

# Microsporidia: diverse, dynamic, and emergent pathogens in aquatic systems

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**Microsporidia cause important diseases in aquatic organisms. Susceptible hosts span a remarkable taxonomic spectrum, from protists to mammals. Known genera represent a small fraction of extant taxa in global aquatic systems. Transmitting horizontally or vertically, effects range from cryptic to catastrophic; individual level effects being extrapolated to populations and ecosystems. Debate over positioning within the eukaryotes and internal structuring of the phylum has benefited from molecular phylogenetic approaches to taxonomy. Similar tools offer new perspectives on transmission between hosts of differing trophic status and habitats. Accessible models for host–pathogen interaction are emerging from full genome sequencing projects. Hyperparasitism and the close phylogenetic relationship between taxa infecting invertebrates and vertebrates not only underline a ubiquity in aquatic systems but also potential for zoonotic transfer.**

## The evolution of a discipline

The Microsporidia are a diverse parasite phylum infecting host groups from all major taxa in all environments [1,2]. The vast field of research into Microsporidia has focussed on terrestrial hosts, ranging from those infecting pest and beneficial insects, to important parasites of humans. Yet, despite the fact that almost half of the known microsporidian genera infect aquatic hosts, the emergence of this discipline is more recent. Here, we outline the taxonomic status of the parasites found infecting an incredible diversity of aquatic hosts (from protist to vertebrates) and, further, utilise a clarifying taxonomic framework to highlight some important linkages between those parasites infecting hosts from similar and different ecological set-

tings. Recent research demonstrating potential for extreme morphological plasticity and an ability to infect all known organ and tissue systems is important not only for effects at the individual level but also, in driving change in populations and communities of aquatic hosts. Global change provides urgency to develop our understanding of the role of Microsporidia in ecological communities and their potential to cause emergent diseases in aquatic animals, and in humans.

Microsporidian outbreaks affecting the silkworm industry in Europe were documented in the 1800s. But even prior to these reports, pathogens later shown to be microsporidians were reported infecting fish (e.g., *Glugea anomala* in stickleback [3]). By the turn of the 20th century, researchers had also provided evidence that microsporidians were also significant pathogens of aquatic invertebrates including freshwater crayfish and marine crabs [4,5]. Although such work established the field of microsporidiology in aquatic hosts, the contextualisation of discoveries in the aquatic realm with those occurring in terrestrial settings did not occur until the first taxonomic frameworks were erected in the mid-20th century [6]. Early attempts to classify known taxa [7] proceeded to the grouping of known taxa to genera [8], comprehensive systematic reviews [9], and erection of the phylum Microspora (later Microsporidia Balbiani, 1882) by 1977. Establishment of the phylum brought together research in aquatic and terrestrial microsporidiology and led to further refinement of taxonomic frameworks between the mid-1980s and 2000 [10–13]; by 2012, over 187 genera (1500 species) were recorded [14]. Parallel to research and opinion regarding internal organisation of the phylum has been intensive debate on its relative position within eukaryotic phylogenies. Prevailing phylogenetic evidence provides strong support for placement of microsporidians as divergent fungi rather than protists [15]. Although this may have been expected to necessitate their classification according to rules of the International Code for Botanical Nomenclature (ICBN), current opinion is that taxa within the phylum should continue to be classified according to the rules of the International Commission on Zoological

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Nomenclature (ICZN) [16,17]. Regardless of higher ordering, it is now well accepted that integrated use of available data (host type, ecology, pathology, ultrastructure, and phylogenetics) should be employed when attempting to classify novel pathogens within the phylum [18,19]. In aquatic hosts, an increasingly efficient taxonomic rationale provides the necessary backdrop for recognition of the role of Microsporidia in individual and population modulation, for studies on their potential emergence in novel hosts and locations, and for realising the potential for zoonoses in specific taxa.

### Diversity of underwater microsporidians

Of the 187 genera described to date [14], almost half are known to infect aquatic organisms. Excluding genera which infect aquatic life stages of insects, approximately 20 genera infect fish, 50 genera infect aquatic arthropods, and at least 21 genera infect aquatic non-arthropod invertebrates, protists, and hyperparasites of aquatic hosts (Tables 1–3). Historic ability to detect microsporidian infections based upon external clinical signs [4] has been augmented by application of pathological and molecular diagnostic approaches, allowing for detection of cryptic and subclinical infections [20]. In addition, access to hosts from a wide range of aquatic environments has expanded the phylum considerably [21]. Microsporidians occur in hosts inhabiting freshwater, brackish, and marine environments and from a wide array of habitats therein, including temporary water bodies, lakes and rivers, estuaries, rocky shorelines, open ocean, and the deep ocean floor.

All of the 20 genera infecting fish occur in hosts from the class Osteichthys (bony fish). To date, no examples have been reported from cartilaginous fish (such as sharks) or from jawless cyclostomes (such as hagfish). A predominant

focus on commercially exploited or model taxa within the 30 000 extant osteichthyds provides the assumption that microsporidian parasites are probably vastly underreported within this group. In addition, the taxonomic range of invertebrate and protistan hosts known to be susceptible to infection by microsporidians appears even more remarkable. Although the majority infect aquatic arthropods (Box 1), parasitism has also been reported in the Arachnida [22], Mollusca [23,24], Hydrozoa [25], Nematoda [26], Rotifera [27], Clitelata [28], Kinorhyncha [29], Acanthocephala [30], Phylactolaemata [31–33], Oligochaeta [34,35], Cestoda [36,37], Digenea [38,39], Monogenea [40], and Dicyemida [41]. They also infect protists from the Gregarinasina [42–44], Amoebozoa [45], and Ciliophora [46,47]. Coupling the capacity to infect such a wide taxonomic range of hosts, and the relative lack of attention applied to pathogen profiling of aquatic organisms, it is apparent that many thousands of microsporidian taxa remain undescribed in aquatic hosts. Furthermore, the remarkable demonstration of infection capacity across almost all trophic levels within the invertebrate phyla (and indeed within cohabiting aquatic vertebrate hosts) is suggestive that trophic transfer of microsporidians in aquatic environments remains a probable but largely unexplored phenomenon [48]. The presence of microsporidian pathogens within protists, such as gregarines, and as hyperparasites of fish pathogens, such as digeneans, proposes a potential vector role for these hosts to higher invertebrates and to fish, over evolutionary timescales. Improved phylogenetic information for members of the Rudimicrospora (e.g., *Mechnikovella* sp. infecting gregarine symbionts of invertebrate hosts) offers an obvious route to investigate this hypothesis [49].

**Table 1. The described genera of Microsporidia infecting fish**

Genus	Host class <sup>a</sup>	Example host	Target organ/tissue	Taxonomic attribution <sup>c</sup>
<i>Amazonspora</i>	Osteichthyes	<i>Hassar orestis</i>	Gill	Azevedo and Matos, 2003
<i>Dasyatispora</i> <sup>b</sup>	Osteichthyes	<i>Dasyatis pastinaca</i>	Musculature	Diamant <i>et al.</i> , 2010
<i>Glugea</i> <sup>b</sup>	Osteichthyes	<i>Gasterosteus aculeatus</i>	Various	Thelohan, 1891
<i>Heterosporis</i> <sup>b</sup>	Osteichthyes	<i>Pseudocrenilabrus multicolor</i>	Musculature	Schubert, 1969
<i>Ichthyosporidium</i> <sup>b</sup>	Osteichthyes	<i>Crenilabrus melops</i>	Musculature	Caullery and Mesnil, 1905
<i>Kabatana</i> <sup>b</sup>	Osteichthyes	<i>Oncorhynchus tshawytscha</i>	Musculature	Lom <i>et al.</i> , 2000
<i>Loma</i> <sup>b</sup>	Osteichthyes	<i>Oncorhynchus tshawytscha</i>	Gill	Morrison and Sprague, 1981
<i>Microfilium</i>	Osteichthyes	<i>Lutjanus fulgens</i>	Gill	Faye <i>et al.</i> , 1991
<i>Microgemma</i> <sup>b</sup>	Osteichthyes	<i>Chelon labrosus</i>	Liver	Ralps and Matthews, 1986
<i>Microsporidium</i>	Osteichthyes	<i>Prosopium williamsoni</i>	Various	Balbani, 1884
<i>Myosporidium</i> <sup>b</sup>	Osteichthyes	<i>Merluccius capensis</i>	Musculature	Baquero <i>et al.</i> , 2005
<i>Neonosemoides</i>	Osteichthyes	<i>Tilapia zilli</i>	Gill	Faye and Togubaye, 1996
<i>Nucleospora</i> <sup>b</sup>	Osteichthyes	<i>Oncorhynchus tshawytscha</i>	Kidney	Hedrick <i>et al.</i> , 1991
<i>Ovipleistophora</i> <sup>b</sup>	Osteichthyes	<i>Rutilus rutilus</i>	Ovary	Pekkarinnen <i>et al.</i> , 2002
<i>Paranucleospora</i> <sup>b</sup>	Osteichthyes	<i>Salmo salar</i>	Haematopoietic cells	Nylund <i>et al.</i> , 2010
<i>Pleistophora</i> <sup>b</sup>	Osteichthyes	<i>Mugil auratus</i>	Various	Gurley, 1893
<i>Potaspora</i> <sup>b</sup>	Osteichthyes	<i>Potamorhaphis guianensis</i>	Abdominal lining (serosa)	Casal <i>et al.</i> , 2008
<i>Pseudoloma</i> <sup>b</sup>	Osteichthyes	<i>Danio rerio</i>	Nervous tissues	Matthews <i>et al.</i> , 2001
<i>Spraguea</i> <sup>b</sup>	Osteichthyes	<i>Lophius piscatorius</i>	Nervous tissues	Weissenberg, 1976
<i>Tetramicra</i> <sup>b</sup>	Osteichthyes	<i>Scophthalmus maximus</i>	Musculature	Matthews and Matthews, 1980

<sup>a</sup>Hosts are classified into the class Osteichthys.

<sup>b</sup>Nucleotide sequence data available within NCBI database (accessed at time of writing).

<sup>c</sup>Taxonomic attribution refers to original description of genus.

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