ABSTRACT: Trematodes serve as outstanding hosts for a variety of parasites. This paper restricts those parasites to three groups of non-related taxa parasitizing trematodes and forming invasive spores similar in external morphology, which is why in the past these three groups of parasitic eukaryotes were united into the taxon “Sporozoa” (Kudo, 1924). (1) Trematode-infecting microsporidia (type Microsporidia Balbiani, 1882: Rozellomycota: Holomycota) are represented by more than 30 species. Among those, the species with sequenced barcode (SSU rDNA) are phylogenetically associated with either microsporidia from invertebrates, as the species of the genus Unikaryon (7 species), or fish microsporidia, as the species of the genera Pleistophora and Ovipleistophora or alike forms (4 species). However, most of the species that we place in the incertae cedis group, are known only by light-microscopy descriptions. Those were attributed by the authors to the genera Nosema (14 species) and Microsporidium (8 species), but in fact their taxonomic affiliation, phylogenetic position, and origin remain unknown. (2) Trematode-infecting haplosporidia (type Haplosporida Caulleri Mesnil, 1899: Ascetosporea: SAR) are represented by only one genus Urosporidium with a broad range of hosts among marine helminths and free-living invertebrates. The literature describes 10 Urosporidium spp. infecting trematodes. (3) Myxosporidia or Myxozoa (subclass Myxospora Butchli, 1881: class Myxozoa Grasse, 1970: Cnidaria: Holozoa) infect mainly fish. All three species known from trematodes, belong to the genus Fabespora, and, likely, switched to hyperparasitism from fish. These three spore-forming groups demonstrate a diversity of characteristics and group-specific physiological mechanisms in addition to common adaptations responding to similar environmental conditions. These forms developed from genetically dissimilar material and exemplify an amazing power of convergent evolution, a phenomenon A.A. Dobrovolskii and other Russian scholars of parasitology demonstrated for a variety of parasitic groups.

KEY WORDS: Convergent evolution, Trematoda, Haplosporidia, hyperparasitism, Microsporidia, Myxozoa, Nosema, Pleistophora, Unikaryon, Urosporidium.
Гиперпаразитические спорообразующие зукариоты (Microsporidia, Haplosporidia и Myxozoa) — паразиты в трематодах (Platyhelminthes)

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Резюме: Трематоды хорошо известны как хозяева разнообразных паразитических организмов. В настоящей статье рассмотрены представители трех неродственных таксонов зукариот, представители которых паразитируют в трематодах и формируют инвазионные споры, сходные по внешней морфологии, из-за чего в прошлом эти три группы паразитических зукариот объединялись в тип Sporozoa (Kudo, 1924). (1) Микроспоридии (тип Microsporidia Balbiani, 1882: Rozellomycota: Holomycota) представлены более чем 30 видами. Виды с отсеквенированным баркодом (участок rDNA) филогенетически связаны либо с микроспоридиями беспозвоночных, как виды рода Unikaryon (7 видов), либо с микроспоридиями рыб, как виды родов Pleistophora и Ovipleistophora (4 вида). Однако большинство видов, которые мы поместили в группу incertae sedis, известны лишь по светооптическим описаниям и отнесены авторами описаний к родам Nosema spp. (14 видов) и Microsporidium spp. (8 видов). (2) Гаплоспоридии (тип Haplosporida Caulleri et Mesnil, 1899: Ascetospora: Unikaryon) представлены только одним родом Urosporidium, имеющим широкий спектр хозяев среди морских беспозвоночных, как паразитических, так и свободноживущих. В литературе описано 10 видов, заражающих трематод. (3) Миксоспоридии или Myxozoa (п/класс Myxospora Butchli, 1881: класс Myxozoa Grasse, 1970: тип Cnidaria: Holozoa), заражающих, главным образом, рыб. Все 3 вида, известные из трематод, принадлежат к роду Fabespora, и, очевидно, перешли к гиперпаразитированию с рыб. Эти три генетически неродственные группы «Sporozoa» демонстрируют разнообразные признаки и физиологические механизмов, специфичные для каждой группы, но также и сходные адаптации к паразитизму, выраженные, в частности, в сходстве морфотипов и некоторых особенностях патогенеза. В целом, описанные группы зукариотических микробиорганизмов представляют собой наглядный пример конвергентной эволюции — феномена, многократно описанного А.А. Добровольским и другими представителями Российской школы паразитологии на различных группах паразитов. Как цитировать эту статью: Sokolova Yu.Ya., Overstreet R.M. 2020. Hyperparasitic spore-forming eukaryotes (Microsporidia, Haplosporidia, and Myxozoa) parasitizing trematodes (Platyhelminthes) // Invert. Zool. Vol.17. No.2. P.93–117. doi: 10.15298/invertzool.17.2.01

Ключевые слова: конвергентная эволюция, Trematoda, Haplosporidia, гиперпаразитизм, Microsporidia, Myxozoa, Nosema, Pleistophora, Unikaryon, Urosporidium.
Introduction

This review is dedicated to Andrey Aleksandro维奇 Dobrovolskii, a brilliant university professor having a bright personality, a man of the highest culture and integrity, and an outstanding parasitologist specializing in trematodes. His fascinating lectures on protistology, invertebrate zoology, parasitology, and particularly on trematode life cycles, made listeners fall in love with the creatures that he discussed as well as with Nature and Science in general. These lectures inspired students of several generations, including the first author of this paper, to remain in the field of parasitology throughout their lives. This paper contains the overview of the current state of research on eukaryotic parasites of trematodes, thus covering subjects that always were in the focus on Prof. Dobrovolskii’s interests, namely the biology of trematodes and the phenomenon of hyperparasitism. The fact that large parasites have smaller parasites and that they yet have smaller parasites has thrilled biologists for centuries, possibly before pointed out in an early poem (Swift, [1733] 1910). In conjunction with the microscope’s invention, a mathematician (De Morgan, 1915) developed a rhyme based on Jonathan Swift’s poem, “Big fleas have little fleas upon their backs to bite ’em; and little fleas have lesser fleas, and so ad infinitum.” The first comprehensive review of the known literature on hyperparasitic associations among helminths including parasites of trematodes, appeared in 1946 (Dollfus, 1946).

Trematodes seem to provide an acceptable home to a variety of eukaryotic parasites, like microsporidia, myxozoa, haplosporidia, ciliates, flagellates, and amoebae as well as bacteria and viruses. Complicated life cycles of trematodes that, in the course of their lifespans, infect several hosts belonging to various trophic levels, providing exceptional opportunities for the parasites to hitchhike between various invertebrates and vertebrates, particularly those in marine and freshwater ecosystems. Parasitizing trematodes should facilitate host-switching, spreading infections throughout the habitat, and horizontal gene transfer among secondary and primary hosts of the hyperparasites.

As an example, a parasite that we are not treating in detail (Overstreet, 1976b), we note a diplomonad flagellate (Hexamita sp.) in the intestine of Crassicutis archosargi (Digenea) but not in its fish host, the sheepshead (Archo-sargus probatocephalus), similar to a larger species of Hexamita in reproductive systems and eggs of Deropristis inflata (Digenea) in the American eel, Anguilla rostrata, from near Woods Hole, Massachusetts (Hunninen, Wichterman, 1938). Several authors (e.g., Dollfus, 1946; Overstreet, 1976b) discuss these other protists. A few trematodes of herbivorous hosts in Mississippian, such as the common mullet small haploporids (< 1 mm long) Xiha fastigata (previously known as Dicrogaster f.) and Saccocoe-lioides beauforti (recently referred to as Culuwia b.) contain motile bacteria in their excretory vesicles. A couple of attempts to extract the bacteria using capillary tubes to collect, culture, and identify (or sequence) were unsuccessful (RMg, unpublished data), but we encourage others to achieve this with the same or other hyperparasitic bacteria and techniques. The bacteria in the haploporids seem to be non-harmful symbionts unlike the bacterium Edwardsiella ictaluri in the metacercaria of the diplostomoid Bolbophorus damnificus, which readily kills the hyper-host (commercial catfish, Ictalurus punctatus) and unlike other discussed associative bacteria (Overstreet, Lotz, 2016).

The purpose of this publication is to discuss the non-related spore-forming, eukaryotic parasites in trematodes, namely 1) Microsporidia (type Microsporidia Balbiani, 1882: Rozellomyctota: Holomycota), 2) Haplosporidia (type Haplosporida Caulleri, Mesnil, 1899: Ascetomycota: Sar), and 3) Myxosporidia or Myxozoa (subclass Myxosporea Butchli, 1881: class Myxospora Grasse, 1970: Cnidaria: Holozoa). In fact, the World Register of Marine species (WoRMS) places them in three kingdoms (Fungi, Phylum Microsporidia; Chromista, Phylum Cercozoa; and Animalia, Phylum Cnidaria). From recent phylogenies in the Tree of Life (Fig. 1) joining plants and animals, the first group (Microsporidia) shows a close relation-
Fig. 1. Tree of Life (modified from Adl et al., 2019) demonstrates phylogenetic position of Microsporidia (Holomycota; Rozellamycota), Haplosporidia (SAR, Ascetosporea), and Myxosporidea (Holozoa, Cnidaria).

Microsporidia has yet to be established. Recent studies based on molecular data revealed a few peculiar phylogenetic associations of trematode-infecting microsporidia from crustacean and fish hosts with overlapping habitats, particularly marine and estuarine ones (Fig. 2). They suggest trophic transfer of microsporidian species, particularly those of the Clade 5 “Marinosporidia” (Vossbrinck et al., 2014; Stentiford et al., 2017a; Sokolova, Overstreet, 2018; Bojko et al., 2020). Presumably, some microsporidian taxa from the Clade 5 might have exploited life strategies of various parasites, including trematodes, to gain additional opportunities for transmission either within polyxenous life cycles or through predation of the infected host tissues by a potential alternative host (Stentiford et al., 2017a). However, direct evidence of a multi-host invertebrate-fish parasite life cycle has been demonstrated only for Paranucleospora theridion, which uses a salmonid fish (Atlantic salmon, Salmo salar, or rainbow trout, Oncorhynchus mykiss) as an intermediate host and an ectoparasitic copepod (Lepeophtheirus salmonis or Caligus elongates) as a definite host (Freeman et al., 2003; Nylund et al., 2010; Freeman, Sommerville, 2011). We stress that hyperparasitism has been commonly reported among “higher” microsporidia (Phylum Microsporidia; Class Microsporea, sensu Sprague, 1977). Noteworthy that metchnikovellids (Phylum Microsporidia; Class Rudimicrosporea, Order Metchnikovellida sensu Sprague, 1977), the basal and diverged group of the phylum Microsporidia, are all gregarine-infecting hyperparasites (Sokolova et al., 2013, 2014). In addition to trematodes, hyperparasitic microsporidia also infect Myxozoa, both myxosporean developmental sequences from fish (Kudo, 1939; Diamant, Paperna, 1985) and actinosporian sequences from oligochaetes (Morris, Freeman, 2010); paramyxids (Stentiford et al., 2017b); cestodes (Dissaneiakte, 1957; Canning, Gunn, 1984; Poddubnaya et al., 2006); and parasitic copepods (Nylund et al., 2010; Freeman, Sommerville, 2011). Hitchhiking in other parasites, and particularly trematodes, may be considered as one potential route of transmission and radi-
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Fig. 2. Phylogenetic tree combined from several SSUrDNA-based analyses (Stentiford et al., 2017a; Lovy, Friend, 2017; Sokolova, Overstreet, 2018) of the fragment of the Clade V (Marinosporidia). This class contains mostly fish-infecting species (fish icons), but also several peculiar phylogenetic associations (exclamation marks) suggesting presumable role of hyper-parasites, like trematodes, in potential host switching between fish and crustacean hosts (shrimp icons). Species parasitizing trematodes, are indicated by asterisks. The outgroup Clade IV contains the only known microsporidium with a polyxenous fish-crustacean lifecycle (Desmozoon lepeophtherii).

Рис. 2. Филограмма, объединяющая несколько филогенетических анализов на основании МCрДНК (Stentiford et al., 2017а; Lovy, Friend, 2017; Sokolova, Overstreet, 2018), демонстрирует связи внутри Клады V (класс “Marinosporidia”). Эта клада состоит, в основном, из видов, заражающих рыб (изображение рыбы), но также содержит несколько странных филогенетических ассоциаций (восклицательные знаки), которые предполагают роль гиперпаразитов (возможно, трекатод) в смене хозяев с рыб на ракообразных (изображение креветки) и обратно. Виды, паразитирующие у трекатод помечены звездочками. Внешняя группа, Класс IV, содержит единственный вид микроспоридии (Desmozoon lepeophtherii) с подтвержденным поликсенным (рыба-ракообразное) жизненным циклом.
ation of microsporidia (Stentiford et al., 2017a). Potential host-switching among infected trematode hosts or between trematodes and their hosts might have been facilitated by an exceptional ability of trematodes to suppress host innate immune responses. Mechanisms of this phenomenon, like suppression of macrophage activation through inhibiting Toll-like receptors (TLRs) and inhibition of inflammatory responses by parasite glycans, have been recently revealed and intensively studied (Mabbott, 2018). Thus infection with trematodes potentially could enable penetration of generally opportunistic microsporidia by creating immune-privilege niches.

To our knowledge, as many as 34 species of microsporidia have been reported from digenean hosts (Table 1), and this number continually grows: Victor Sprague in his comprehensive for the time “Annotated list of species” (Sprague, 1977) mentioned only 17 microsporidia infecting trematodes. Given the facts that the field has been understudied and most findings of microsporidia in trematodes are fortuitous, such a large number indicates that microsporidian infections in trematodes are fairly common in nature. Seven of the described species belong to the genus *Unikaryon*, four belong to the two closely-related genera of fish microsporidia, *Pleistophora* and *Ovipleistophora*, and the remaining 23 species occur distributed among the genera *Nosema* (14 species) and a collective taxon *Microsporidium* (8 species). However, we place them into an *incertae sedis* group, as they are described on the basis of light microscopic observations only that is not sufficient for discrimination. In contrast, electron microscopic observations exist for two of the four species of *Pleistophora-Ovipleistophora* and for all seven species of *Unikaryon*. Unfortunately, GenBank-accessible SSUrDNA sequences currently exist for only two species of microsporidia parasitizing trematodes (*U. legeri*, KX364285 and *O. diplostomuri* KY809102). Consequently, rDNA-based phylogenetic relationships of most species infecting trematodes remain obscure. Most described species are known from rediae and sporocysts developing in the first intermediate host, a mollusk, or in metacercariae developing in the second intermediate host which could be a mollusk, crustacean, or fish. Microsporidia and microsporidia-infected worms have never been isolated from birds, the definitive host of many marine species of trematodes (Shigina, 1986).

The genus *Unikaryon* Canning, Lai et Lie, 1974 with its type-species, *U. pyriformis* (see Canning et al., 1974), is composed of specialized parasites of helminths, mostly trematodes, but also cestodes (Sene et al., 1997). Currently, it includes two species of trematodes known from fishes and three species known from mollusks (Azevedo, Canning, 1987). In addition, two new yet undescribed species that share morphological similarity and >95% of SSrDNA sequence identify with *U. legeri*, have been recently isolated from crab intermediate hosts (RMO, YYS, unpublished) (Table 1). All species of *Unikaryon*, except one, are known from larval stages, predominantly encysted metacercaria (see Table 1 for references). Probably, many species, infecting metacercariae in invertebrate hosts and currently attributed to *Nosema* (e.g., *N. rhionicia* and *N. strigeoideae*) and to *Microsporidium* (e.g., *M. spelotremae*), belong to *Unikaryon*. The distinguishing morphological characters of *Unikaryon* spp. include the presence of prespore diplokaryotic stages in the life cycle, disporoblastic sporogony, and uninucleate spores with large posterior vacuoles. Spores are often arranged in pairs within a sporoporous vesicle membrane, which might be either robust or fragile, and occasionally reside in voluminous parasitophorous vacuoles individually or in pairs (Canning, Nicholas, 1974) (Fig. 3).

A few microsporidia infecting trematodes belong to the closely-related genera *Pleistophora* and *Ovipleistophora*. Representatives of these genera predominantly infect adult trematodes parasitizing vertebrate hosts. Species in both genera produce multinucleate plasmodia transforming into sporophorous vesicles with multiple dimorphic micro- and macros pores (Table 1). These microsporidia seem to have switched to trematodes from fishes and potentially could
**Table 1. Microsporidia species described in digenean hosts.**

| Parasite | Host; Life cycle stage; Tissue tropism | Hyper-host | Spore size; Pt* length, µm; No coils | Locality | References |
|----------|----------------------------------------|------------|--------------------------------------|----------|------------|
| *U. piriformis* Canning, Lai et Lie, 1974 (type-species) | *Echinoparyphium duni*, *Echinostoma audyi* (*Echinostomatidae*); Exp**: *Shistosoma mansoni*; Redia, cercaria; parenchyma | *Lymnea rubigenosa*, *Indoplanorbis exustus* (*Gastropoda*); freshwater snails | 3.8 x 2.7; Pt 150 (>15 coils) | West Malaysia | Canning et al., 1974 |
| *U. diplostomi* Shigina et Grobov, 1972 | *Diplostomum spathaceum*, *D. indistinctum*, *D. paraspathaceum* (*Diplostomatidae*); Sporocysts, cercariae, metacercariae; parenchyma, tegument, cyst wall lysis | *Salmo irideus*; *Cyprinus carpio*; *Rutilus rutilus*; *Gobio gobio*, + 4 spp. (*Perciformes*); freshwater fishes; Exp: *Lebistes reticulatus*; *Lymnea spp.* | 3.5 x 1.8; 4–5 coils | Moscow Region, Russia | Shigina, Grobov, 1972; Shigina, 1986 |
| *U. legeri* (Dollfus, 1912) KX364285 | *Gymnophalus somateriae*, *Meioygmophallus minutus* (*Gymnophallidae*); Metacercariae; Parenchyma | *Cardium eduli* and other marine molluses (*Bivalvia*) | 2.9 x 1.7; Pt 35; 6–6.5 coils | France, Great Britain, Portugal | Dollfus, 1912; Canning, Nicholas, 1974; Azavedo, Canning, 1987; Stentiford et al., 2017a |
| *U. allocreadii* Canning et Madhavi, 1977 | *Allocreadium fasciatus* (*Allocreadiidae*); Adult; parenchyma | *Aploneus melasigma*, (*Cyprinodontiformes*); freshwater fishes | 3.5 x 2.7; Pt 30; 4–5 coils | Andra Pradesh, India | Canning, Madhavi, 1977 |
| *U. slaptonleyi* Canning, Barker, Hammond, Nicholas, 1983 | *Echinoparyphium recurvatum* (*Echinostomatidae*); Redia, sporocysts, metacercariae; parenchyma, germinal tissues; Exp: *Fasciola hepatica*, *Schistosoma mansoni* | *Radix peregra*, *Planorbis planorbis* (*Gastropoda*); freshwater snails | 5 x 2.8; 17–21 coils | Devon, England | Canning et al., 1983 |
| *Unikaryon sp.1* | *Microphallus* sp. (*Microphallidae*); Encysted metacercaria; parenchyma | *Panopeus herbstei* (*Brachyura*); marine crab | 2.3 x 1.3; 6 coils | Tampa Bay, Florida, USA | YYS, RMO, unpublished |
| *Unikaryon sp.2* | *Diacetabulum* sp. (*Microphallidae*); Encysted metacercaria; tegument | *Pachygrapsus transversus* (*Brachyura*); marine crab | 2.4 x 1.2; 4 coils | Molasses Key, Florida, USA | YYS, RMO, unpublished |

*Pt — polar tube, figures correspond to the length in micrometers; length; **Exp — experimental infection.
Table 1 (continued).
Таблица 1 (продолжение).

**Pleistophora** and **Ovipleistophora**

| Parasite                                | Host; Life cycle stage; Tissue tropism                                                                 | Hyper-host                                                                 | Spore size; Pt* length, µm; No coils | Locality              | References                  |
|-----------------------------------------|-------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|--------------------------------------|------------------------|----------------------------|
| Pleistophora (Glugea) danilevskyi Pfeiffer, 1895 | Encyclometra bolongensis, Telorchis ercolanii (Telorchiidae); Adult; parenchyma, generalized          | *Natrix natrix*, *Lacerta* sp., *Chalcides tridactylus* (Reptilia: Squamata) snakes; *Emys orbicularis* (Reptilia: Testudines) turtle; *Rana temporaria* (Amphibia: Anura) frog | Multicellular plasmodia. Microspores: 3–4. Macrospores: 6–7; Pt 70 | Italy, Poland, Belgium, Switzerland | Guyénot, Naville, 1924; Canning 1975; Sprague, 1977 |
| Pleistophora sp. Paperna, Sabnai, Castel, 1978 | *Heterophyes heterophyes* (Heterophyidae); Metacercarial capsule                                      | *Liza ramada* (Mugiliformes), marine fish                                  | 3.7 x 1.7; Pt. 250; 17–19 coils     | Atlantic, Mediterranean Sea | Paperna et al., 1978   |
| Pleistophora sp. Lie, Basch, Umathevy, 1966 | *Echinostoma* spp. (26 species), *Echinoparyphium* spp. (Echinostomatidae); Sporocysts, rediae, cercariae | *Lymnea rubiginosa* (Gastropoda)                                            | Data not available                  | Central Malaya (State of Negri Sembilan) | Lie et al., 1966        |
| Ovipleistophora diplostomuri Lovy et Friend, 2017 KY809102 | *Posthodiplostomum minimum* (Diplostomatidae); Metacercaria and fibrotic encapsulation of cyst wall | *Lepomis macrochirus* (Perciformes), freshwater fish                        | Microspores: 4.3 x 2.5, 6–9 coils in 1 row; Macrospores in separate SPV: 7.5 x 4.7; 19–43 coils in 1–4 rows | New Jersey, USA          | Lovy, Friend, 2017         |
Table 1 (continued).
Таблица 1 (продолжение).

**Incertae sedis groups: “Nosema Naegeli, 1857” and Microsporidium Balbiani, 1884**

| Parasite                  | Host; Life cycle stage; Tissue tropism                                                                 | Hyper-host                           | Spore size; Pt* length, µm; No coils | Locality                      | References                     |
|---------------------------|---------------------------------------------------------------------------------------------------------|--------------------------------------|--------------------------------------|-------------------------------|---------------------------------|
| *Nosema diphterostomi* Levron, Ternengo, Toguebaye et Marchand, 2004 | *Diphterostomum brusinae* (Zoogoidae); Adult; gut epithelium, connective tissue                       | *Diplodus annularis* (Perciformes), marine fish | 2.1 x 1.4; 6–7 coils            | Corsican Mediterranean Coast, France | Levron et al., 2004            |
| *N. dollfusi* Sprague, 1964 | *Bucephalus cuculus* (Bucephalidae); Cercariae, metacercariae                                          | *Crassostrea virginica* (Bivalvia)    | 3 x 1.7                              | Atlantic, Chesapeake Bay, Maryland, USA | Sprague, 1964                  |
| *N. echinostomi* Brumpt, 1922 | *Echinostomatidae*; Cercaria, metacercariae, cyst walls                                                 | *Limnea limnosa; L. palustris, Succinea sp., Helisoma campanulatum* (Gastropoda) | 4.7 x 2.8                            | Paris, France; Lake Michigan, USA; Lake Dolgoye, Leningrad, Russia | Brumpt, 1922; Hussey, 1973; Voronin, 1974; Canning, 1975; Shigina, 1986 |
| *N. eurytremae* Canning, 1972 (= *Perezia helminthorum* Canning et Basch, 1968)                      | *Eurytrema pancreaticum* (Dicrocoeliidae); Sporocysts, cercariae (in snails), metacercariae (in grasshoppers); tegument, peripheral parenchyma; *Postharmostomum gallinum* (Brachylaimoidea); similar pathogenesis in snails | *Bradybaena similaris* (Gastropoda); *Conocephalus maculates* (Insecta: Orthoptera) | 3.9 x 2.31; 10–12 coils | Malaysia                        | Canning, Basch, 1968; Canning, 1972; Lie, Basch, 1970; Colley, 1975; Colley et al., 1975; Higby et al., 1979 |
| *N. gigantica* Canning et Madhavi, 1977                                                              | *Allocreadium fasciatus* (Allocreadiidae); Adult; parenchyma; Co-infection with *U. allocreadium* | *Apolocheilus melastigma* (Cyprinodontiformes), freshwater fish | 7.9 x 4.9; Pt 190; c.12 coils | India                          | Canning, Madhavi, 1977          |

* *Microsporidium* is not an available name *sensu stricto* but used as the legitimate name of a collective group for unidentified species, or if the genus for the new species cannot be recognized.
| Parasite | Host; Life cycle stage; Tissue tropism | Hyper-host | Spore size; Pt* length, µm; No coils | Locality | References |
|----------|----------------------------------------|------------|-------------------------------------|----------|------------|
| *N. lepocreadii* Canning et Olson, 1980 | Lepocreadium manteri (Lepocreadiidae); Adult; female gonads | *Leuresthes tenuis* (Atheriniformes), marine fish | 3.5 x 1.5; 10 coils | Pacific, San Diego, USA | Canning, Olson, 1980 |
| *N. monorchis* Levron. Temengo, Toguebaye et Marchand, 2005 | *Monorchis parvus* (Monorchiidae); Adult; gut, uterus epithelium | *Diplodus annularis* (Perciformes), marine fish | 3.2 x 2.5; 16–17 coils | Corsican Mediterranean Coast, France | Levron *et al*., 2005 |
| *N. podocytoyloides* Tonguebye, Quillchini, Diagne, et Marchand, 2014 | *Podocytoyloides magnatetis* (Opecoelidae); Adult; parenchyma | *Parapristipoma octolineatum* (Perciformes), marine fish | 3.6 x 2.6; 11–16 coils | Atlantic, near Dakar, Senegal | Toguebaye *et al*., 2014 |
| *N. rhionica* Voronin 1974 (*Unikaryon*?) | *Mesostephanus appendiculatus* (syn. *Cercaria rhionica*) (Cyathocotyliidae); Sporocysts, cercariae; parenchyma | *Melanopsins praemorsa* (Gastropoda) | 4.3 x 2.9; Pt 190 | West Caucasus, Kura River Basin | Voronin, 1974 |
| *N. strigeoideae* Hussey, 1971 (*Unikaryon*?) | *Diplostomum flexicaudum* (Diplostomatidae); Mother and daughter sporocysts, cercariae, metacercariae; Exp. | *Stagnicola emarginata* (Gastropoda) | 4.9 x 3.0; Pt > 100 | Michigan, USA | Hussey, 1971 |
| *N. vasicola* Canning, Lai et Lie, 1974 | Plagiorchiidae; Rediae, cercariae; parenchyma | *Lymnaea rubiginosa* (Gastropoda) | 3.1 x 1.6 | West Malaysia | Canning *et al*., 1974 |
| *N. xiphidiocercariae* Voronin, 1974 | Plagiorchiidae; Sporocysts, cercariae, metacercariae; parenchyma | *Lymnaea palustris* (Gastropoda) | 4.4 x 2.3 | Moscow Region, Russia; freshwater basins | Voronin, 1974 |

* Our conjectures regarding the parasite species basing on published data on morphology, hosts and pathogenesis are indicated in brackets in italic font.
| Parasite | Host; Life cycle stage; Tissue tropism | Hyper-host | Spore size; Pt* length, µm; No coils | Locality | References |
|----------|--------------------------------------|------------|--------------------------------------|----------|------------|
| Nosema sp. 1 Palmieri, Lai, Sullivan, Cali, 1978 | Fasciola gigantea, Echinostoma auyi, Tracheophillus sp. (Fasciolidae, Echinostomatidae); Sporocysts, cercariae; Digestive and reproductive glands | Lymnaea auricularia rubiginosa (Gastropoda) | Data not available | USA | Palmieri et al., 1978 |
| Nosema sp. 2 Palmieri, Lai, Sullivan, Cali, 1978 | Fasciola gigantea, Echinostoma auyi, Tracheophillus sp.; same pathogenesis | Lymnaea auricularia rubiginosa (Gastropoda) | Data not available | USA | Palmieri et al., 1978 |
| Perezia helminthorum Canning et Basch, 1968 (Microsporidium?) | Eurytrema pancreaticum, Postharmostomum gallinum (Brachylaimidae); Sporocysts, cercaria, and metacercaria | Bradybaena similaris (Gastropoda) | 3.5 x 2.0; Pt 75 | Near Kuala Lumpur, Malaysia | Canning, Basch, 1968 |
| Microsporidium sp. Martin, 1936 | Digenea; Sporocysts | Succinea sp. (Gastropoda), marine snail | Data not available | Woods Hole Region, Massachusetts, USA | Martin, 1936; Shigina, 1986 |
| Microsporidium sp. Smith, 1959 | Megalodiscus (Cladorchiidae) temperatus; Sporocyst, redia, cercaria; Also in limpet tissues | Ferressia novangliae? (Gastropoda), freshwater limpet | Data not available | Ann Arbor Area, ichigan | Smith, 1959; Shigina, 1986 |
| M. dobrovolskyi Ginetsinskaya, 1968 | Paralepoderma cloacicola (Plagiorchidiidae); larvae | Natrix natrix (Reptilia: Squamata: Serpentes) | Data not available | Khar'Kov, northeast Ukraine | Ginetsinskaya, 1968 |
| M. distomi (microspores of Pleistophora-like species?) | Glyphelmins linguatula; Adult; gonads (yolk cells) | Bufo marinus (Anura) frog | 2 x1 (in groups and individual) | Brazil | Lutz, Splendore, 1908; Shigina, 1986 |

* Our conjectures regarding the parasite species basing on published data on morphology, hosts and pathogenesis are indicated in brackets in italic font.
**Table 1 (continued).**

| Parasite | Host; Life cycle stage; Tissue tropism | Hyper-host | Spore size; Pt* length, µm; No coils | Locality | References |
|----------|---------------------------------------|------------|--------------------------------------|----------|------------|
| *M. ghigii* (microspores of *Pleistophora*-like species?)*® | *Telorchis ercolanii* (Telorchiiidae); Adult; tegument epithelium; parenchyma | *Natrix natrix* (Squamata), freshwater snake | 2–2.5 x 1; (in groups and individual) | Italy | Guyénot, Naville, 1924; Shigina, 1986 |
| *Microsporidium* sp. Schäller, 1959 | *Cercaria* sp. (3 species); Sporocysts and cercariae | *Tropidiscus* sp. (Gastropoda) | 2.3–3.4 x 1.1–1.5 µ | Eastern Germany; freshwater basins | Schäller, 1959; Shigina, 1986 |
| *M. spelotremae* Guyénot, Naville et Ponse, 1925 (*Unikaryon ?)*® | *Spelotrema* sp.; Metacercaria: parenchyma, generalized | *Carcinus maenas* (Brachyura) | 3.5 x 1.5 Pt 106 | France, England | Guyénot et al., 1925; Canning, 1975 |

**Experimental infection**

| Parasite | Host; Life cycle stage; Tissue tropism | Hyper-host | Spore size; Pt* length, µm; No coils | Locality | References |
|----------|---------------------------------------|------------|--------------------------------------|----------|------------|
| *Anncaliia* (Nosema, *Brachiola algerae* (Vavara et Undeen, 1970) | Exp. *Fasciola hepatica*; *Schistosoma mansoni*; Sporocysts | * Biomphalaria glabrata* (Gastropoda), freshwater snail | Regular spores of *A. algerae* 3.5 x 2; 9–11 coils | Exp: England | Vavara, Undeen, 1970; Lai, Canning, 1980; Franzen et al., 2006 |

* Our conjectures regarding the parasite species basing on published data on morphology, hosts and pathogenesis are indicated in brackets in italic font.
Fig. 3. Two new microsporidia of the genus *Unikaryon* isolated from trematodes infecting crabs: a–e — *Unikaryon* sp.1 from encysted metacercaria of *Microphallus* sp. in *Panopeus herbstii* from Tampa Bay, Florida, USA; f — *Unikaryon* sp. 2 from encysted metacercaria of *Diacetabulum* sp. in *Pachygrapsus transversus* from Molasses Key, Florida, USA. a — the infected metacercarian cyst (IC) is much larger than uninfected ones (UC). Unstained smear, light microscopy, DIC; b — infected (IC) and uninfected cysts (UC) on thick sections stained with methylene blue, bright field light microscopy; c — infected metacercaria in scanning electron microscope: the parasitophorous vacuole (PV) is tightly packed with spore duplets. d — a duplet of spores enclosed in sporophorous vesicle membrane (arrow), at higher magnification, transmission electron viroscopy (TEM); e — parasitophorous vacuole (PV) filled with sporophorous vesicles, TEM; f — *Unikaryon* sp. 2 exclusively infects submerged secretory epithelial cells in the trematode tegument. Arrow indicates the limits of the sporophorous vesicle that encloses two spores, TEM (membranes are poorly preserved because of initial fixation in paraformaldehyde).

Рис. 3 Два новых вида микроспоридий рода *Unikaryon* из третмод, заражающих крабов: a–e — *Uniklaryon* sp.1 из инцистирующихся метацеркарий *Microphallus* sp. в *Panopeus herbstii* из Tampa Bay, Florida, USA; f — *Unikaryon* sp. 2 из инцистирующихся метацеркарий *Diacetabulum* sp. в
play a role in distribution of microsporidia among fishes, snakes, amphibians, and reptiles associated with an aquatic habitat and often hosting trematode parasites. For example, *Pleistophora danileewskyi* infects the trematode *Telorchis ercolanii* from the intestine of the grass snake, *Natrix natrix*, but also was recorded from snake tissues free of trematodes, as well as from lizards, turtles, and frogs that share habitats with the grass snake (Guyénot, Naville, 1924; Canning, 1975). One of four species identified as *Pleistophora* sp. was isolated from a gastropod and infected encysted metacercaria (Lie et al., 1966). Since ultrastructural studies were not conducted, and life cycle and morphological details were omitted from the original description, we strongly believe that this species was misidentified. Authors probably mistook parasitophorous vacuoles containing spores of *Unikaryon*, for sporophorous vesicles, characteristic for species of *Pleistophora*.

*Pleistophora* spp., as a rule, infect fish musculature (Sanders et al., 2010; Stentiford et al., 2013). In contrast, representatives of the closely-related genus *Ovipleistophora* that are morphologically and genetically similar to *Pleistophora* spp., infect oocytes, spermatocytes, and fibroblasts within ovaries and testes of perciform fishes (Summerfelt, Goodwin, 2010). The recently described *Ovipleistophora diplostomuri* infects fibroblasts, but only those that form fibroblastic capsules around metacercarial cyst walls of the diplostomoid trematode *Posthodiplostomum minimum* from internal organs of the bluegill sunfish, *Lepomis macrochirus*. *O. diplostomuri* clusters with trematodes infecting ovaries of perciform fish (Lovy, Friend, 2017). Tissue tropism similar to that of *O. diplostomuri* occurred in a microsporidium infecting fibroblasts of metacercarial capsules of a heterophyid trematode (*Heterophyes heterophyes*) in the thinlip grey mullet, *Chelon (=Liza) ramada* (Paperna et al., 1978). The authors assigned the microsporidium to *Pleistophora* sp., but more likely it is in fact conspecific with *O. diplostomuri* (Lovy, Friend, 2017). The unique tropism of *Ovipleistophora* spp. may reflect the opportunistic nature of microsporidia. *Ovipleistophora mirandella*, the type-species (Pekkarinen et al., 2002), infects fibroblasts in ovaries and testes that are known as immunologically privileged organs. *O. diplostomuri*, in turn, infects fibroblastic formations encapsulating the metacercarial cyst wall protected by trematode-induced immunosuppression. Hence, in some ways these two species share similar tissue tropism, both infecting fibroblasts in immunologically protected sites. *O. diplostomuri* intermediate hosts — trematodes *Posthodiplostomum minimum* and *Heterophyes heterophyes* parasitizing bluegills and mullets, respectively, produce long lasting infections in fish with 100% prevalence (Lovy, Friend, 2017). Long-term trematode-fish associations might have helped creating specialized immunoprotective niches for microsporidia. Development of fish-related *Pleistophora*-like microsporidia in the metacercarial cyst-wall encapsulation composed of trematode secretion and fish host fibroblasts, exemplifies such a niche.

More than 20 species of trematode-infecting microsporidia have been placed in the genera *Nosema* and *Microsporidium*. According to the characteristics and host ranges provided by the authors, some of those species could be provisionally identified as *Unikaryon* spp. or *Pleistophora* spp. None of them has been sequenced, and hardly any of them appear to belong to the
Hyperparasitic Microsporidia, Haplosporidia, and Myxozoa parasitizing trematodes

genus *Nosema*. We treat those species as an *incertae sedis* group (see Table 1 for the list and associated references).

A series of experimental studies on virulence, host range, and mass production of trematode-infecting microsporidia was driven by a potential ability of these hyperparasites to biologically control the pathogenic trematodes *Fasciola hepatica* and *Schistosoma* spp. that pose a serious threat to human health and cattle breeding worldwide. Suppressing trematode multiplication at parthenogenetic stages in molluscs by infecting the latter with microsporidia served as the major strategy for those experiments. *Nosema eurytremae*, with its unusually wide trematode host specificity, successfully propagated in lepidopteran larvae under experimental conditions (Higby et al., 1979; Pilley et al., 1978). Surprisingly, *Anncaliia algera* was selected as the most preferred microsporidian species to be used in biological control (Lai, Canning, 1980). The latter species with dual natural host specificity in both mosquitoes and humans has unique generalist properties, allowing for experimental infections in a broad range of hosts and cell lines (Sokolova et al., 2019).

Also, using *N. strigeoideae* against *Diplodostomum spatheceum* infecting eye lenses of commercial and other fishes was explored (Palmieri et al., 1976). However, all these biological control studies using microsporidia in trematodes peaked in late 1970’s – early 1980’s (Shigina, 1986), did not have further development.

Overall, we conclude that microsporidia of trematodes are drastically understudied even though the complicated trematode polychenous life cycles probably played an important role in dissemination of microsporidia among invertebrate and vertebrate hosts connected by trophic chains, especially in marine habitats with low density of inhabitants and limited transmission options.

**Haplosporidia**

All the described Ascetosporea haplosporidians infecting trematodes belong to the genus *Urosporidium* Caullery, Mesnil, 1905. The taxon seems small, including four species by WoRMS and nine species in a recent review (Azevedo, Hine, 2017). By examining Table 2, one can see there are at least 14 species, including 4 unnamed ones, and probably several more exist.

Most species of *Urosporidium* infect trematodes, and those that do not still infect worms: turbellarian, cestode, nematode, and even a polychaete (the type species). Seven different families of trematodes have been reported as hosts, which indicates a wide range of hosts, especially when considering the other listed worm hosts (Table 2). Molecular phylogenies show haplosporidians are cercozoans related to Foraminifera and Radiolaria and probably date back to the Cambrian (Azevedo, Hine, 2017). Strict jackknife consensus tree of parsimony analysis of SSU rDNA sequence data of two species of *Urosporidium* show them to be sister to the other known haplosporidian genera (Burreson, Ford, 2004), but maximum likelihood trees show it to be nested among species of *Haplosporidium*; however, this tree remains unresolved (Azevedo, Hine, 2017).

Microscopy shows species of *Urosporidium* to have an internal flap of wall material covering the spore orifice as opposed to an external hinged lid in those of *Haplosporidium* and *Minchinia*, none of which infects trematodes (Azevedo, Hine, 2017). The flask-shaped spores of most species have one or more extensions, commonly referred to as tails (Table 2), and their number and length are not consistent; the size of spores does not necessarily present comparable values because some preparations are fixed, and others are fresh, under intense pressure, in sectioned material, or in ultrastructural images. Consequently, values should be used as a guide only and not as a taxonomic character. As the listed and additional species are examined more critically, including investigation by molecular techniques, changes in the characteristics of *Urosporidium*, other haplosporidian genera, and associated nomenclature will be made. For example, a few species of *Haplosporidium* are reported from worms, such as *Haplosporidium malacobdellae* in the nemerte-
Table 2. *Urosporidium* Caullery et Mesnil, 1905 species described in trematodes and other hosts.

| Parasite | Host | Life cycle stage; tissue tropism | Hyper-host | Spore size | Locality | References |
|----------|------|----------------------------------|------------|------------|----------|------------|
| *Urosporidium fuliginosum* Caullery et Mesnil, 1905 (type species) | Not in trematode; in coelom of *Polychaeta, Syllis gracilis* (*Syllidae, Annelida*) |  | 5 µm, 1 tail up to 15 µm long | English Channel, France | Caullery, Mesnil, 1905 |
| *U. astomatµm* Menke, 1968; probably nomen nudum | *Parvatrema donacis* (*Gymnophallidae*); metacercariae | *Donax variablis* (*Bivalvia*) | 5–6 x 6–7 µm, 1 tail up to 11 µm long | Port Aransas to Galveston, Texas | Sprague, 1954; Mackin, Loesch, 1954; Menke, 1968 |
| *U. cannoni* Anderson, Newman et Lester, 1993 | Not in trematode; in tubellarian *Stylochus* sp. (*Polyclada*) | Associated with commercial oyster (*Bivalvia*) | 4.8–5.2 µm, 11 to 13 tails | Moreton Bay, Queensland, Australia | Anderson *et al.*, 1993 |
| *U. charletyi* Dollfus, 1944 | Not in trematode, in cestode *Catenotaenia dendritica* | *Sciurus vulgaris* (*Rodentia*) | ~ 15 µm, 1 tail 16–20 µm long | Indre-et-Loire, central France | Dollfus, 1941; 1944; 1946 |
| *U. constantae* Howell, 1967 | *Bucephalus longicornutus* (*Bucephalidae*); sporocysts and embryonic cercariae | *Ostrea lutaria* (*Bivalvia*) | 4–5 µm, single tail 10–12 µm long | New Zealand, both islands | Howell, 1967 |
| *U. crescens* De Turk, 1940 | *Microphallus basodactylophallus, M. turgidus, Levinseniella capitanea,* and possibly *M. nicolli* and *Megalophallus* sp. (*Microphallidae*); sporocysts, cercariae, and encysted metacercariae | *Callinectes sapidus, Palaemonetes spp.* | 5–6 µm, 1 tail | East coast and Gulf of Mexico, USA | De Turk, 1940; Couch, 1974; Overstreet, 1978; Shields, Overstreet, 2007 |
| *U. jiroveci* Ormières, Sprague et Bartoli, 1973 | *Gymnophallus nereicola* (*Gymnophallidae*) and unidentified *Monorchidae; sporocysts* | *Abra ovata* (*Bivalvia*) | 5.5–7.0, 1 tail 12–14 µm | Beauduc, France, Mediterranean Sea | Ormières *et al.*, 1973 |
Table 2 (continued).
Таблица 2 (продолжение).

| Parasite | Host Life cycle stage, tissue tropism | Hyper-host | Spore size | Locality | References |
|----------|--------------------------------------|------------|------------|----------|------------|
| *U. jiroveci* Ormières, Sprague et Bartoli, 1973 | *Gymnophallus nereicola* (Gymnophallidae) and unidentified Monorchidiidae; sporocysts | *Abra ovata* (Bivalvia) | 5.5–7.0 µm, 1 tail 12–14 µm | Beauduc, France, Mediterranean Sea | Ormières *et al*., 1973 |
| *U. pelseneeri* (Caullery et Chapellier, 1906) | Bucephalidae (*Bucephalus haimeanus*?); *Bacciger bacciger* (Fellodistomidae) as *Cercaria pectinate*; sporocysts | *Donax trunculus, D. vittatus, Barnea candida* (Bivalvia) | 4.5–5.5 µm, 1–3 tails 10–11 µm | English Channel, France | Caullery, Chapellier 1906; Guyénot, 1943; Dollfus, 1925; Sprague, 1970 |
| *U. spisuli* Perkins, Zwerner et Dias, 1975 | Not in trematode; in juvenile ascaridoid nematode tentatively identified as *Paranisakiopsis pectinis* by Perkins *et al*., 1975 but probably *Sulcascaris sulcata* (see Lichtenfels *et al*., 1978) | *Spisula solidissima* (Bivalvia) | 3.8–6.9 x 3.0–5.9 µm wide, 2–3 tails 15–17 µm | Virginia, North Carolina, USA | Perkins *et al*., 1975 |
| *U. tauricum* Zaika et Dolgikh, 1963 | Unidentified Hemiuridae; redia | *Rissoa splendidia* (Gastropoda, Rissoidea) | 5.5–7.5 µm, 1 tail 15–45 µm | Ukraine, Black Sea | Zaika, Dolgikh, 1963 |
| *Urosporidium* sp. of Mackin, Loesch, 1954 | Bucephalidae; sporocysts | *Crassostrea virginica* (Bivalvia) | 3–5 x 57 µm | Mobile Bay, Alabama, USA | Mackin, Loesch, 1954 |
| *Urosporidium* sp. Carballal, Díaz, Villaiba, 2005 | Not in trematode; in tubellarian *Paravortex cardii* (Polyclada) | *Cerastoderma edule* (Bivalvia) | 4–5 µm, 3 tails | Galicia NW, Spain | Carballal *et al*., 2005 |
| *Urosporidium* sp. Le, Kang, Hong, Park, Choi, 2015 | *Parvatrema duboisi* (Gymnophallidae); non-encysted metacercariae | *Ruditapes philippinarum* (Bivalvia) | 3.1–4.3 x 3.9–5.5 µm, loop-like filaments | West and south coasts of Korea | Le *et al*., 2015 |
| *Urosporidium* sp. Reece, Siddall, Stokes, Burreson, 2004 | *Styctodora lari* (Heterophyidae) | *Batillaria australis* (Gastropoda) | AY449714 | Sydney, New South Wales, Australia | Reece *et al*., 2004; Azevedo, Hine, 2017 |
Fig. 4. Pepper spot disease in blue crabs caused by a *Urosporidium crescens* (Haplosporida) infection in *Microphallus basodactylophallus* (Microphallidae).

a — life cycle of the digenean *M. basodactylophallus*. The adult worm in the intestine of the raccoon discharges eggs in the host feces which are eaten by and hatch in at least six snail species serving as first intermediate hosts. From the enclosed larva, numerous swimming cercariae are produced asexually. These penetrate the blue crab and encyst as spherical metacercariae. When hyperparasitized by *U. cresens*, the encysted worm and its cyst wall enlarge to an easily visible size (from about 350 µm to over 650 µm in diameter), with brownish spores giving the heavily infected metacercaria a black appearance. Non hyperparasitized worms develop to adults if eaten by a proper bird or mammal final host (modified from Overstreet, 1978); b — spores from hyperparasitized metacercaria on smear of tissues of the crab with pepper disease. Haplosporidian spores stained red with Giemsa, scale bar — 5 µm; c — cooked crabmeat showing two areas with *M. basodactylophallus* metacercariae hyperparasitized with *U. cresens* (“pepper spots”, arrows); d — live spores of *U. crescens* in the trematode, scale bar — 5 µm.

A few species of *Urosporidium* can influence commercial sales of the hyper-hosts such as the surf clam with infected nematode and blue crab with pepper spot-buckshot (Fig. 4). In both cases, the spores are brownish but appear black to the naked eye. For example, consumers of the blue crab do not want to eat crabs with disease...
symptoms, such as the pepper spots. These spots are metacercariae that are packed with cysts and spores of *U. crescens*, which have caused the metacercariae and cyst wall to enlarge several times that of an uninfected metacercariae. As it turns out, if the consumer was to eat infected crabs raw, the uninfected metacercaria could cause a human infection with the trematode, but the hyperinfected metacercaria would not.

Pathological responses in cercariae and metacercariae cause mortality of the cercariae and castration of the metacercariae. This seems to be true for all species examined (Azevedo, Hine, 2017).

**Myxozoa**

The first myxosporidian described from a trematode was *Fabespora vermicola* (Fig. 5) infecting the apocreadiid *Crassicutis archosargi* in Mississippi (Overstreet, 1976b). The infection was rare and RMO has not seen it in *C. archosargi* since. Visual attempts made at the time of original collection to encounter it in the sparid fish host, *Archosargus probatocephalus*, to determine if both the fish and trematode contained the infection were also unsuccessful. However, in 1980, William Font, who was on sabbatical in RMO’s laboratory, did find what was probably the same species of *Fabespora* (Table 3) in the cryptogonimid *Metadena cf. spectanda* in the sciaenid fishes *Micropogonias undulatus* and *Cynoscion arenarius* in Davis Bayou, Ocean Springs, Mississippi, from near where infected individuals of *A. probatocephalus* initially occurred (W. Font, R. Overstreet, unpublished). The trematode was identified as *Metadena spectanda* (Overstreet, 1971) from *M. undulatus* and another sciaenid fish, with the caveat that the species may differ from the larger Brazilian specimens used in the original description. This problem to determine if all trematode specimens from sciaenids in both South and North America are conspecific can now be solved with DNA sequencing. Sequencing could also solve the question as to whether all the myxosporidian (*Fabespora*) material from Mississippi is conspecific, relat-
| Parasite                        | Helminth host                          | Hyper-host                        | Locality                      | References            |
|--------------------------------|----------------------------------------|-----------------------------------|-------------------------------|-----------------------|
| *Fabespora vermicola*          | *Crassicutis archosargi* (Apocreadiidae) | *Archosargus probatocephalus*      | Mississippi, Gulf of Mexico   | Overstreet, 1976a     |
| *Fabespora* sp.                 | *Metadena cf. spectanda* (Cryptogonimidae) | *Micropogonias undulatus* and *Cynoscion arenareus* | Mississippi, Gulf of Mexico | Present study          |
| *Fabespora* sp. of Siau, Gasc, Maillard, 1981 | *Sparicotyle chrysophrii* (as *Allopodocotyle chrysophrii*, Opecoelidae) | *Sparus aurata*                  | Mediterranean Sea         | Siau *et al.*, 1981   |
| *Myxidium giardi* (?)* Cépède, 1906 | Not in trematode; in monogenean *Pseudodactylogyrus bini* (Pseudodactylogyridae) | *Anguilla anguilla*               | Northwest Spain            | Aguilar *et al.*, 2004 |
| *Myxidium incompavermi* Freeman et Shinn, 2011 | Not in trematode; in monogenean *Diplectanocotyla gracilis* (Diplectanidae) | *Megalops cyprinoides*           | Peninsular Malaysia        | Freeman, Shinn, 2011   |
| *Myxidium* sp. of Freeman, Yoshinaga, Ogawa et Lim, 2009 | Not in trematode; in monogenean *Platycephalotrema*, probably *P. ogawai*¹ as *Haliotrema* sp. (Ancyrocephalidae) | *Platycephalus* sp.              | Lake Hamana, Japan        | Freeman *et al.*, 2009 |

¹According to figure by Freeman *et al.* (2009) by Delane Kritsky (see Kritsky, Nitta, 2019).
ed to another, and related to *Fabespora* spp. in fishes.

Another record of infection in a trematode was also identified as *Fabespora* sp., probably a different species (Siau et al., 1981). It occurred in the opecoelid *Sparicotyle chrysophrii* in *Sparus aurata* from the French Mediterranean Sea (Table 3), and the authors described ultrastructural aspects of sporogenesis as an earlier paper did (Weidner, Overstreet, 1979). The unusual presence of bundled microfilaments (identified as microtubules by Siau et al., 1981) in the extracellular space between the valvogenic and interior cells of the sporoblast attaching to the plasma membranes of both capsulogenic and germinative cells apparently allows the spores to propel themselves through host tissues by undulating their valves (Overstreet, 1976a; Weidner, Overstreet, 1979). Early developmental myxozoan stages occurred within and around trematode gonads; the mature disporous spores were enclosed in membrane and passed from the parenchyma to and through the tegument. Heavily infected specimens had necrotic gonads and a lack or paucity of eggs. In *M. undulatus* infections were found in 1 of 22 worms in the pyloric caeca and in 1 of 6 in the intestines, whereas in *C. arenarius* in 4 of 11 worms in the caeca and in 0 of 15 in the intestine, suggesting infections typically occur in young individual trematodes (W. Font, R. Overstreet, unpublished). *Fabespora* spp. also occur in fishes. The type-species, *Fabespora nana*, for which DNA has not been sequenced, infected the Knout goby, *Mesogobius batrachocephalus*, in the Black Sea (Naidenova, Zaika, 1969) as well as the gall bladder of the cusk-eel *Ophidion rochei* but not *M. batrachocephalus* near Karadag in the Black Sea (Yurakhno, 2013). Unnamed species occurred in *Merluccius hubbsi* in the Argentine Sea (Cantatere et al., 2016) and in *Centropomus undecimalis* from Tampa Bay, Florida (Landsberg, 1993). Landsberg found the spores in the fish host’s feces and questioned whether they had originally come from a trematode. The relationship between fish infections in the Black Sea and those from trematodes needs to be established.

Other platyhelminths also host myxosporidians (Table 3), such as *Myxidium giardi* being free (not encysted) in the ventral region near the opisthaptor of the monogenean *Pseudodactylogyrus bini* on the branchial tissues from 1 of 323 examined *Anguilla anguilla* but in none of the related monogenean on the same fish from northwestern Spain (Aguilar et al., 2004). *Myxidium incomptavermi* was reported from a gill-infesting monogenean (*Diplectanocotyla gracilis*) on *Megalops cyprinoides* in Malaysia (Freeman, Shinn, 2011). It was also detected by PCR in the kidney, spleen, and intestinal tract of the tarpon fish host. Sequences of 1,702 base pairs of SSU rDNA showed that *M. incomptavermi* occurred robustly at the base of the multivalvulidan clade (*Kudoa, Sphaerospora*, and *Unicapsula*) alongside with another species from Japan (Freeman et al., 2009; Table 3). These taxa were placed distantly from the unrelated freshwater and marine *Myxidium* clades. It is important to determine where *Fabespora* spp. from trematodes fit in that tree. All myxosporidian species infecting Platyhelminthes cause severe pathological alterations in the worm hosts.

**Conclusions**

Microsporidia in trematodes are common and are represented by several species. Trematode-infecting microsporidia with clarified phylogenetic position descend from the species infecting invertebrates (*Unikaryon*) and fish (*Pleistophora* and *Ovipleistophora*-like species). However phylogenetic position and origin of most microsporidia recovered from trematodes, remain unknown.

The representatives of only one Haplosporidia genus, *Unikaryon*, are known to infect trematodes, and this genus has a broad host range among marine parasitic and free-living marine invertebrates.

All trematode infections with myxosporidia were recovered from fish; they are caused by species belonging to different clades of Myxozoa, and have switched to trematodes from fish hosts.
Parasitic “sporozoans” demonstrate diversity of characters and physiological mechanisms specific for each group, alongside with common adaptations in response to similar environmental conditions that have created morphologically alike forms from genetically dissimilar material. Indeed, the described above microscopic organisms exemplify an amazing power of convergent evolution, the phenomenon that A.A. Dobrovolskiy and other scholars of the Russian school of parasitology explicitly demonstrated on a variety of parasitic groups (Dogiel, 1962; Ginecynskaya, Dobrovolskii, 1978).

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