bufo dorbignyi	Uruguay	Cordero (1919)
Bufo marinus	Brazil	Carini (1932)
Bufo marinus	Brazil	Kudo and Sprague (1940)
Bufo marinus	Germany?	Lühe (1899)
Melanophryniscus stelzneri	Uruguay	Cordero (1919)
Hylidae		
Hyla pulchella	Uruguay	Cordero (1919)
Hyla raddiana	Uruguay	Cordero (1919)
Ololygon nebulosa	Brazil	Carini (1932)
Ololygon rubra	Brazil	Carini (1932)
Hylidae (Pelodryadidae)		
Litoria caerulea	Australia	Delvinquier (1986)
Litoria dentata	Australia	Delvinquier (1986)
Litoria fallax	Australia	Delvinquier (1986)
Litoria latopalmata	Australia	Delvinquier (1986)
Litoria lesueri	Australia	Delvinquier (1986)
Litoria nasuta	Australia	Delvinquier (1986)
Litoria nyakalensis	Australia	Delvinquier (1986)
Litoria peronii	Australia	Delvinquier (1986)
Litoria revelata	Australia	Delvinquier (1986)
Litoria rubella	Australia	Delvinquier (1986)
Litoria tyleri	Australia	Delvinquier (1986)
Litoria verreauxii	Australia	Delvinquier (1986)
Leptodactylidae		
Leptodactylus prognathus	Uruguay	Cordero (1919)
Leptodactylus latinasus	Uruguay	Cordero (1919)
Leptodactylus ocellatus	Brazil	Lutz (1889)
Leptodactylus ocellatus	Uruguay	Cordero (1919)
Leptodactylus ocellatus	Brazil	Cordero (1928)
Limnomedusa macroglossa	Uruguay	Cordero (1928)
Odontophrynus americanus	Uruguay	Cordero (1928)
Physalaemus signifer	Brazil	Carini (1932)
Pelurodema bibroni	Uruguay	Cordero (1919)
Myobatrachidae		
Crinia parinsignifera	Australia	Delvinquier (1986)
Limnodynastes ornatus	Australia	Delvinquier (1986)
Limnodynastes peronii	Australia	Delvinquier (1986)
Limnodynastes tasmaniensis	Australia	Delvinquier (1986)
Limnodynastes terraereginae	Australia	Delvinquier (1986)
Uperoleia laevigata	Australia	Delvinquier (1986)
Mixophyes fasciolatus	Australia	Delvinquier (1986)
Ranidella parinsignifera	Australia	Delvinquier (1986)
Pseudidae		
Lysapsus mantidactylus	Uruguay	Cordero (1919)
	***Myxidium serotinum* Kudo et Sprague, 1940**	
Anura		
Bufonidae		
Bufo debilis debilis	U.S.A.	McAllister *et al*. (1989)
Bufo terrestris	U.S.A.	Kudo (1943)
Bufo valliceps valliceps	U.S.A.	McAllister *et al*. (1989)
Bufo woodhousii woodhousii	U.S.A.	McAllister *et al*. (1989)
Bufo americanus charlesmithi	U.S.A.	McAllister *et al*. (1995)
Bufo speciosus	U.S.A.	McAllister *et al*. (1995)
Hylidae		
Pseudacris clarkii	U.S.A.	McAllister (1991)
Pseudacris streckeri streckeri	U.S.A.	McAllister (1987)
Acris crepitans blanchardi	U.S.A.	McAllister *et al*. (1995)

Hyla avivoca	U.S.A.	McAllister *et al*. (1995)
Hyla chrysocelis	U.S.A.	McAllister *et al*. (1995)
Hyla cinerea	U.S.A.	McAllister *et al*. (1995)
Pseudacris crucifer crucifer	U.S.A.	McAllister *et al*. (1995)
Pseudacris streckeri illinoensis	U.S.A.	McAllister *et al*. (1995)
Ranidae		
Rana clamitans	U.S.A.	Kudo (1943)
Rana pipiens	U.S.A.	Kudo and Sprague (1940)
Rana sphenocephala	U.S.A.	Kudo (1943)
Rana sp.	U.S.A.	Kudo and Sprague (1940)
Rana berlandieri	U.S.A.	McAllister *et al*. (1995)
Rana blairi	U.S.A.	McAllister *et al*. (1995)
Rana catesbeiana	U.S.A.	McAllister *et al*. (1995)
Rana clamitans melanota	U.S.A.	McAllister *et al*. (1995)
Rana utricularia	U.S.A.	McAllister *et al*. (1995)
Leptodactylidae		
Syrrhophus cystignathoides campi	U.S.A.	McAllister *et al*. (1995)
Microhylidae		
Gastrophyne carolinensis	U.S.A.	McAllister *et al*. (1995)
Gastrophyne olivacea	U.S.A.	McAllister *et al*. (1995)
Caudata		
Ambystomatidae		
Ambystoma texanum	U.S.A.	McAllister and Upton (1987)
Ambystoma annulatum	U.S.A.	McAllister *et al*. (1995)
Ambystoma opacum	U.S.A.	McAllister *et al*. (1995)
Ambystoma tigrinum mavortium	U.S.A.	McAllister *et al*. (1995)
Plethodontidae		
Eurycea quadridigitata	U.S.A.	McAllister *et al*. (1995)
Desmognathus fuscus conanti	U.S.A.	McAllister *et al*. (1995)
Hemidactylium scutatum	U.S.A.	McAllister *et al*. (1995)
Plethodon caddoensis	U.S.A.	McAllister *et al*. (1995)
Plethodon ovachitae	U.S.A.	McAllister *et al*. (1995)
Plethodon serratus	U.S.A.	McAllister *et al*. (1995)
Salamandridae		
Notophthalmus viridescens louisianensis	U.S.A.	McAllister *et al*. (1995)
Sirenidae		
Siren intermedia nettingi	U.S.A.	McAllister *et al*. (1995)
	***Myxidium haldari* Sarkar, 1982**	
Anura		
Hylidae		
Hyla arborea	India	Sarkar (1982)
	***Myxidium lesminteri* Delvinquier, Markus et Passmore, 1992**	
Anura		
Bufonidae		
Bufo garmani	South Africa	Delvinquier *et al*. (1992)
Heleophrynidae		
Heleophryne natalensis	South Africa	Delvinquier *et al*. (1992)
Ranidae		
Tomopterna krugerensis	South Africa	Delvinquier *et al*. (1992)
Tomopterna cryptotis	Namibia	McAllister and Freed (1996)
	***Myxidium chelonarum* Johnson, 1969**	
Reptilia		
Pseudemys scripta scripta	U.S.A.	Johnson (1969)
Chelydra serpentina serpentina	U.S.A.	Johnson (1969)
Kinosternon sonoriense	U.S.A.	Johnson (1969)
Sternotherus odoratus	U.S.A.	Johnson (1969)
Graptemys pulchra	U.S.A.	Johnson (1969)
Graptemys pulchra pseudographica	U.S.A.	Johnson (1969)
Pseudemys nelsoni	U.S.A.	Johnson (1969)
Pseudemys scripta elegans	U.S.A.	Johnson (1969)
Pseudemys s. scripta × elegans	U.S.A.	Johnson (1969)
Pseudemys floridana floridana	U.S.A.	Johnson (1969)
Pseudemys concinna hieroglyphica	U.S.A.	Johnson (1969)
P. c. concinna × hieroglyphica	U.S.A.	Johnson (1969)
Chrysemys picta picta	U.S.A.	Johnson (1969)
Deirochelys reticularia	U.S.A.	Johnson (1969)

***Myxidium americanum* Kudo, 1919**		
Reptilia		
Trionix spinifera	U.S.A.	Kudo (1919)
***Myxidium mackiei* Bosanquet, 1910**		
Reptilia		
Trionix gangeticus	India	Bosanquet (1910)
Lissemys punctata andersonii	India	Helke and Poynton (2005)
***Myxidium danilewskyi* Laveran, 1897**		
Reptilia		
Emys orbicularis	France	Laveran (1897)
***Chloromyxum careni* Mutschmann, 1999**		
Anura		
Pelobatidae		
Megophrys nasuta	Indonesia	Mutschmann (1999)
***Chloromyxum protei* Joseph, 1905**		
Caudata		
Proteidae		
Proteus anguineus	Austria	Joseph (1905)
***Chloromyxum salamandrae* Upton, McAllister et Trauth, 1995**		
Caudata		
Plethodontidae		
Eurycea multiplicata griseogaster	U.S.A.	Upton *et al*. (1995)
Eurycea multiplicata multiplicata	U.S.A.	Upton *et al*. (1995)
Eurycea neotenes	U.S.A.	Upton *et al*. (1995)
***Myxobolus hylae* Johnston et Bancroft, 1918**		
Anura		
Hylidae		
Hyla aurea	Australia	Johnston and Bancroft (1918)
***Myxobolus chimbuensis* Ewers, 1973**		
Anura		
Hylidae (Pelodryadidae)		
Litoria darlingtoni	New Guinea	Ewers (1973)
Litoria thesaurensis	New Guinea	Ewers (1973)
***Myxobolus bufonis* Upton, Freed, Freed, McAllister et Goldberg, 1992**		
Anura		
Bufonidae		
Bufo maculatus	Cameroon	Upton *et al*. (1992)
***Myxobolus fallax* Browne, Sheltinga, Pomering et Mahony, 2002**		
Anura		
Hylidae (Pelodryadidae)		
Litoria fallax	Australia	Browne *et al*. (2002)
***Myxobolus ranae* Guyénot et Naville, 1922**		
Anura		
Ranidae		
Rana temporaria	Switzerland	Guyénot and Naville (1922)
***Hoferellus anurae* Mutschmann, 2004**		
Anura		
Hyperoliidae		
Afrixalus dorsalis	Nigeria	Mutschmann (2004)
Hyperolius concolor	Ghana	Mutschmann (2004)
Hyperolius sp.	Tanzania	Mutschmann (2004)
***Sphaerospora ohlmacheri* Desser, Lom et Dyková, 1986 (*Chloromyxum ohlmacheri* Whinery, 1893)**		
Anura		
Ranidae		
Rana castesbeiana	Canada	Desser *et al*. (1986)
***Caudomyxon caudatum* Upton, McAllister et Trauth, 1995 (*Chloromyxum caudatum* Thélohan, 1894)**		
Caudata		
Salamandridae		
Triton cristatus	France	Upton *et al*. (1995)

M. fallax, *M. ranae*, *M. bufonis* and *Chloromyxum careni*. However, it is not clear whether these species are specific for their hosts, since in most of the descriptions only one host species was observed. *Myxobolus hylae* was observed only in *Hyla aurea* but not in sympatric *H. caerulea* in Australia (Cleland and Johnston 1910, Johnston and Bancroft 1918). However, the authors did not report how many specimens were observed. Browne *et al*. (2002) examined four hylids and four myobatrachids from locations where *Litoria fallax* was infected with *Myxobolus fallax*, and found that the specimens were not infected.

Clearly more research is needed to clarify this question.

Life cycle

As far as the author is aware there are no studies on the life cycle of myxosporeans infecting amphibians and reptiles. Taking into account the two host life cycle described for the first time for *Myxobolus cerebralis* by Wolf and Markiw (1984) and latter observed for a great number of different species of myxosporeans infecting fish, it is highly probable that the same type of cycle exists for the parasites of amphibians and reptiles.

The abundance of the presumptive invertebrate hosts is likely to explain the distribution of *Myxidium immersum* in Australia. According to Delvinquier (1986), variations in the distribution of possible intermediate host(s) could explain the scarcity of *M. immersum* in North Queensland. On the other hand, abundance of the intermediate host(s) could lead to the high percentage of infection in southern Queensland.

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